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THE RELATIONSHIP BETWEEN SOCIAL BEHAVIOR AND GENITAL SWELLING IN CAPTIVE FEMALE CHIMPANZEES: IMPLICATIONS FOR MANAGING CHIMPANZEE *(Pan troglodytes)* GROUPS

M. A. Bloomsmith
S. P. Lambeth
P. L. Alford
The University of Texas M. D. Anderson Cancer Center

ABSTRACT: This study was conducted as a portion of a project investigating relationships among reproductive cycling, aggression, and wounding in captive chimpanzees. Changes in behavior associated with the genital swelling of 11 adult female chimpanzees socially housed in four different groups were measured using 282 hours of data gathered within a 20-month period. The females' perineal swellings were rated daily using a five-point scale indicating level of tumescence. Behaviors recorded when the animals were detumescent were compared with behaviors when their sexual swellings were maximal. In addition to the subject's genital swelling rating, two factors, the male-to-female ratio in the groups and the presence or absence of a tumescent female other than the focal animal, were also included in the analysis. Multiple regression analysis revealed significant effects of each of the three factors. Significantly higher levels of sexual behavior and lower levels of submission were associated with the tumescent stage of cycling. Scores for affiliation, aggression, abnormal behavior, inactivity, locomoting, and being followed did not vary significantly with swelling phase. Group structure (male-to-female ratios) affected affiliation, locomoting, being followed, and aggression levels. Affiliation, submission, and locomoting were influenced by the presence of a tumescent female in the group. Proximity to other adult females increased during the tumescent stage of swelling, but proximity to adult males did not change. The group structure and whether or not a tumescent female was present affected various aspects of proximity to all age/sex classes of group members. Some findings from this study may be explained by the long-term stability of group membership in the colony studied, and implications for colony management are discussed.

INTRODUCTION

The studies of female chimpanzee (*Pan troglodytes*) behavioral changes associated with estrous cycling and ovulation have focused

Address correspondence to Mollie Bloomsmith, Ph.D., The University of Texas, M. D. Anderson Cancer Center, Science Park, Department of Veterinary Resources, Route 2, Box 151-B1, Bastrop, Texas 78602.

mainly on sexual behavior (Coe, Conolly, Kraemer, & Levine, 1979; Lemmon & Allen, 1978; Wallis, 1982; Yerkes & Elder, 1936). More recently, some investigators have measured influences on other behaviors (Goodall, 1986; Wallis & Lemmon, 1986; Wallis, 1986). These findings have been described in terms of female sexuality, behavioral changes associated with pregnancy, and the evolution of the chimpanzee mating system. The purpose of our study was to examine from an applied perspective, whether reproductive cycling, the presence of other cycling females, and group composition affected female behaviors and to determine whether such effects need be considered in the management of chimpanzee colonies.

The female chimpanzee's perineal region increases in size and turgidity as she approaches the time of ovulation. This genital swelling apparently attracts males by providing a visual cue for female reproductive status (Dixson, 1983 cited in Wallis, 1986; Graham, 1981). Rates of copulation, genital inspection, food sharing, and grooming are all affected by female chimpanzees' cycles (Harcourt, 1981; Lemmon & Allen, 1978; Wallis, 1986), as is the relative occurrence of male or female initiation of some of these social interactions (Wallis, 1986). Free-ranging females have been described as showing various levels of sociality, grooming, copulating, "nervousness," submission, and "assertiveness" at different points in their cycles (Goodall, 1986).

Goodall emphasized the strong influence of this factor by stating that "the presence or absence of cycling females is without doubt the single most significant factor in overall patterning of the chimpanzee community from year to year" (1986, p. 158). Females with a genital swelling may be in the company of many males as they travel and forage, but a female with no swelling is generally not near adult males (Goodall, 1986). The congregation of males around sexually receptive females sets up the circumstances for male-male competition for access to ovulating females, although in the wild this competition is not necessarily expressed by intermale aggression (Harcourt, 1981).

