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Short communication

The effects of predictable and unpredictable feeding schedules on the behavior and physiology of captive brown capuchins (*Cebus apella*)

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Abstract

Responses to different feeding schedules in group living capuchins (*Cebus apella*) were evaluated. Animals were fed on a predictable schedule for 6 weeks followed by 6 weeks on an unpredictable schedule (varied by early, on-time, or late feedings). Behavior was sampled via scan sampling at 1 min intervals 1 h pre-feed and 1 h post-feed. It was hypothesized that meal unpredictability would alter behavior and fecal cortisol concentrations. Major differences in behavior typically associated with stress or anticipation (e.g. abnormal behavior, self-directed behavior) were not observed when feedings were switched to an unpredictable schedule. However, differences in other behavioral measures suggest that a predictable schedule is better for the well being of the animals. In the predictable schedule animals spent more time in proximity, activity, and social behavior. Though some changes in behavior during the unpredictable phase were positive (e.g. more foraging, less tension), they were restricted to on-time and early feeds. More negative changes in behavior were seen in the unpredictable phase, specifically on on-time and late feed days. In particular, in the hour before feeding animals spent less time in proximity, less time engaged in social behavior, and more time inactive. This pattern suggests that anticipation of feeding is particularly pronounced when

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feeding times are delayed in an unpredictable manner. Cortisol concentrations were significantly higher during the unpredictable phase than the predictable phase. Subjects did not habituate to the unpredictable feeding schedule, as evidenced by sustained elevated cortisol concentrations during the sixth week of the unpredictable feeding schedule when compared to cortisol concentrations during the predictable phase. The results of both the behavioral and physiological data suggest that predictable feeding schedules may be most beneficial to the well being of captive capuchins.

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Captive animals often have established, predictable feeding schedules due to caretaker and experimental constraints. Such routine husbandry procedures should be evaluated as to their effects on animals' well being, as the predictability and uncontrollability of these schedules may be stressful. Such stress may be manifested behaviorally, through higher rates of stereotypic or abnormal behavior, or physiologically, through an elevation of cortisol concentration.

The influence of feeding schedules on well being appears to be complex. Predictable feeding schedules may lead to anticipatory and stereotyped behavior, as has been documented in a variety of captive animals, including primates (François' langurs; Krishnamurthy, 1994) and carnivores (bears, leopards, and pumas; Carlstead, 1998). However, there is considerable evidence indicating that predictable events are less stressful than unpredictable events when the event is not under the animals' control (Weinberg and Levine, 1980). This would seem to indicate that for many (if not most) laboratory animals, a predictable feeding schedule would be less stressful. Once on a feeding schedule, whether predictable or unpredictable, animals likely become adapted to that schedule and deviations from it may produce behavioral responses. Johannesson and Ladewig (2000) discovered that dairy calves always fed on an irregular schedule did not exhibit behavioral or growth deficits. However, in calves that were fed on a regular schedule that then became irregular, behavioral changes were observed. The calves anticipated feedings and the delay in feeding time resulted in the display of anticipatory behavior.

Capuchin monkeys (*Cebus* spp.) are New World primates known for their behavioral flexibility, cognitive abilities, and propensity for object manipulation. Due to these characteristics, they are commonly studied in captivity for both behavioral and biomedical purposes (Fragaszy et al., 2004). The aim of the present study was to evaluate the effects of predictable and unpredictable feeding schedules on physiological and psychological measures of well being in capuchin monkeys. It was expected that both behavior and cortisol concentrations would differ during predictable and unpredictable feeding schedules.

1. Method

1.1. Subjects

Six socially housed brown capuchins (*Cebus apella*) served as subjects for this study. Animals were housed indoors in the Hiram College Capuchin Laboratory in an enriched

enclosure measuring 3 m × 4 m × 3m. Primate chow was available ad libitum from two feeding stations; fruit was dispersed daily throughout the enclosure.

1.2. Procedure

Morning feeds were not manipulated throughout the study. Afternoon feeds were on a predictable schedule (6 weeks) followed by an unpredictable schedule (6 weeks) for this study. During the predictable schedule, the afternoon feeding occurred at 15:00, which had been the set afternoon feeding time for these animals for over 3 years. Data were collected on a total of 29 days during this schedule. During the unpredictable schedule, feeding times randomly varied from 13:00 to 17:00. The unpredictable schedule consisted of 11 early feedings (between 13:00 and 14:00), 10 on-time feedings (between 14:30 and 15:30), and 12 late feedings (between 16:00 and 17:00). Data were collected on a total of 33 days during the unpredictable schedule. The order of treatment presentation was random during the unpredictable phase.

Scan sampling (Martin and Bateson, 1993) on all individuals was conducted every minute for 1 h pre-feed and 1 h post-feed. Behavioral data collected included abnormal (including coprophagy, feces manipulation, head toss or spin), agonistic, forage, inactive, non-social, self-directed, social, tension (pacing or staring at the door), and vocalization. It was also noted whether or not each subject was in proximity to another (defined as within one body length of another) each scan. Observations were conducted from behind a one-way mirror, so subjects were unable to see or hear the observer. At feeding time, the caretaker entered the room, fed the animals and swept the floor. The caretaker spent no longer than 15 min in the room.

