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THE RELATIONSHIP BETWEEN STABILITY OF ACTIVITY RHYTHMS AND DOMINANCE BEHAVIOR IN MALE MICE

A Thesis

by

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Submitted to the Graduate School Appalachian State University in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE

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## ABSTRACT

THE RELATIONSHIP BETWEEN STABILITY OF ACTIVITY RHYTHM AND DOMINANCE BEHAVIOR IN MALE MICE. (August 1985) James Michael Orcutt

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This research investigated the relationship between the stability of activity rhythm and social status in laboratory mice (*Mus musculus*). The three hypotheses tested were: 1) dominant mice attend more to the photoperiod than to social factors in establishing their activity rhythms, while subordinates must be attentive to both the photoperiod and social factors, 2) dominant mice are more stable in activity rhythm than subordinates, and 3) dominant mice are more active than subordinates.

Four pairs of male house mice were used in the study. The two mice in each pair were separated by a wire mesh which allowed them to establish their rhythms semi-independently of the other individual. After a few days the mesh was removed allowing direct

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contact between the pair of mice. Approximately twentythree hours later the mesh was replaced and the twentyfour hours of data before and after contact were correlated to show disruption or stability of activity rhythms. The treatment was repeated once to determine if the results were consistent.

The dominant mice showed little or no disruption in activity rhythm while the subordinates activity was disrupted. The results indicated that dominant mice were not concerned with the activities of the subordinate, but were more concerned with environmental factors. The subordinate must attend to both environmental factors and activity of the dominant. Also, dominant mice were more active and showed more stable rhythms than subordinates. A discussion of how the results fit with strategies which mice use in the natural environment is presented.

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## DEDICATION

This is dedicated to my mother, my sister Jayne, my brothers John and Jeff and to the memory of my father. I love you all.

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## INTRODUCTION AND LITERATURE REVIEW

The ecology of social animals encompasses many interrelated factors. Among the most important is their response to the physical and social pressures of the environment. Surviving predation, hunger, and other environmental stress are only some aspects of an animal's success; another aspect is how the individual contributes to the survival of the species by reproduction. These factors are often treated as if they were independent and are rarely investigated at the same time.

If an animal's behavior is considered as an adaptation to the demands of the environment, social or physical, it can be assumed that a behavior adapted to the physical environment may not always be adaptive to the social environment and vice versa. The degree to which the social and physical environments affect the behavior of animals such as mice can be determined by placing individuals in a situation where responses to social and physical environmental variables can not be made independently. The behavioral changes made by the animal will reflect the relative importance of a given physical or social environmental variable for that animal in that situation.

This investigation is an attempt to determine the relationship between activity rhythm of mice (an important physical parameter) and social status (an important social parameter). It is assumed that a given mouse must attend to both social and physical factors to be evolutionarily successful. Dominant mice are able to attend more closely to physical factors because they are not threatened by social factors. Subordinate mice are threatened by social factors, such as agonistic encounters with dominant mice, and are not able to attend closely to the environment.

The social system of mouse populations has been studied extensively. Mice are known to establish dominance heirarchies within small groups usually composed of a dominant male with two or three sexually mature females, several immature juveniles and one or more subordinate males (Berry 1970; Selander 1970; Dewsbury 1984). The dominant individual has priority over the other members of the group concerning food, water, and acquisition of mates. In addition, recent research has suggested that dominant individuals may have priority over the others regarding the most preferred times to be active (Regal and Connolly 1980). Since mice make up a considerable part of the dietary needs of a large group of predators,

it is beneficial for a mouse to be active during the hours which are the safest, i.e. night (Daan 1981).

Much research has been done on dominance heirarchies of mice and other rodents (Mackintosh 1970; Sadlier 1970; Bovet 1972a; Benton et al. 1980; Meaney and Stewart 1981), and on activity rhythms of rodents (Berry 1970; Ziesenis et al. 1975). But there has been comparatively little research done on the relationships between dominance and activity rhythms (Bovet 1972b; Regal and Connolly 1980). A primary reason that so little research has been conducted in this area is the separate and often distinct research methods developed for the analysis of activity rhythms and for social behavior. There are also fundamental problems associated with the concept of dominance.