Since adult male chimpanzees form the cohesive unit around which free-ranging chimpanzee groups are organized, it is logical to establish multi-male groups of captive chimpanzees (Fitch, Merhalski, & Bloomsmith, 1989). Such arrangements are also a practical means of allowing social housing for the large number of adult male chimpanzees in captivity, but there are advantages and disadvantages for the group members (see Fitch et al., 1989 discussion). In our colony, an analysis of veterinary wounding records indicated an increase in the total number of wounds inflicted in multimale-multifemale social groups when at least one of the group's females displayed a maximal genital swelling (Alford, Bloomsmith, Keeling, & Beck, 1990; Lambeth, Bloomsmith, & Alford, 1990). This wounding is

probably an outcome of male-male competition and is certainly a problem for the colony manager, although it is acknowledged that some aggression among captive chimpanzees is "normal" and to be expected even among well-socialized groups.

This study was the first in a group of studies designed to identify and characterize factors influencing captive chimpanzee agonism. A second study will measure levels of agonism when female group members are at different points in their reproductive cycles (Bloomsmith, Lambeth, & Alford, accepted) and a third study will test a strategy for reducing the agonism potentially associated with the cycling of females. Although the spatial constraints of captivity may influence the effects of female cycling on social behavior, some influences on social interactions would still be predicted from the strength of the findings with free-ranging subjects. Based on those findings, we expected to find in the present study that changes in female affiliation, agonism, sexual behavior, and proximity to adult males would be associated with changes in genital swelling. This information could then be used to identify the female's role in the increase in wounding associated with cycling females, as documented in our colony records.

METHODS

Animals

The animals were 11 sexually mature, nongravid, female chimpanzees (*Pan troglodytes*) socially housed with adult males, adult females, and immature chimpanzees in four different groups. Social groups of 2 to 4 adult males, 2 to 5 adult females, and 2 to 5 immatures were housed in enriched outdoor corrals (22 m in diameter) with access to additional indoor quarters. During observation periods focal animals and their groups were limited to the outdoor portion of their enclosures. The animals' ages ranged from 10 to 26 years old.

Data Collection

A total of 282 hours of data were collected between May 1988 and January 1990, with a range of 18 to 30 hours of data collected per chimpanzee. Each chimpanzee was observed between one and three times weekly at various times throughout the day. Data collection consisted of 15-min focal animal observations (Altmann, 1974) with data recorded at 10-s intervals.

The behavioral categories were affiliative interactions (rest in contact, move in contact, groom, play initiation, play, embrace), aggressive interactions (threat, brusque rush, attack), submissive inter-

actions (avoid, crouch/bob, pant-grunt, bared-teeth scream, present in an agonistic context, flee), sexual behavior (receive genital exploration, present in a sexual context, receive mount/thrust, move away from a mounting male, explore genitals of another), and other behaviors (inactive, locomote, abnormal, being followed by another animal, and "other"). (See Appendix for operational definitions.)

Proximity of the focal animal to her group members was also recorded during the same intersample interval. The identity of each chimpanzee in the proximity of the focal animal was recorded. Proximity was defined as two individuals being within 1 m of each other. The mean percentage of agreement by observers across all behavioral categories was 92%, as measured monthly, and the mean percentage of agreement on proximity scores by four observers was 93%.

The degree of swelling of the sexual skin of each female was recorded daily by one of two trained members of the caregiving staff. A 5-point scale (with ratings of 0 to 4) was used to rate the swellings (Graham, 1981). Behavioral data collected on days when the genital swelling was rated as a "2" were excluded to clearly differentiate the two ends of the scale, and the remaining information was separated into two categories as described below. The interobserver reliability on the swelling ratings was 84% agreement.

Data Preparation and Analysis

The scan-sampling behavioral data were summarized for each session to estimate the percentage of time the chimpanzee was engaged in each behavior. This information was then compiled and grouped across all animals by the five stages of the female's estrous cycle. Data were then combined into two categories, the detumescent condition (ratings of 0 or 1) and the tumescent condition (ratings of 3 or 4).

