Some comparative aspects of yawning in Betta splendens, Homo sapiens, Panthera leo, and Papio sphinx

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Students of behavior have neglected yawning. It is rarely mentioned in animal behavior texts, and even books that would seem to be particularly relevant, such as Hinde's (1972) Non Verbal Communication, do not include yawning in the index. In physiology the standard texts such as Starlings Human Physiology (Davson & Eggleton, 1962) or the revised Johns Hopkins Atlas of Human Functional Anatomy (1977) devote only a few vague sentences to yawning, if it is mentioned at all. There is no precise knowledge of the eliciting stimuli, functions, development, or topography of yawning. Darwin (1873) described yawning in humans as an act of deep inspiration, followed by a lengthy, forceful expiration with simultaneous strong contraction of many skeletal muscle groups, and occasionally accompanied by lacrimation. Yawning is sometimes described as a reflex, and Moore (1942) reported that yawning is one of the first reflexes observed in newborn human infants.

Fatigue (Cramer, 1924; Mayer, 1921), drowsiness and boredom (Barbizet, 1958; Provine & Hamernik, 1986), hunger and satiety (Barbizet, 1958) have all been suggested as stimuli for yawning. A widely held hypothesis is that oxygen insufficiency causes yawning, but Starlings Human Physiology does not mention this possibility, and Barbizet found the evidence for it to be inconclusive. Frequent or excessive yawning may accompany certain diseases of the central nervous system, particularly frontal lobe tumors and epidemic encephalitis, a contagious inflammation of the brain (Brock & Krieger, 1963). Gastric diseases, brain stem lesions, and certain varieties of epilepsy may also be accompanied by pathological yawning (Barbizet, 1958). On the other hand, Geigel, a Gerrnan physician, suggested that "a seriously sick person does not yawn, and when he does yawn again the danger is pasC (cited by Cramer, 1924).

More recent research has indicated the involvement of a central cholinergic mechanism in the initiation of yawning by rats (Urba-Holmgren, Gonzalez, & Holmgren, 1977), with a positive modulating effect of serotonin (Urba-Holmgren, Holmgren, Rodriguez, & Gonzalez, 1979). Low doses of drugs that stimulate dopamine neurons also induce yawning in rats (Mogilnicka & Klimek, 1977). Injections into brain or cerebrospinal fluid of ACTH, melanocyte-stimulating hormone, or peptides having similar hormonal activity induce a stretching and yawning syndrome in several species. There is an association between yawning and some elements of sexual behavior (Huston, 197 1), and Phoenix and Chambers (1982) found that injections of testosterone produced yawning by male and female rhesus macaques. Holmgren, Urba-Holgrem, Aguilar, and Rodriguez (1980) found that testosterone treatment restored cholinomimetically induced yawning in castrated male rats and increased yawning in normal and androgenized fernales.

Darwin (1873) noted that yawning occurred Aring displays of "passion" and threat in baboons; rhesus macaque fernales have also been observed to yawn during sexual excitement (Dewsbury, 1978). Nonhuman primates yawn in a variety of other contexts, and Hall (1962) described a "gaping" or ~yawning" response made by captive patas monkeys, Erythrocebus palas, when confronted with a mirror. He reported that the response was similar to the yawning he had observed in field studies of wild chacma baboons and that Hinde and Rowell (1962) had observed in captive rhesus macaques. Hall (1962, p. 1258) reported that "the young fernale, in particular,

frequently made ..'yawning' responses in which, while staring towards the reflection, she lowered the head while opening the mouth to fullest extent, then raised the head again in normal horizontal position. This reaction would occur with the animal in the sitting, normal standing, or lowcrouched postures." Calling such behavior yawning is simply a useful description because its functional variations and relations to other behaviors have not been determined.

Herbivores have seldom been observed yawning (Barbizet, 1958; Cramer, 1924; Heusner, 1946), but warm, well-fed, drowsy members of the Félidae often yawn (Leyhausen, 1979), and domestic Canids may yawn in certain social play situations (Bekoff, 1974). Dumpert (192 1) asserted that yawning was universal in mammals and birds, and Cramer (1924) reported that amphibians and certain reptiles also yawn. Although it is clear that members of these classes may open their mouths widely on occasion, it is not at all clear that they are yawning when they do so.