The concept of dominance is a general term used to describe an individual's social status. There are at least two schools of thought concerning dominance. One is, as Bernstein (1980) believes, that dominance is an artifact of a relationship between individuals, and not an individual trait or characteristic. The other is that dominance, or the lack of it, is a trait of each individual (Benton et al. 1980; Parmigiani et al. 1982a; Parmigiani et al. 1982b). Much of the difference between the two perspectives is due to the lack of a universally accepted measure of dominance.

Benton et al. (1980) attempted to resolve the problem of measurement by comparing seven of the most commonly used tests to determine social status. Their results showed little correlation between the tests, which suggested that the tests were measuring factors which may or may not be associated with social status. Benton et al. (1980) were able to conclude that the measure of territoriality was one of the most useful measures they compared. Kaufmann (1971) and Dewsbury (1978) both suggested that the dominance heirarchy is closely associated with territoriality in mice. Mackintosh (1970) provided additional support from his study on territory formation in mice. He recorded aggressive attacks to assess territoriality which he linked directly to dominance. Sadlier (1970) demonstrated that mice use aggression to establish dominance heirarchies, such that the most aggressive is the most dominant. Therefore, dominance has been shown to have at least two components which can be measured - aggressiveness and territoriality.

Both components, aggression and territoriality, have been shown to depend to a great extent upon the ability to recognize other individuals (Archer 1968; Ropartz 1968; Brain et al. 1982a; Brain et al. 1982b; Kareem and Barnard 1982; Parmigiani and Brain 1983).

Although visual and tactile stimuli are both important in recognition, they are negligible in comparison to olfactory stimuli. Though the level of aggression a dominant mouse shows towards an intruder is usually very high, when the dominant is rendered anosmic he will be non-aggressive towards any intruder (Brain et al. 1982a; Ropartz 1968). Archer (1968) was able to show that over time mice became habituated to the particular odors of other mice which lessened the level of aggression within the group. Ropartz (1968) and Brain et al. (1982a) found similar results from their studies. This habituation to odors of other mice may explain the lower aggression in stable groups than between individuals who are not familiar with each other. Group housed mice are known to scent mark each other which can also contribute to the reduction in levels of aggression by producing a group scent which each member can recognize (Kareem and Barnard 1982).

An individual's scent can also communicate social status. According to Parmigiani et al. (1982a) Mainardi and Pasquali (1973) found that female mice were able to distinguish between males of different social status by olfaction, preferentially selecting dominant males. This has been supported by DeFries

and McClearn (1970) and Horn (1974) in similar studies who found that when mice were allowed to establish a dominance heirarchy the dominant male sired approximately ninety percent of the offspring.

The advantages of a dominance heirarchy are important not only to the survival of the dominant individual, but also to the group's survival. Stable groups resulting from the formation of dominance heirarchies exhibit few instances of aggression between group members (Mackintosh 1970).

In addition to the studies on social structure, much research has been directed towards activity rhythms. Berry (1970) in his paper on the ecology of the wild house mouse (Mus musculus), explained how the activity rhythm of the mice was associated with the photoperiod in such a way that the onset of activity occurred just after sunset and concluded just before sunrise. Ziesenis et al. (1975), working with deer mice (Peromyscus maniculatus), found that aggression, in addition to activity, was a rhythmic function of the They were able to correlate aggression photoperiod. to activity, such that the periods of high aggression coincided with the periods of high activity. Through the work of Berry (1970), Ziesenis et al. (1975) and Regal and Connolly (1980), it is clear that mice

exhibit a biphasic (two peaked) distribution of activity which is dependent on the photoperiod.