The scan-sampling proximity data were summarized by adding the number of points at which the focal animal was within 1 m of an adult male, an adult female, or an immature group member during each observation session. This information was then compiled across focal animals by the genital swelling phase, as described above.

Because of their potential influence on behavior, two other factors were also analyzed: the presence of another tumescent female and the adult male-to-female ratio in the animal's social group. There was another tumescent female present (other than the focal animal) during approximately 35% of the observations. During 90% of the data collection sessions, the male-to-female ratio was either 1:1 (three adult males and three adult females) or 1:2.5 (two adult males and five adult females). The remaining 10% of the data were collected under a variety of group compositions. Because these data were too few for analysis, they were excluded.

Data were analyzed by applying multiple regression techniques, which in some cases were followed by an analysis of variance test applied to residuals. All tests were two-tailed, and an alpha of 0.05 was used to determine significance. Several transformations on the original data led to no improvement in the information derived from the data.

RESULTS

A multiple regression measuring the effects of three factors (genital swelling, presence of a tumescent female, and group composition) was computed for each of the eight dependent measures of interest. Each factor significantly affected at least one dependent measure (see Table 1 for individual values). When tumescent, the focal animals showed a statistically significant increase in sexual behavior. Their level of submissive behavior was reduced, but the reduction did not satisfy the alpha level set. The presence of a nonfocal tumescent fe-

TABLE 1
Statistical Relationships Between the Three Factors of Interest and the Eight Dependent Measures.

	Factor		
Dependent Measure	*Phase of Genital Swelling*	*Presence/Absence of Nonfocal Tumescent Female*	*Group Structure*
Aggression	NS	NS	NS[2]
Submission	−.06; NS[1]	NS[2]	NS
Affiliation	NS	.04; $p = .003$	.19; $p < .001$
Sexual Behavior	.13; $p < .001$	NS	NS
Abnormal Behavior	NS	NS	NS
Inactivity	NS	NS	NS
Being Followed By Another	NS	NS	−.07; $p = .025$
Locomotion	NS	−.03; $p = .006$	−.10; $p < .002$

A three-factor multiple regression was computed for each dependent measure. The standard coefficient and the associated p value for each factor is reported.

[1] $p = .06$

[2] A two-factor multiple regression was computed for each dependent measure which excluded the genital swelling factor. Subsequently the residuals were analyzed by ANOVA to measure an effect of genital swelling. Two additional dependent variables, submission (−.07; $p = .02$) and aggression (.06; $p = .04$), were determined to be significantly related to the presence of a nonfocal tumescent female and group structure respectively. Relationships to genital swelling phase were unchanged.

male reduced levels of submission and locomotion among the chimpanzees and increased their affiliation. The focal animals living in a group with a male-to-female ratio of 1:2.5 showed more affiliation, showed less locomotion, and were followed less often than those living in a 1:1 group structure. Focal animals in the 1:2.5 group structure engaged in approximately three times as many scans with affiliation as those in the 1:1 structure (20% versus 7% of the data scans). Approximately three-quarters of this affiliative behavior recorded in each of the group structures was social grooming.

Due to concern over reduced statistical power from including three factors in the multiple regressions on infrequently occurring dependent measures, additional analyses were performed. Multiple regressions were computed to remove the variance associated with group structure and other tumescent females, and the residuals were then tested for an effect of genital swelling using an ANOVA. The multiple regressions with only these two factors revealed a significant relationship to two other dependent measures: the 1:2.5 group composition was associated with more aggression than the 1:1 group structure; the incidence of submissive behavior was significantly higher when there was no other tumescent female in the group. The ANOVA results for effects of genital swelling were identical to those found using the three-factor multiple regression.

The patterns of association with other individuals in the group were examined by summarizing and analyzing the proximity data in three ways. First, the absolute values for the incidence of proximity to group members were calculated. Multiple regression of absolute proximity values for genital swelling phase, the presence of a tumescent female in the focal animal's group, and group composition showed significant effects (Table 2).