Fecal samples were collected from each subject three times each week in the morning (between 08:00 and 11:00) for the duration of the study. Subjects were transferred into individual cages and samples collected upon voiding. Cortisol concentrations were determined using procedures developed by Sousa and Ziegler (1998).

1.3. Data analysis

All analyses were conducted using SPSS for Windows, Version 11.5, and alpha was set at 0.05. The mean proportion of scans for proximity and each behavior category were calculated for each subject to provide a measure of time spent engaged in each of the behaviors. Prior to analysis, these mean individual proportions were arcsine transformed to ensure normal distributions (Zar, 1984). The behavioral effects of feeding routines were then analyzed using a two-factor within-subjects MANOVA. The two factors analyzed were schedule of the feed (predictable, early, on-time, and late) and the timing of the observation (pre- or post-feeding). Tukey post-hoc tests were used to make direct comparisons between the predictable feeding schedule and other feeding schedules (early, on-time and late) as warranted. Mean individual cortisol concentrations during the predictable and unpredictable phases were compared using a Wilcoxon test as the data violated the assumption of homogeneity of variance.

2. Results

The mean (\pm S.D.) percentage of time in the behavioral categories during each phase, both before and after feeding is displayed in Table 1. The schedule of feeding (predictable, early, on-time, or late) had a significant effect on foraging ($F_{3,15} = 20.15$, $p < 0.05$), inactive ($F_{3,15} = 3.34$, $p < 0.05$), social behavior ($F_{3,15} = 19.01$, $p < 0.05$), tension ($F_{3,15} = 8.47$, $p < 0.05$), and proximity ($F_{3,15} = 11.27$, $p < 0.05$). There was more foraging and less tension at early feeds ($p < 0.05$). Tension was also lower for days when animals were fed on-time during the unpredictable schedule, but animals spent less time in proximity and in social behavior ($p < 0.05$). On days that animals were fed late, animals were more inactive and less social ($p < 0.05$).

A main effect of timing of observations was found for foraging ($F_{1,5} = 93.51$, $p < .05$), inactive ($F_{1,5} = 8.10$, $p < 0.05$), nonsocial ($F_{1,5} = 65.47$, $p < 0.05$), social ($F_{1,5} = 27.17$, $p < 0.05$), proximity ($F_{1,5} = 15.47$, $p < 0.05$) and vocalization ($F_{1,5} = 18.52$, $p < 0.05$) behavior. Foraging, food-related vocalizations, inactivity, and nonsocial activity increased after feeding while social behavior and proximity decreased.

There were significant interaction effects between schedule of feed and observation time for agonistic ($F_{3,15} = 5.12$, $p < 0.05$), foraging ($F_{3,15} = 40.26$, $p < 0.05$), inactive ($F_{3,15} = 3.97$, $p < 0.05$), nonsocial activity ($F_{3,15} = 4.53$, $p < 0.05$), social ($F_{3,15} = 5.49$, $p < 0.05$), tension ($F_{3,15} = 5.85$, $p < 0.05$), and proximity ($F_{3,15} = 6.39$, $p < 0.05$). Overall, agonistic behavior was low for all schedules ($< 1\%$); it was highest on on-time and late days after feeding. There was more nonsocial behavior and inactivity and less social behavior and time spent in proximity during the pre-feed period of on-time and late days compared to predictable or early days. Tension was highest in the hour before feeding for the predictable and late feeds. While tension decreased after feeding on most schedules, it actually increased on early feed days.

Mean individual cortisol concentrations ranged from 5.12 to 36.52 ng/g during the predictable phase, and from 7.37 to 103.07 ng/g during the unpredictable phase. The median cortisol concentration during the unpredictable phase (Mdn = 43 ng/g) was significantly higher than the concentration during the predictable phase (Mdn = 7.71 ng/g) (Wilcoxon $z = -2.20$, $p < 0.05$).

In order to determine whether the monkeys habituated to the unpredictable feeding schedule, mean individual cortisol concentrations from the final week of the unpredictable phase ($n = 3$ for each subject) were compared to mean individual cortisol concentrations during the predictable phase. Cortisol concentrations were significantly higher during the sixth week of unpredictable feeding (Wilcoxon $z = -1.99$, $p < 0.05$) when compared to the unpredictable phase.