In this report I describe observations of yawning by a fish (Betta splendens), by a carnivore (Panthera leo), and by two primate species (Papio sphinx and Homo sapiens) in a variety of settings. Because mere opening of the mouth is not necessarily the saine as yawning, in all of this research 1 defined yawning as a slow opening of the mouth, maintenance of the open position for more than 3 s, followed by a more rapid closure of the mouth.

Siamese Fighting Fish (Belta splendens)

While doing research on the aggressive threats and other social behaviors of Betta splendens (Baenninger, 1966; Baenninger, 1984), 1 observed yawning during encouriters with conspecifics and with mirror images but not in their solitary behavior. For this reason 1 hypothesized that yawning would occur primarily when conspecifics were visible, and particularly in aggressive, intruder-resident interactions. Myrberg (1972) described yawning of bicolor damselfish, Eupomacentrus partitus, and discovered that it accompanied transitions between various social behaviors, particularly agonistic responses and nest entrances and exits.

Experiments and Observations All fish were purchased froin a commercial supplier and were housed in Miter glass aquaria for 1 mo before observations. They were observed from behind a screen during the light-on phase of a 12-hr light cycle. They were fed a small amount of frozen brine shrimp daily. Aquaria were cleaned every 4 days. Yawning by 15 isolated fish was observed for twenty 1-hr intervals in the light-on portion of their daily light-dark cycles. During these sessions the observer viewed fish under 15-W white illumination through holes cut in opaque material that prevented fish from seeing the observer. Under these circumstances only a single yawn was observed. This constitutes a rate of 0.003 yawn/fish-hour. The frequency of yawning increased greatly when 7 pairs of male Siamese fighting fish were observed while separated by clear Plexiglas partitions. Of the 14 fish, 12 yawned between one and seven times during a single 1-hr observation that followed 24 hr of visual isolation. There were 41 yawns during 14 fish-hours, a rate of 3.0 yawns/fish-hour. The 12 fish that yawned did so an average of 3.5 times per hour. There was no evidence of yawning contagion in these observations; a minute-by-minute analysis of responses did not show any temporal pattern of yawns, either between or within the protagonisis. That is, in only one instance did members of a pair both yawn during the saine or successive minutes, but 2 other fish were observed to yawn repeatedly during successive minutes. These multiple yawns were not reciprocated by the fish on the other side of the transparent partition.

After these paired observations every fish was again isolated for 24 hr, after which each pair was again observed for 1 hr while separated by clear Plexiglas. This time 3 (différent) fish failed to yawn, and 27 yawns were recorded, a mean of 2.5 yawns for each fish thai yawned and a rate of 1.9 yawns/fishhour. This decrease between the first and the second observation was significant by a sign test ($p < .05$, two-tailed). If yawning were associated with absence of stimulation or lack of stimulus change, one might expect the rAponse to increase after isolation and repeated exposure to the saine conspecific. Instead, like the biting response in repeated pair encounters of this species

(Baenninger, 1984), the pattern I am referring to as yawning appears to wane.

Table 1
Yawning Rates (Yawns / Subject-Hour)

Subject	Condition	Rate
Humans	Morning subway	0.0054
	Afternoon subway	0.48
	Crowded subway	0.006
	Uncrowded subway	0.24
	Donnitory cafeteria	0.009
	Aerobie exercise class	0.0012
	Evening leisure time	3.6
	Lecture class	24.6
	Library	0.9
	Laboratory experiment	0.15
Fish	Isolated	0.003
	Separated, paired	
	Initial	3.0
	24 hr	1.9
	Fighting	
	Initial	6.0
	24 hr	0.75
	Separated, paired, with mirror	
	Initial	3.9
	24 hr	4.6
	48 hr	3.1
	Separated, paired, without mirror	
	Initial	4.5
	24 hr	2.1
	48 hr	1.7
Lions	Grouped	1.2
Mandrills	Grouped	0.78