The relationship between social status and activity rhythm is a relatively new area of study. Regal and Connolly (1980), working with rats, found a clear distinction between the activity rhythm of the subordinate and the two higher ranked rats, from a group of three females. This work is supported by previous work of Calhoun (1962) and Crowcroft and Rowe (1963). Calhoun (1962), working with rats, found that subordinates were active during times which were not only different than the dominant's but were considered to be non-preferred times as well. Preferred times were those which coincided with darkness so that the individual's chances for survival were enhanced. Crowcroft and Rowe (1963), working with mice (Mus musculus), observed that subordinates avoided contact with the dominant individuals by being active at different times. Regal and Connolly (1980) mentioned the idea of temporal territories, where the dominants are active during the most preferred times and the subordinates are active during less preferred times.

Bovet (1972b) showed similar results with longtailed field mice (Apodemus sylvaticus). The group of

mice he observed consisted of two males and two females living in a large terrarium. He observed the group for several months and concluded that the subordinates were active during "communal" times which were distinctly different from the dominant's. This further suggests the possibility of temporal territories based on social status.

The relationship between social status and activity rhythm is consistent with the general ideas regarding the dominant's superior "Darwinian fitness" (Hahn and Haber 1982). The dominant is generally perceived to possess the most desirable characteristics, and therefore, has a greater chance for survival. There are several important advantages given to the dominant which enhance his ability to survive. Among these advantages are mate selection, priority of the resources within the territorial borders, and activity during the most preferred times. Much controversy surrounds the idea of temporal territories, with many investigators considering them to be artifacts of an unnatural setting where the subordinate, due to limited territory, must avoid the dominant by being active at different times (Dewsbury 1984). The subordinates within natural systems have the option to escape from the territory controlled by the dominant.

There is considerable controversy regarding activity levels of dominant versus subordinate mice. Thiessen (1966) considered subordinates to be more active than dominants based on organ weights, however, others believe just the opposite is true (Mackintosh 1970; Parmigiani and Pasquali 1980; Regal and Connolly 1980).

The primary objective of this research, to examine the relationship between activity rhythm and dominance behavior in males of the species Mus musculus, is focused on three hypotheses. The first hypothesis is that dominant individuals exhibit activity rhythms which are correlated to the physical environment (photoperiod), whereas subordinate individuals organize their activity rhythms according to the social environment (behavior of the dominant). The null hypothesis is that both dominant and subordinate mice are equally attentive to the same environmental factors. A second hypothesis is that dominant mice exhibit greater stability of activity rhythm than their subordinate counterparts. This hypothesis is based on the assumption that dominant mice attend more to the photoperiod than do subordinates. The null hypothesis in this case is that both dominant and subordinate mice

exhibit equally stable activity rhythms. The third hypothesis is that dominant mice are more active than subordinate mice. Dominant mice are often patrolling their territorial borders and enforcing their dominance on other members of the group (Mackintosh 1970). This type of activity should produce a measureable difference between two mice of different social status (Parmigiani and Pasquali 1980). The null hypothesis is that both dominant and subordinate mice are equally active.

## MATERIALS AND METHODS

In the attempt to examine the relationship between social status and activity rhythm, many methodological problems had to be solved. Although Regal and Connolly (1980) conducted work similar to that which is presented here, many of their methods had to be changed, and considering the research as a whole, the present approach was highly eclectic. Descriptions of the materials will be presented first followed by a detailed discussion of the methods.

Four pairs of laboratory bred house mice (Mus musculus) were chosen for the experiment based on their availability and their general acceptance by others working in this area. The mice, which were all males, were acquired from the animal room on the Appalachian State University campus. Their origin, and therefore, any genetic information, is unknown. All individuals, prior to experimentation, had been group housed with access to females and were considered to be sexually mature adults at the time of their use. This precludes an inability to participate in the formation of a dominance heirarchy (Mackintosh 1970; Lore and Flannelly 1977).

The laboratory was approximately 4.3 meters long by 3.3 meters wide. Since the photoperiod has been shown to be extremely important in activity rhythms the laboratory's photoperiod was kept constant throughout the investigation at a standard 12 hour light, 12 hour dark schedule with lights on from 0600 to 1800 hours. Temperature was maintained between 18 and 25 degrees Celsius. Extraneous odors were removed by a ventilation system. Access to the room was strictly limited to once or twice a day to record wheel running activity and to make sure the food and water were in constant supply. Only during periods of observation, which will be discussed later, were there more than two visits per day into the laboratory. These procedures were designed to keep the conditions as stable as possible, and to minimize influences which may adversely affect the results.