When tumescent, animals had higher scores of proximity to other adult females; there was no change in their proximity to adult males or to immatures. The presence of a tumescent female in the focal animal's group also increased the score for proximity to other adult females. Chimpanzees in the group with a 1:2.5 male-to-female ratio were near other group members more than those in a 1:1 male-to-female ratio. Higher levels of proximity to adult females and to immatures were measured, but there was no difference in proximity to adult males.

The second treatment of the proximity data was adjusted for the number of available partners by dividing the absolute proximity values by the numbers of group members in the appropriate age/sex class. These adjusted proximity values were then analyzed by a multiple regression. Genital swelling had no effect on any of the adjusted proximity scores. The presence of a tumescent female in the focal animal's group increased her proximity both to adult males and to adult

TABLE 2
Statistical Relationships Between the Three Factors of Interest and the Proximity Measures.

	Factor		
	Phase of Genital Swelling	*Presence/Absence of Nonfocal Tumescent Female*	*Group Structure*
Absolute Proximity Scores:			
To Adult Males	NS	NS	NS
To Adult Females	.08; $p = .01$	.10; $p = .002$	.13; $p < .001$
To Immatures	NS	NS	.23; $p < .001$
To All Group Members Combined	.06; $p = .04$	.09; $p = .007$	.22; $p < .001$
Proximity Scores Adjusted for Number of Partners:			
Mean to Each Adult Male	NS	.06; $p = .05$	.08; $p = .01$
Mean to Each Adult Female	NS	.07; $p = .04$	.06; NS[1]
Mean to Each Immature	NS	NS	.14; $p < .001$
Mean to Each Group Member	NS	.07; $p = .04$	.17; $p < .001$
Percentage of Proximity to Each Age/Sex Class:			
To Adult Males	NS	−.07; $p = .05$	NS
To Adult Females	NS	.11; $p < .001$	NS
To Immatures	NS	NS	.14; $p < .001$

A three-factor multiple regression was computed for each dependent measure. The standard coefficient and the associated p value is reported.

[1] $p = .06$

females. These adjusted proximity scores for all age/sex classes of group members were higher in the group with a 1:2.5 composition.

The third summary of the proximity data was made to calculate the percentage of the proximity scores that were directed toward each of the three age/sex classes previously identified. Multiple regressions for each age/sex class revealed that genital swelling had no effect on

the percentage of the proximity scores associated with age/sex class. The presence of a nonfocal tumescent female significantly increased the percentage of proximity to adult females and to adult males, but had no effect on the proximity to immature group members. Only the percentage of total proximity to immature group members was affected by group composition, with a greater level of proximity in the 1:1 groups.

The copulation rate was calculated for all focal animals combined. In 118.5 hours of observation when females were at the low stage of swelling, one copulation was observed, giving a rate of .008 copulations per hour. When females were at the high stage of swelling, five copulations were observed during 134.5 hours, giving an hourly rate of .04. (As mentioned in Methods, data from females with a tumescence rating of 2 [29 hours] were not analyzed.)

DISCUSSION

In this study, the behavior of adult female chimpanzees was influenced by their own reproductive cycling, by the presence of other cycling females in their social groups, and by the ratio of adult males to adult females in their social groups. These factors affected different aspects of female behavior. Consistent with previous studies (Goodall, 1986; Wallis, 1986), the incidence of sexual behavior rose during the tumescent stages of females' cycles. Genital explorations of the focal females doubled between the detumescent and tumescent stages and was the most frequent sexual interaction. Copulations were infrequent, with only six observed during the 282 hours of observation. This is much lower than copulation rates reported in the wild (Goodall, 1986; Tutin, 1979; Tutin & McGinnis, 1981) or in other captive populations (Coe et al., 1979).