The possibility of an association between yawning and biting was studied in a third set of observations. Novel pairs were formed by placing 5 individual male Bettas in the 12liter aquaria of 5 resident males which had been living in thern alone for 1 wk. The yawning and biting responses of both residents and intruders were counted during the first hour together; after 23 hr together, these responses were again counted for 1 tir. During the first hour the two pairs performed 153 bites and 60 yawns (6.0 yawns/fish-hour). After 24 hr there were 92 bites, but only 8 yawns (0.75 yawn/fish-hour). In one pair the intruder was severely damaged by the resident and showed neither biting nor yawning responses. Putting pairs of fish together was necessary in order to measure biting, but because of the aggressiveness of these fish toward conspecifics, this study was run with a small number of subjects. It appears that both biting and yawning responses wane with continued exposure to the same conspecific and that actual combat increases the initial yawning rate, compared with the rate when fish have only visual contact. In the final study, 14 pairs of naive male fish,

isolated in 1-liter aquaria, were visually exposed Io each other. Their yawning responses to a single conspecific in 1 hr were recorded. Fish were then isolated again, but a mirror was placed against the aquaria of seven pairs (14 fish) so that each subject could view its own image instead of a conspecific; the rernaining seven pairs saw neither mirrors nor fish. Twenty-four hours later the yawning responses to the original pair mernber were again counted, This procedure was then repeated after 48 hr. Under these circumstances, with the mirror present for two 24-hr intervals, there was only slight waning of yawning responses. There were 55 yawns in response to pair members during the initial hour (3.9/fish-hour), 64 after 24 hr of mirror viewing (4.6/fish-hour), and 43 after a second 24-hr period of mirror viewing (3. 1 /fish-hour). The no-mirror control pairs essentially replicated the results of the second study, by showing clear evidence of a waning of yawns over repeated exposure to a conspecific: Initially there were 65 yawns (4.5/fishhour); 24 hr later there were 29 (2. 1 /fish-hour); and during the final pair encouriter 48 hr later, there were 24 yawns (1.7/ fish-hour). Having a mirror present during isolation from conspecifics appears to counteract the waning of yawning that normally occurs in repeated pair encounters.

The rate of yawning by members of this species is dramatically increased by the presence of a single conspecific. There were 300 times as many yawns/hour when fish were in visual contact with a conspecific. During actual combat the rate of yawning was again doubled initially, although it waned after prolonged fighting, perhaps due to physical exhaustion. Presence of a mirror while fish were isolated prevented waning of yawns in visual pair encounters that were separated by 24-hr intervals. The possibility that yawning is an aspect of agonistic threatening in this species is clear, but it has not previously been documented (Simpson, 1968).

Lions (Panthera leo)

Captive African lions were observed for 100 hr in an attempt to answer the following questions: (a) Do lions (like humans) make sounds, or stretch, when they yawn, and are they more likely to yawn in some postures than in others? (b) Do lions yawn at high frequencies, and are there particular environmental events that modify those frequencies? (c) Docs contagion of yawning occur among members of this species? (d) Is there any evidence for contagion of yawning between lions and people?

Method : Observations of yawning were conducted for 100 hr at the Philadelphia Zoo in the lion bouse from July 21, 1982, to March 25, 1983. The house contained 5 lions, 3 females and 2 males. Each animal had its own tiled cage, but except at feeding time (3:00 p.m.) 4 of the lion3 were kept in pairs. The observer sat on a wooden bleacher located 10 m from the cages so that all 5 lions could be seen simultaneously. Behavior was scan-sampled for one bundred 1-hr periods at différent times from 9:00 a.m. to 5:00 p.m. Temperature, time, and the incidence of yawning were recorded, as was the time between yawns (an interyawn interval of 20 s was established as an arbitrary criterion for contagion). The approximate number of people entering the lion house during the hour and the number of people in front of a lion's cage when it yawned were recorded in order to determine whether yawning frequency was correlated with the number of human observers present. A lion's position when it yawned was recorded (standing, sitting, or lying down), as was the occurrence of stretching or making a sound during yawns.

Results : During 100 hr of observation, the 5 lions yawned 592 times, a rate of 1.2 yawns/lion-hour. No relation was found between the number of yawns per hour and the mean number of people entering the lion house per hour ($r = .14$), nor was any relation found between the number of yawns per hour and the number of people standing in front of the cage when a yawn occurred ($r = .09$). The time of day was related to the frequency of yawning, however. During the morning there were relatively few yawns (0.8/lion-hour), but there was a progressive increase before feeding tirne (to 1.8 yawns/lionhour between 1:00 and 2:00 p.m.). During and after feeding there was a sharp decline in the frequency of yawns (0.35 yawn/lion-hour).