Once inside the laboratory the mice were initially housed in separate plastic boxes measuring approximately 15cm x 7cm x 7cm, with food and water ad libitum. After seven to fourteen days they were each transferred to their own metal cage, which measured approximately 25cm x 14cm x 11cm. Attached to each cage was a large running wheel, 35cm in diameter (Carolina Biological

Supply Company, stock # 67-4540). The metal cages are standard in many rodent activity studies (Richter 1979; Regal and Connolly 1980). Two cages were attached by a wire mesh (lcm square) which served as a removable partition between the two mice. The running wheels were connected to a six-channel event recorder, which was located outside the laboratory.

During the full contact procedures outlined below, the mice were observed to determine their dominance relationship. To facilitate the observations, most of which occurred during darkness, a red-filtered light was used. The use of red light to observe rodents has been thoroughly investigated in the past. Findley (1959) and Southern (1955) both found that rodents could not perceive red light. McGuire et al. (1973) confirmed the previous findings concerning the lack of significant effects of red light on activity rhythms or on other photoperiod dependent events. The mice were marked by fur clipping or dyeing to aid in identification during observations. Mice which were both dark in color were clipped; the mice which were both light in color were dyed. These methods are commonly practiced by other investigators (Berry 1970; Mackintosh 1970; Sadlier 1970).

As previously mentioned, the methods used in this investigation were developed from a variety of sources, with many perfected through considerable trial and error. A general outline of the treatment methods is presented below, followed by a more descriptive discussion of the important aspects of data collection and analysis.

- Adjustment Two male mice of approximately the same age and weight were isolated in separate plastic boxes under laboratory conditions for a period of time not less than seven days. This procedure was designed to allow the mice to adjust to the laboratory conditions prior to experimentation.
- 2) Limited Contact I The mice were introduced to the cleaned and sterilized metal cages with running wheels attached. Although the mice were separated by a wire mesh, visual, auditory, olfactory and limited tactile communication could occur. During this procedure, data were collected each day on wheel running activity and activity rhythms for approximately six days. The procedure was designed to allow a baseline of data to be collected for each mouse.

- 3) Full Contact I At the conclusion of Limited Contact I the wire mesh which separated the mice was removed. The mice were observed during this part of the experiment to determine each individual's social status. No activity data could be collected during this time since there was no accurate way to attribute the activity of either mouse to a particular wheel. This part of the experiment was approximately 23 hours long.
- 4) Limited Contact II The mice were again separated, being put back to their original metal cages, with the wire mesh replaced. Fresh bedding was provided to each mouse. This procedure was designed to test the effect that treatment (Full Contact I) had on the activity of the mice in relation to their baseline. This lasted for three to five days during which time activity data were collected as noted in Limited Contact I.
- 5) Full Contact II At the conclusion of Limited Contact II the procedure of Full Contact I was repeated. This was done to test the stability of the dominance relationship established in Full Contact I.

- 6) Limited Contact III At the conclusion of Full Contact II the mice were handled as described in Limited Contact II. After this part of the experiment the pairs were removed from the laboratory, however, Pair Three was retained for the next procedure.
- 7) Separation After the conclusion of Limited Contact III, the mice from Pair Three were completely separated to opposite sides of the laboratory. They were in metal cages with activity wheels allowing activity rhythm data to be collected. This procedure was designed to test the assumption that a change in an individual's activity rhythm during treatment was due to social factors and not physical factors of the environment. This lasted approximately seven days.

There were two types of activity data collected during the three Limited Contact periods described above: 1) total wheel revolutions, or wheel running activity, and 2) activity rhythm data. Wheel running activity was measured directly from the numerical counters on each wheel. The counters measured how many wheel revolutions each mouse had completed since the previous day; this allowed a careful record to be kept

of the activity of each mouse during the Limited Contact periods. There is considerable controversy regarding activity levels of dominant versus subordinate mice.