In addition, females with a maximal genital swelling showed a tendency toward exhibiting less submissive behavior than those in a detumescent stage of their cycle. The reduction in submissive behavior could result from at least two situations. Fewer aggressive actions may be directed toward the females during tumescent stages of their cycles, therefore eliciting fewer submissive responses, or females may respond to the same social situations differentially, based upon their cycling status. Which situation best explains these findings cannot be discerned from these data because the collection technique did not incorporate sequences of behavior. However, Goodall stated that female chimpanzees in Gombe became "more assertive during maximal swelling" (1986, p. 483). Unseen and submissive females that normally remained at the perimeters of the social group would become visible and approach dominant males, sometimes begging for food

when cycling. Similarly, Nishida stated that "estrus seems to eliminate an adult female's shyness and makes her bold and aggressive" (1979, p. 103). Findings from the current study indicate that a similar phenomenon may be manifested in captive females.

No behaviors other than sex and submission were affected by genital swelling phase. It should be noted that rating genital swellings is not equivalent to detailed hormonal information, which would more closely represent the phase in each female's reproductive cycle. It is possible, for example, that some of these females' cycles were anovulatory. The methods used have the shortcoming of not accounting for such events.

Based upon our previous finding of increases in the number of wounds inflicted in multimale-multifemale groups when there was a female with a tumescent swelling present, one might expect that adult females would be involved in more aggressive episodes themselves. Our findings contradict that hypothesis. Further examination of our wounding records after this study was completed have indicated that the effect of tumescent females on rates of wounding has been eliminated in recent years in some groups with long-term stability (Alford et al., 1990; Lambeth et al., 1990). Unfortunately, since data for the current study were collected only on groups that had been stable over a long period of time, we cannot discern whether females may have been directly involved in the increase in wounding measured in past years.

The presence or absence of a tumescent female group member has an indirect impact on the behavior of other female group members. Females engage in more affiliation, less submission, and less locomoting when a group member has a tumescent swelling. These changes seem to be generally consistent with a more relaxed, less socially tense atmosphere when at least one other female group member is displaying a maximal swelling. There is no evidence, for example, that adult males redirect aggression from tumescent females toward other (nontumescent) females in the group. It is important to note that this finding relates only to adult females. Members of other age/sex classes may respond differently.

Finally, the adult composition of the groups also seems to have an impact on several behaviors that could be related to the level of social tension in the group. These results should be viewed with caution however, because only one of the groups studied had a group composition of 1:2.5. In the group with a 1:2.5 male-to-female ratio, the females were more affiliative, spent less time locomoting around the enclosure, and were also followed by another animal less often. However, these females also engaged in more aggression. Perhaps two adult males could not control female aggression as effectively as can males in a 1:1 group structure. One possible explanation for the

positive relationship between levels of affiliation and of aggression is that social grooming (the behavior that composed most of the category of affiliative behavior) may be a tension-reducing, reconciliatory behavior that may increase in association with agonistic episodes (Nieuwenhuijsen & de Waal, 1982). In other words, perhaps these females fought more, so they reconciled (e.g., groomed) more.

Most unexpectedly, affiliation and the proximity of females to adult males were not affected by changes in genital swelling. Females did not show an increase in the number of times they were near males, nor was there any evidence for a bias toward a greater percentage of proximate activity to involve males at times of maximal swelling. Contrary findings would have been predicted based on relevant literature that describes increased prosocial interactions (Coe et al., 1979; Harcourt, 1981), particularly male-initiated interactions, as females' cycles progress toward ovulation (van Lawick Goodall 1968; Goodall 1986; Wallis, 1986). The group structure had various effects on proximity to other group members, as did the presence of a tumescent female.

The extremely low rate of sexual activity, the lack of effect of reproductive cycling on affiliative behavior, and the lack of an increase in proximity to males during tumescent stages of cycling are in contrast to other published findings. Each of these results may be influenced by a particular feature of the chimpanzee colony studied, and so may not be generalizable. This colony has shown a decrement in reproductive performance (e.g., number of conceptions) in the last few years, and a subjectively noticed reduction in sexual behavior. We hypothesize that this effect may be due to long periods of stability in group membership (in most cases at least 7 years when the data were collected) and a resulting "boredom" with available sexual partners. A similar effect of familiarity on captive chimpanzee sexual interactions has been documented (Allen, 1981; Coe et al., 1979). An objective study of this phenomenon in The University of Texas colony is planned, but the effect appears to be so strong that we feel confident in hypothesizing an influence on intragroup interactions. While the generalizability of these findings may be somewhat constrained because of the influence of group stability, this information certainly can be applied to other settings in which long-term group stability is maintained. Larger social groups of chimpanzees are becoming more common as laboratories and zoos are attempting to improve the social conditions for their chimpanzee residents. This information will be useful to apply as those groups remain intact over many years.