Of a total of 592 yawns, only 19 (3.1 %) occurred within 20 s of another yawn. No instances of multiple yawns by the same individual were seen. Only 4.5% of the yawns were accompanied by a stretch, and sounds were never detected during yawns. Lions yawn most often when they are lying down. Of 592 yawns, 435 occurred when the lion was lying down; 122 occurred while the animal was standing, and 35 occurred while sitting (with only rear quarters contacting the floor). In the winter months the temperature was kept Illween 70 and 75*F, but in the summer the temperatures in tl* lion house climbed past 80*F, and the highest temperature recorded was 85'F. Yawning was most frequent when the temperature was between 70 and 74 (corrected for the number of observations in that temperature range) and declined when the temperature fell below or rose above this range. Yawning by lions occurred most often just before feeding, when they presumably are hungry, and when room temperature is warin, but not hot. It was not contagious, and the presence of large numbers of humans did not affect the frequency of yawns by lions. They yawned most often while lying down.

Mandrills (Papio sphinx)

The open-mouthed aggressive threat is a common behavior in a number of primate species. To what extent is this response discriminable from yawning, and does its frequency covary with yawning? Are there reliable variations in yawning frequency over the course of a day? Is there any evidence of social facilitation or contagion of yawning in this species of Old World monkey?

Method : Mandrills were observed in the rare marnmal house of the Philadelphia Zoo during March and April of 1983 and in March and April of 1985. Two females were housed with one male, and a younger male had a private cage but could see his conspecifics. The animals were enclosed in tiled, soundproof glass cages. At feeding time (3:00 p.m.) males ate in separate cages, and the fernales ate together in one cage. To make observations, the observer stood about 2 m from the cages and observed for 1-hr intervais during different times of the morning and afternoon. Time, temperature, and the number of yawns performed during each hour were recorded as well as whether yawns occurred within 20 s of each other. The number of people standing in front of a cage when yawning occurred was recorded, as was the approximate number of people who entered the rare mammal house during an observation period. Positions of mandrills while yawning and whether they stretched during yawns were recorded as well as the sex of the yawner.

Results : Two différent types of yawns occurred in the males. In one type the animal raised its head and opened its mouth so widely that its teeth were exposed, particularly the large canines that are characteristic of males. This response lasted 4-5 s and was never seen in females. In the second type of yawn, the head was raised only slightly, and the mouth did not open widely enough to expose the teeth, which remained covered by the lips. This response lasted only 1-2 s and was shown by both sexes. Only these shorter duration responses were scored as yawns. It appears likely that these were true yawns, whereas the longer duration response was really a "bared-teeth display" shown exclusively by males in primate species during hostile encouriters. Yawning was never observed just before or after sleep episodes, and only 8% of the yawns occurred while the animal was lying down. The remaining 92% occurred while animals were in a sitting posture, but yawning was never obsmed while an animal was standing.

During 36 hr of observation, there were 111 yawns by the 4 mandrills, a rate of 0.78 yawn/mandrill-hour. There was no significant correlation between the number of yawns per hour and the number of people in the rare mammal house ($r = .26$), nor was there a correlation of yawns per hour with the number of people in front of the cage when yawns occurred ($r = .17$). Ambient temperature did not vary as much as in the lion house and was uncorrelated with rate of yawning by mandrills. There was a clear relation between the number of yawns per hour and the time of day. One hour before the animals were fed, there was an increase in yawning frequency, from a mean of 1.5 yawns/mandrill-hour between 1:00 and 2:00 p.m. to 6.5 between 2:00 and 3:00 p.m. After

feeding, the frequency again decreased to 2.0; all animals finished feeding by 3:30 p.m. Yawning contagion was not apparent (by a 20-s criterion for the interval between yawns by différent individuals). Multiple yawns by individuals were noted, that is, when a mandrill yawned, it occasionally repeated the response within a few minutes. The two mouth-opening responses (the bared-teeth displays and the true yawns) bore no temporal or sequential relation to each other.