The collection of the activity rhythm data was accomplished using an event recorder which was attached independently to each wheel. The recorder presented a record of how active each mouse was in each time unit. The basic time unit was arbitrarily chosen to be 2.5 minutes long. The data was first scanned to determine if the mice were active (signified by two or more wheel revolutions) during each 2.5 minute interval. If considered active, the mouse was assigned a "1" for that interval; if inactive during the interval, the mouse was assigned a "O". The total number of intervals, within each hour, a mouse was found to be active were summed. Although the use of an hour was arbitrarily chosen, there is some basis for its use in the literature (Regal and Connolly 1980). The total score for a mouse indicated how many of the 2.5 minute intervals the mouse was active within each hour and did not show absolute activity. The scores ranged from "0", inactive, to "24", extremely active (there are twentyfour 2.5 minute intervals in an hour). The hour

scores were used further in the statistical analyses and will be referred to as "hour scores." (See Appendix A for hour scores of each pair).

Autocorrelation was the primary statistic used in this study. Its use to detect rhythms was reviewed by Binkley (1976), although this technique has apparently not been used in previous research of the present type. Autocorrelation was based on an assumption that the mice were exhibiting an activity rhythm with a period length of twenty-four hours, as expected, with a stable photoperiod. By correlating the hour scores of one day with the scores of the previous day, for each mouse, it was possible to measure the stability of their activity rhythms. A rhythm was considered stable if the autocorrelation between the two days was significantly different from zero. The mice from each pair were compared over the Limited Contact periods by their mean autocorrelation values. [Statistics in this study follow Sokal and Rohlf (1981) unless otherwise noted.]

Comparisons of activity rhythms could take any of three possible forms: both mice could be stable, one mouse could be stable and the other unstable, or both mice could be unstable. The first possibility occurred regularly and was evaluated by determining if there was

a significant difference between the two mean autocorrelation values for each mouse. (The individual with the highest value was considered more stable). The second possibility was infrequent and led to the obvious conclusion that one was stable and the other unstable. The third possibility, with both mice unstable, never occurred. However, evaluating data of this type would be carried out like that for both mice being stable. In addition to the autocorrelation technique, two analyses were used from the Statistical Package for the Social Sciences on hour scores (Hull and Nie 1981). The first analysis was the Box-Jenkins Time Series Analysis; this to the author's knowledge has never been used to analyze behavioral data of this The results of the Box-Jenkins analysis provided type. strong support for the use of autocorrelation by demonstrating that the mice exhibited consistent twentyfour hour periods of activity rhythms. Further support for the periodicity of rhythm was shown by the use of multiple regression on hour scores.

Observational data collected when the mice were in Full Contact allowed one to determine the dominance relationship between the two mice of each pair. The data were collected during several 15 minute periods of

observation randomly spaced through the Full Contact periods. The categories which were observed were 1) winner, defined as that individual which did not exhibit submissive behaviors during agonistic encounters, 2) initiator, defined as that individual who approached or attacked the other, and 3) cage, which was the home cage (either A or B) where the interaction occurred. Previous research has described the dominant individual as highly territorial and the most successful winner of fights (Crowcroft 1955; Brain and Al-Maliki 1978; Benton et al. 1980). The winner of a fight was defined as dominant. Other behaviors were observed to determine if they also related to dominance and to amount of activity and activity rhythms. In most cases one observer (the author) recorded the observational data, however, other individuals cooperated in multi-observer tests of interrater reliability. (Reliability was 89 percent or greater in all the tests).

The methods and materials used in this research were designed to be as non-invasive as possible to minimize the impact of external stimuli on the behavior and activity of the mice which may otherwise have affected the results.

## RESULTS

A basic assumption underlying the entire investigation is that the environmental variable of the photoperiod was the zietgeber for the activity rhythm of the mice and that any shift in rhythm was due to the treatment (Full Contact) and not chance variations. To test this, members of Pair Three were separated to opposite sides of the lab for seven days after Limited Contact III and their activity rhythms (mean autocorrelations) were found to be not significantly different from that before treatment (Limited Contact I). This provides support for the assumption that shifts in activity rhythm are not due to the primary environmental variable (photoperiod) but to social factors.