The current results indicate that chimpanzee behavioral management problems may change as colonies are housed in stable groups over long periods of time (see Nieuwenhuijsen & de Waal, 1982 for evidence of decreasing aggression over time). For example, reduced

breeding performance may become a problem rather than agonism and wounding problems resulting from intermale competition for females. In the future, we will more fully examine these issues by studying the effects of reproductive cycling on wounding and on group measures of agonism, and by examining the effect of familiarity on sexual behavior.

From a behavioral management perspective, these findings indicate that, in our colony with multimale chimpanzee groups, changes in the genital swellings of females do not seem to lead to any problems that demand the attention of colony managers. Our original goal of documenting the females' role in increased group agonism during certain phases of their cycle has been changed, as further analysis has shown that this agonism is eliminated with long-term stability in group membership (Bloomsmith, et al., accepted). There is probably little a colony manager can do to arrange groups so that at least one tumescent female is present, but this may have beneficial effects on other group females. These data indicate that group structure can be manipulated by colony managers, perhaps to influence levels of female affiliation or aggression. Since these behaviors varied together, it may be that groups with particular structures require more careful monitoring for problems with aggression. If a colony manager wanted to encourage a particular female's expression of social behavior, a group containing more females than males may be an appropriate choice. On the other hand, if female aggression is really a problem, having an equal number of adult males as adult females may help to reduce the problem. Certainly, stability in group membership should be encouraged from the point of view of creating a more peaceful and safe environment for chimpanzees, as long as one realizes that problems with breeding performance may then have to be addressed.

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APPENDIX: Operational Definitions of Behaviors Analyzed

Affiliative Behavior

Play Initiation—Includes a variety of behaviors, such as run-past, slapping the ground or rolling in front of another individual, that culminate in a play bout. Usually accompanied by a play face.

Social Play—Includes rough-and-tumble play (fast-paced, vigorous locomotion, wrestling, hitting, pulling, chasing, biting, etc.) and quiet play (slower-paced, gentle tickling, finger and toe manipulating, etc.). Never accompanied by piloerection; may be accompanied by play-face and/or laughing.

Embrace—Usually ventro-ventral contact of two individuals. One or both may have arms around the other. Hands are *relaxed* (i.e., not clutching fur of the other). In some instances an animal may embrace another from the side or the back.

Rest in Contact—Physical contact with another animal that is not recorded under a different behavioral category. Animals are not locomoting and are touching one another.

Move in Contact—Physical contact with another animal that is not recorded under a different behavioral category. Animals are locomoting and are touching. Carrying an infant is excluded.

Social Groom—Picking through hair or at skin and removing debris with hands and/or mouth. Does not include pulling hair out. Focal animal may direct or receive this, or it may be mutual.

Agonistic Behavior

Avoid—Focal animal moves away as another approaches or moves out of the path of another. May involve a flinching movement (slight ducking of the head or head and shoulders).

Crouch/Bob—Focal animal lowers its body by flexing its arms and legs until it is in a horizontal position touching or nearly touching the substrate. May tuck its head between drawn up shoulders or press its face against the ground. Vertical, repeated movement of the head or head and shoulders in an "up-and-down" pattern.

Pant Grunt—Rapid, rhythmic series of grunts or barks directed toward another. Sometimes accompanied by crouching or bobbing (after Bygott, 1979).

Bared Teeth Scream—Mouth widely opened, lips fully retracted from teeth and gums with high-pitched, intense intermittent screams (after van Hooff, 1974).