Discussion of Fish, Lions, and Mandrills

Visual contact with conspecifics or mirror images appears to be necessary for yawning to occur it all in Siamese fighting fish, and the highest rate of yawning occurs when visual, tactile, and chernical contact are possible among fish. As with aggressive biting, the response habituates with prolonged visual or physical contact. In the two mammal species, individuals had presumably habituated to one another through prolonged contact and familiarity. The male mandrills occasion ally showed a bared-teeth display to each other, presumably as a threat, but no such aggressive displays were observed in the lions. Siamese fighting fish in the laboratory yawned exclusively in social settings, so the response is probably also an aspect of aggressive displays in this species.

The clearest result of the zoo observations was the increase in yawning just prior to feeding time which occurred in both lions and mandrills. Feeding may well be the major event of the day for zoo animals (aside from cage cleaning and randomly occurring social interactions), so this finding appears contrary to the belief that yawning is associated with lack of stimulation. As with the fish, the anticipation of major stimulus events may be associated with an increase in yawning by lions and mandrills. Another possibility is that lions, mandrills, and fighting fish all yawn in anticipation of metabolically expensive events such as feeding or fighting. Increased oxygen consumption and metabolic rate characterize such behaviors, but increasing respiration rate might accomplish the saine adaptive outcome.

Humans (Homo sapiens)

Data on yawning frequency by people were collected in several différent publie situations. The procedures used in each of these operant level determinations are described together with the results from each sampling situation. The frequency of yawning by riders on Philadelphia's Broad Street subway line was observed in a series of observations lasting from 10 to 30 min. The number of people present was estimated, and an attempt was made to record every yawn by sitting at one end of the subway car and facing the other riders. A scan-sampling method was used, with a 10-s period taken for each end-to-end scan of the car (Altmann, 1974), but yawns were always recorded if they were noticed. Most of the observations were made between 7:30 and 9:30 a.m. and between 5:30 and 8:00 p.m. As expected, yawning was a relatively low-frequency event. The duration of each observation period was multiplied by the estimated average number of people present during the observation, and the resulting product (person-hours) was the denominator in assessing the relative frequency of yawning. In a total of 12,130 person-hours of subway observation, only 95 clear yawns were recorded. Sixty-five of the yawns occurred during morning observations, when 12,067 person-hours were observed; 30 of the yawns occurred after noon during the remaining 64 person-hours of observation. Thus, the relative frequency of yawning was much greater during the afternoon and evening observations (about 0.48 yawn/person-hour versus 0.0054 in the morning).

The relative frequency of yawning was much greater when fewer people were present (less than 15). Ten yawns occurred during the 44 person-hours when fewer than 15 riders were in the subway car (about 0.24 yawn/person-hour); 85 yawns were made during the 12,086 person-hours in which more than 15 riders were present (about 0.006 yawn/person-hour). During 30-min observations at lunch and dinner in dormitory cafeterias of Temple University, the observer recorded yawning at large tables where 7-22 other students were also eating lunch or dinner. During 43.5 hr of observation, spread over 2 mo, there were only four yawns observed-two at lunch and

two at dinner (approximately 0.009 yawn/personhour). Yawning while eating at communal dining tables appears to be an infrequent event. Five 45-min aerobics classes comprising 15 students produced a total of four yawns, an average yawn frequency of 0.00 12 yawn/person-hour, one of the lowest recorded in any situation observed. Intense, rhythmic physical exertion does not appear to be associated with frequent yawning. Whether this is due to direct inhibition by exercise or to concentration on another activity is presently unknown.

Leisure activities in dormitories were associated with higher yawning rates than was eating or aerobics. While students were watching TV, conversing casually, or drinking beer in groups of three or more, the student observer counted 92 yawns during 5 tir. With a mean of five students in the group, this produced a frequency of 3.6 yawns/person-hour. Seventeen meetings of a mathematics class (calculus) were observed by a student observer for 40-min periods in the middle of the class meeting. A total of 248 yawns occurred during these observations, a rate of 24.6 yawns/person-hour. This was the highest rate of yawning obtained in any of these observations. Finally, yawning was observed in the campus library on 25 occasions during the middIe of the semester. Recording was limited to the five tables adjacent to the observer's position, and sessions lasted for 20 min. A mean of 8 students were present at the tables being observed. Fifty-nine yawns occurred under these circumstances, a frequency of approximately 0.9 yawn/person-hour.