The results are presented in support of the three hypotheses and while the null hypotheses are not mentioned each of the alternate hypotheses are accepted based on the rejection of their respective null hypotheses. The three hypotheses addressed by the research require an unequivocal measure of dominance, therefore, the results of the behavioral analysis are presented first, followed by the results of the analysis of activity rhythms and wheel running activity.

The behavioral data collected during the Full Contact periods were used to determine the social status of each mouse. In a pair, the mouse that was the winner more times in each Full Contact period was considered dominant. During Full Contact I the following mice were dominant: IA, IIB, IIIA and IVA (Table I). During Full Contact II mice IIB, IIIA and IVA were dominant indicating that a consistent dominance relationship had been established in Pairs Two, Three and Four (Table II). The first pair reversed their status so that during Full Contact II mouse IB was dominant. The third pair showed very few of the observed behaviors which made the assessment of dominance difficult under the methods previously used. Other behaviors had been observed which indicated that mouse IIIA was dominant in each Full Contact period: mouse IIIA exhibited upright posture and stole food from IIIB. [The upright posture is a behavior which has been commented on in the literature as dominant behavior, Grant and Mackintosh (1963).1

With the dominance relationship of the four pairs of mice known, one can consider the three hypotheses. The first hypothesis is that the dominant mice organize

Table I

# Type and Number of Behaviors by Mice

During Full Contact I

4ice <sup>1</sup>	N <sup>2</sup>	Initiator	Winner	Cage <sup>3</sup>	Social Status
A	00	19 (0.95)*	18 (0.90)*	0 (00.00)	Dominant
В	0.4	1 (0.05)	2 (0.10)	10 (1.00)*	Subordinate
IA	16	4 (0.25)	2 (0.13)	0 (0.00)	Subordinate
IB	0	12 (0.75)*	14 (0.87)*	16 (1.00)*	Dominant
VA	VC	18 (0.75)*	18 (0.75)*	7 (0.29)	Dominant
VB	F J	6 (0.25)	6 (0.25)	17 (0.71)*	Subordinate

\* Significant difference between values, p < 0.05 (Normal approximation of binomial distribution).

1 Numbers refer to pair, letters refer to individual.

2 Numbers of interactions observed.

3 Home Cage (A or B) where interaction occurred.

Note: Values in parentheses are percent of total for the pair.

Table II

## Type and Number of Behaviors by Mice

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Mice <sup>l</sup>	N <sup>2</sup>	Initiator	Winner	Cage <sup>3</sup>	Social Status
IA	c	0 (00.00)	0 (00.00)	0 (0.00)	Subordinate
IB	7	2 (1.00)*	2 (1.00)*	2 (1.00)*	Dominant
IIA	11	0 (00.00)	0 (00.00)	27 (0.66)*	Subordinate
IIB	15	41 (1.00)*	41 (1.00)*	14 (0.34)	Dominant
IVA	76	20 (0.80)*	20 (0.80)*	13 (0.52)	Dominant
IVB	C 7	5 (0.20)	5 (0.20)	12 (0.48)	Subordinate

\* Significant difference between values, p < .05 (Normal approximation of binomial distribution).

1 Numbers refer to pair, letters refer to individual.

2 Numbers of interactions observed.

3 Home Cage (A or B) where interaction occurred.

Values in parentheses are percent of total for the pair. Note:

their activity rhythms according to both the physical factors and to social factors (the behavior of dominant To support this hypothesis it is necessary to mice). show: (1) that a dominant's activity rhythm is not affected after contact with a subordinate mouse, and (2) that a subordinate's activity rhythm is affected after contact with a dominant individual. To determine if an individual's activity rhythm was affected during Full Contact the hour scores of the day before Full Contact were correlated with the hour scores of the day after Full Contact (Table III). It was defined that the mice with autocorrelations significantly different from zero show stable rhythms and were not considered to be affected by Full Contact. The results indicated that the mice which were not affected by Full Contact I were: IA, IB, IIB, IIIA, IIIB and IVA. The relationship between social status (dominant or subordinate) and whether affected by Full Contact I or not was tested by a two by two contingency table with the results showing that the relationship was not significant (Fisher's exact test, p=0.214).