Flee—Focal animal moves away from another at full speed. Often accompanied by bared teeth screaming (after van Hooff, 1974).

Threat—Includes head tip (a slight, upward jerking movement of

the chin), arm-raising, arm-waving, wrist-shaking, and lunging toward another animal.

Brusque Rush—Locomotion during which animal moves toward another at full speed often with piloerection (often as a component of a display). Can be a male or female exhibiting this.

Attack—Aggressive interaction involving physical contact. Focal animal hits, tugs, grabs, bites, stomps on, rolls, or repels the other animal involved (after Bygott, 1979).

Sexual Behavior

Receive Genital Exploration—Focal animal's genitals are visually, orally, or manually inspected by another.

Present—Focal animal's posture varies from slight flexion of the arms or turning rump toward another to an extreme crouch with all four limbs folded under it so it is close to the ground. (The context of the behavior is judged to distinguish sexual from agonistic contexts.)

Receive Mount/Thrust—Female remains stationary while a male is mounting her.

Move Away—Female moves away from a male that has "solicited" toward her (sits facing her with thighs rotated laterally, generally has an erection, and exhibits pelvic thrusting); has attempted a genital explore or has attempted a mount.

Genital Explore—Focal animal visually, orally, or manually inspects another animal's anogenital region.

Miscellaneous Behaviors

Inactive—Focal animal is immobile, not engaging in any activity. Includes lying down, leaning, and reclining. The animal appears to be sleeping.

Locomote—Focal animal's whole body is moving through space. Includes walking, climbing, brachiating, etc. If the focal animal is contacting another chimpanzee while locomoting, "move in contact" is recorded rather than locomote.

Abnormal—Includes coprophagy, feces spreading, urophagy, hair plucking, regurgitating, bizarre posturing, self-slapping, rocking, and idiosyncratic stereotypies (Walsh, Bramblett, & Alford, 1982).

Receive Follow—Another animal follows the focal subject.

Other—Behavior not included under any other category in the ethogram.

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BOOK REVIEWS

Spontaneous alternation behavior edited by W. N. Dember & C. L. Richman. Springer-Verlag, New York, 1990, XII + 211 pp.

If an adult rat is placed in the start stem of a T-maze, allowed a choice of one of the arms, and then placed immediately back into the maze and allowed a second choice, about 80% of the rat's second choices will be the arm opposite to that entered in the first trial. This is named *spontaneous alternation behavior*, or *SAB*, and was first observed by Hunter (1914) in a study on discrimination learning. Why would comparative psychologists be interested in such a simple phenomenon?

I started my reading of Dember & Richman's (D&R) book with some expectations I usually experience when reading a collection of chapters, i.e., that heterogeneity of topics and styles will prevail, that it will be hard to find a common theme, and that there will be a lot of "unpublished results" which may not be appropriate for publication in major journals. I was glad to discover that I had been wrong. D&R had put together a very coherent set of chapters which does more than merely review the literature; it conveys a sense of accomplishment uncommon in the animal learning and behavior field. The authors have successfully avoided the further-research-is-necessary cliché, to concentrate on making sense of the impressive amount of information that has been obtained about SAB after several decades of research.

The historical overview presented by W. N. Dember reminds us of some important connections between the early literature on SAB and learning theory. SAB was initially conceptualized in terms of an *exploratory tendency* that would presumably drive rats toward novel places. It was Hull's notion of *reactive inhibition* what shifted attention from the environment to the animal's response. Reactive inhibition was conceptualized as an aversive, temporary state induced by the occurrence of a particular response; within Hull's theory, reactive inhibition was designed to account for some extinction phenomena, such as spontaneous recovery, but its relevance to SAB was obvious. Some early data on the dependence of SAB on relatively short intertrial intervals seemed to confirm the role of reactive inhibition because this aversive state was thought to spontaneously decay in time. SAB entered therefore the *place vs. response* controversy that dominated the field of animal learning during the 1950s. The crucial ex-