Laboralory Experiment : Having collected data on the operant level of human yawning in a variety of situations, a laboratory manipulation of yawning frequency was attempted. One of the phenomena associated with yawning is its contagiousness. Moore (1942) found that people in college libraries and church services yawned in response to the sight of someone yawning; Moore also found that audio recordings and motion pictures induced yawning in experimental subjects. Responses to the auditory stimulus were counted objectively, but subjects reported on their own yawns to the visual stimulus. No attempt was made to disguise the purpose of the stimulus presentations, so that suggestible people may well have yawned in response to perceived demand characteristics of the situation rather than because of contagion per se. In a recent study by Provine (1986), subjects yawned in response to being asked to think about yawning. On the basis of his findings, Provine suggested that yawning may be triggered by still unspecified physiological events or released by witnessing yawns or "yawn-related stimuli." Presumably, recording their own yawns contributed to his subjects' thinking about yawning.

Method : Forty undergraduate psychology students served as subjects. In my laboratory a semiprofessional actor read a passage from Alice in Wonderiand (the mock turtle's story) either live or on a videotape to the students, who were either alone or in pairs. After either one quarter or three quarters of the 7-min reading, the actor paused and yawned audibly, without covering lier mouth. If fatigue or boredom elicited yawning, then more yawns should occur later in the reading, and yawns elicited by seeing the actor yawn should occur in equal numbers after cither interval. Following the reading, in which yawns were recorded by the experimenter, subjects were asked to recall all facial expressions portrayed by the actor and to judge how well they were portrayed. Subjects were also asked how long since they had caten and slept, what sort of mood they were in, whether they yawned or felt like yawning during the reading, and whether they were aware of the reader's yawn.

Results : Only three yawns were elicited during the entire experinient, two in the video condition and one with the live actor; all three were in subjects who were alone. Two occurred within 20 s of the stimulus yawn, and one occurred 3 min later. All three yawns occurred during the last quarter of the reading. These data provide little evidence for the contagiousness of yawning. Most subjects (82%) reported that they were aware of the reader's yawn, and 46% reported that they felt like yawning, although only 3 did so. One yawner had not slept for 14 hr, but the other 2 had slept recently. For the experiment overall, the rate of yawning in the laboratory was O~ 15

yawn/person-hour.

General Discussion

Visual contact with conspecifics or mirror images appears to be necessary for yawning in Siarnese fighting fish, but enforced physical contact resulted in the highest rates of yawning. This procedure was accompanied by aggressive interactions, and it appears that yawning is a type of social response in this species. Like aggressive biting, yawning wanes with prolonged contact of individuals unless mirrors are present. In the two marnmal species observed in captivity, individuals had presumably habituated to one another, so that the absence of social yawning in these species may have resulted front the familiarity of individuals with one another. Yawning niay be a response to interesting stimuli in these three unrelated vertebrates: The fish yawned most in the presence of novel conspecifics, whereas both lions and mandrills yawned most frequently prior to feeding, when they were attentive to the imminent appearance of a caretaker bringing food.

By contrast, the rate of yawning in humans increased when few people were present, when social, physical, or cognitive stimulation was lacking. High rates of yawning were associated with relatively emply subway cars late in the day, with leisure-time dormitory activities (primarily TV walching and desultory conversation), with lecture classes, and with library studying. The lowest rates of yawning observed outside the laboratory occurred in crowded subway cars during morning rush hours, in crowded, communal dining halls where students were conversing, and in aerobic exercise classes. The possibility thus exists that yawning in humans differs functionally from apparently similar responses observed in other vertebrate species. These data indicate that a scarcity of both conspecifics and interesting stimuli may promote yawns in our species, as shown by Provine (1986), whereas the presence of conspecifics and interesting stimuli were associated with yawning in the three other species observed.

Simply feeling bored, as many subjects undoubtedly did while having Alice in Wonderland read to them, was not sufficient to elicit yawning in this experiment. The failure to elicit yawning in the laboratory, associated with the fact that nearly half of the subjects reported feeling like yawning, suggests that anxiety from being under observation may have inhibited any yawning; that would otherwise have occurred. Students participating in experiments are often somewhat anxious, eager to please, and concerned about the impression they make on the experimenter. Future laboratory studies, in which yawning frequencies are objectively recorded by an observer, are needed to assess the possible effects of such social anxiety on human subjects. The present data are insufficient to establish such effects.