The mice not affected by Full Contact II are: IB, IIB, IIIA and IVA (Table III). A comparison between social status and whether affected by Full

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Autocorrelation Showing the Effects of Full Contact on Stability of Activity Rhythms

Mice <sup>1</sup>	Autocor	relations
	Full Contact I	Full Contact II
IA	0.7609*	NA
IB	0.9168*	0.4385*
IIA	0.3748	0.1453
IIB	0.5242*	0.4758*
IIIA	0.7799*	0.6517*
IIIB	0.5948*	0.1070
IVA	0.5708*	0.4377*
IVB	0.3352	0.1215

\* Significantly different from zero (p < 0.05, N=24).

1 Numbers refer to pair and letters refer to individual.

Contact II or not reveals a significant relationship (Fisher's exact test, p=0.029). The fact that each of the mice which were not affected by Full Contact II were also dominant strongly supports the first hypothesis. When both Full Contact periods are pooled the relationship between social status and whether affected by Full Contact or not is significant (Fisher's exact test, p=0.007). With the exception of Full Contact I the data support Hypothesis One.

The mean autocorrelations obtained from Limited Contact I were used to examine the second hypothesis: activity rhythms are more stable in dominant individuals than in subordinates. During this segment of the experiment the mice were separated by a wire mesh so that each mouse was able to establish an activity rhythm independent of the other mouse. When mean autocorrelations were examined for significant differences between members of each pair it was found that IIB, IIIA and IVA exhibited more stable rhythms during Limited Contact I (Table IV). (The level of stability was considered high or low depending on whether an individual exhibited an autocorrelation value significantly greater than the other member of the pair.) The first pair was not used in this analysis since both

Table IV

## Mean Autocorrelations of Mice

During Limited Contact<sup>2</sup>

Limited Contact III	NA	NA	.402	.692*	.610	.437	.557	.400	
Limited Contact II	.782	.828	.584	.741*	.682	.427	.843*	.670	
Limited Contact I	.843	.757	.291	.580*	.821*	.551	.778*	.627	
N	711	/ 11	0.0	C C	15	T T	20	~	
Mice <sup>l</sup>	IA	IB	IIA	IIB	IIIA	IIIB	IVA	IVB	

\* Significantly higher than other in pair, p < .05 (Student t test, two-tailed).

1 Numbers refer to pair, letters refer to individual.

2 Limited Contact periods ranged from three to six days.

had high stability. When the social status (dominant or subordinate) was compared to the level of stability (high or low) for pairs Two through Four a significant relationship was found (Fisher's exact test, p=0.050). Thus the data support Hypothesis Two.

The third hypothesis is that dominant mice are more active than subordinates. To examine this, the activity levels recorded for each mouse during the three Limited Contact periods were compared. The mouse who had mean wheel revolutions per day significantly higher than the other member of the pair was defined as having high activity. The following mice showed high levels of activity: IA, IIB, IIIA and IVA (Table V). The relationship between activity level (high or low) and social status (dominant or subordinate) is significant (Fisher's exact test, p=0.0002). If only mean baseline activity levels, recorded during Limited Contact I, are considered, the relationship between social status and activity level is also significant (Fisher's exact test, p=0.0143). The data support Hypothesis Three.

Data answering other questions relating to activity rhythm and social status which are not directly related to the three major hypotheses were also collected.

Table V

Mean Activity of Mice

During Limited Contact<sup>2</sup>

Mice <sup>l</sup>	Limit Conta	ted I		Limit Conta	ted II	Conta	ted Act III
IA	5830	(0.68)*		5541	(0.58)*	NA	
IB	2737	(0.32)		4039	(0.42)	NA	
IIA	628	(0.10)		1979	(0.23)	4749	(0.45)
IIB	5739	*(06.0)		6666	(0.77)*	5811	(0.55)*
IIIA	7467	*(0.93)*		4276	(0.92)*	3912	(0.87)*
IIIB	607	(0.07)		363	(0.08)	607	(0.13)
IVA	5119	(0.92)*	ų	2108	(0.89)*	646	(0.93)*
IVB	426	(0.08)		270	(0.11)	45	(0.07)

\* Significantly higher than other in pair, p < .05 (Normal approximation of binomial distribution).