3. Discussion

Although this colony had been fed on the same predictable schedule for 3 years, major differences in behavior typically associated with stress or anticipation were not observed when feedings were switched to an unpredictable schedule. However, cortisol concentrations differed between the two feeding schedules, with cortisol concentrations

Table 1

Mean percentage of time (\pm S.D.) *C. apella* engaged in specified behavior for each schedule of feed (predictable, early, on-time, late) and timing of observation (pre- or post-feeding)

Behavior	Predictable pre-feed	Post-feed	Early pre-feed	Post-feed	On-time pre-feed	Post-feed	Late pre-feed	Post-feed
Abnormal	0.98 (\pm 1.92)	0.73 (\pm 1.05)	0.77 (\pm 1.69)	0.50 (\pm 1.04)	2.05 (\pm 4.73)	0.62 (\pm 1.23)	3.52 (\pm 8.03)	0.72 (\pm 1.61)
Agonistic ³	0.27 (\pm 0.27)	0.20 (\pm 0.15)	0.17 (\pm 0.15)	0.20 (\pm 0.19)	0.27 (\pm 0.28)	0.47 (\pm 0.38)	0.07 (\pm 0.05)	0.65 (\pm 0.43)
Forage ^{1,2,3}	11.48 (\pm 4.31)	55.15 (\pm 5.87)	22.80 (\pm 5.90)	58.40 (\pm 5.57)	10.75 (\pm 3.51)	55.22 (\pm 8.15)	10.35 (\pm 4.98)	61.98 (\pm 5.62)
Inactive ^{1,2,3}	11.03 (\pm 6.63)	6.28 (\pm 4.50)	10.17 (\pm 7.57)	8.15 (\pm 5.56)	12.88 (\pm 9.09)	9.67 (\pm 6.93)	13.93 (\pm 9.36)	7.80 (\pm 4.53)
Nonsocial ^{2,3}	35.40 (\pm 6.24)	19.43 (\pm 6.99)	34.75 (\pm 5.80)	16.73 (\pm 2.47)	44.83 (\pm 10.29)	20.22 (\pm 5.89)	42.02 (\pm 11.36)	16.05 (\pm 3.21)
Self-directed	6.27 (\pm 9.30)	2.25 (\pm 1.66)	5.60 (\pm 6.71)	2.72 (\pm 1.98)	5.32 (\pm 8.53)	2.17 (\pm 1.43)	5.52 (\pm 7.21)	1.93 (\pm 1.76)
Social ^{1,2,3}	19.33 (\pm 8.55)	5.52 (\pm 2.52)	17.35 (\pm 8.21)	5.43 (\pm 2.28)	13.50 (\pm 7.36)	2.35 (\pm 1.27)	8.60 (\pm 5.83)	1.82 (\pm 0.74)
Tension ^{1,3}	8.57 (\pm 9.93)	5.75 (\pm 3.55)	4.63 (\pm 5.60)	5.20 (\pm 3.78)	4.95 (\pm 4.86)	3.40 (\pm 2.36)	11.18 (\pm 12.11)	5.18 (\pm 3.11)
Proximity ^{1,2,3}	42.22 (\pm 5.28)	33.31 (\pm 2.33)	43.04 (\pm 6.13)	36.13 (\pm 4.32)	38.01 (\pm 7.71)	28.80 (\pm 3.47)	35.73 (\pm 7.64)	31.66 (\pm 4.97)

Superscripts indicate significant effects at the 0.05 level, where 1, effect of schedule; 2, effect of timing of observations; 3, interaction effect of schedule and timing of observation. Display and vocalization categories not included.

approximately 30% higher during the unpredictable feeding schedule. Physiological measures of stress provided a more sensitive measure of well being in this social group of capuchins.

Some behavioral changes among the different feeding schedules are noteworthy. When the effect of schedule is considered, predictable schedules appeared to be better for the animals. Animals spent more time in proximity, engaged in social behavior, and active during the predictable schedule. The greatest negative effect of schedule was seen for on-time and late feeds, although not in all behavior categories. During on-time and late feeds animals spent significantly more time inactive and significantly less time engaged in social interactions as compared to the predictable schedule. This was most pronounced in the hour before feeding, suggesting that anticipation was greatest on these days. While the increase in tension-related behavior during the predictable schedule was small, this deserves further scrutiny as it does not match other behavior patterns that would indicate increases in stress. Importantly, there was no change in abnormal behavior after animals were placed on an unpredictable feeding schedule.

In capuchins, behavioral indicators of stress are associated with physiological elevations of cortisol (Dettmer et al., 1996). Despite not having a clear behavioral indicator of stress from the capuchins in this study, increases in cortisol concentrations suggest that the unpredictable schedule did cause an increase in stress. As evidenced by the significantly elevated cortisol concentrations, these monkeys were still showing signs of stress after 6 weeks of feeding on an unpredictable schedule. While it may be that animals can eventually habituate to unpredictable feedings, it is important to realize that they may be significantly stressed while in the process of habituation to such a routine.

The difference between our behavioral and physiological measures suggests that the latter was a more sensitive indicator of stress. Based on our findings, we suggest that predictable feeding routines may be less stressful for captive capuchins. However, the same may not hold true for all captive primates. The impact of feeding routines should be assessed both behaviorally and physiologically to determine the best schedule for individual species.

4. Conclusions

Unpredictable feeding schedules negatively affected behavior and physiological well being of a social group of brown capuchins. When these capuchins were fed on a predictable feeding schedule, endocrinological measures of stress were lower and positive behavior patterns were higher. The results suggest that socially housed laboratory capuchins adapt to predictable routines of feeding, and deviations from those routines produce both behavioral and physiological stress.

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