1 Numbers refer to pair, letters refer to individual.

2 Limited Contact periods ranged from three to six days.

Note: Values in parentheses are percent of total for the pair.

Dominance behavior is significantly related to the initiator of an interaction. The initiator of an interaction was the winner in virtually all cases ( $\chi^2$  43.1, df=1, p<.01). On the other hand, the area where the interaction originated (cage of mouse A or mouse B) was not significantly related to dominance ( $\chi^2$  .02, df=1, p>.05).

## DISCUSSION

From an evolutionary perspective, successful organisms must be able to survive and reproduce. Organisms must attend to those environmental factors which might limit survivability and reproduction, often balancing one against the other. In nature predation is the greatest danger to mice; their nocturnal behavior is an adaptation to avoid such predation. A major factor involved in reproductive success is social behavior, therefore, individuals who are successful socially will also be successful in reproduction.

In relation to survival, the individuals who attend closely to the environment's physical factors, especially the photoperiod, are more likely to avoid predation than those who are less attentive. From the results of this study it is clear that dominant mice are more attentive to the photoperiod than subordinate mice. Due to the stability of the dominant-subordinate relationship, after dominance has been established, the dominant has to enforce his social position on only a few occasions. This allows the dominant individual to spend more time attending to the environment's physical factors which

increases his chance for survival. From an evolutionary perspective it is not enough to simply survive, one must also reproduce to be truly successful.

In relation to reproductive success, dominant mice have a distinct advantage over subordinates. DeFries and McClearn (1970) and Horn (1974) found that dominant mice sired roughly ninety percent of the litters with the remaining ten percent attributed to a subordinate. This results from social behavior with the more aggressive dominant male trying to keep the subordinate from mating with the females. The low reproductive success of the subordinate (10%) is greater than that which a subordinate could expect if he left the group. To achieve reproductive success the subordinate mouse must be very attentive to the activity of the dominant so he can mate with females within the group while the dominant is asleep or away. This will limit the chance of a serious fight with the dominant, while at the same time providing an opportunity for reproductive success. In order for the subordinate to attend to the dominant's activity he must be less attentive to the environment. Therefore, the subordinate trades an increased chance of predation for reproductive success.

In most cases the dominant does not drive off the subordinate probably because the subordinate poses no serious threat to the dominant's social status or survivability. In fact, the subordinate may allow the dominant to be more successful in both survivability and reproduction. Since the subordinate helps defend group resources, he is in effect aiding the dominant, who can now spend more time in other pursuits (reproduction or feeding). In return, the subordinate gets access to group resources and in some instances mates. In nature the dominant limits the activity of the subordinate within territorial borders in an attempt to control his use of resources. This was shown in the results of this study by lower wheel activity of the subordinate when compared to the dominant.

The major hypotheses of this study fit nicely into the framework of natural systems. If three assumptions are made: 1) that the subordinate will be more attentive to the dominant than the dominant is to the subordinate, 2) that dominant mice are more active than subordinate mice are, and 3) that a given mouse cannot attend to both the photoperiod and the activity of another mouse equally well, social status can be defined by the stability of activity rhythm and the level of activity. With the exception of Limited Contact I, the relationship between high stability of activity rhythm and dominant status was significant, as was the relationship between dominant status and a high level of activity. It follows that if social status can be predicted from these criteria before there is an opportunity to engage in agonistic behavior, then the disposition for social status must be a trait as Benton et al. (1980) suggests. The fact that the activity rhythm of the dominant mice were not affected after Full Contact while the subordinate's were, supports the assumption that the subordinate pays attention to the dominant mouse.

As does most research of an exploratory nature, this study opened up many new areas of research which may be fruitful. The dominance reversal noted in the first pair, in particular, represents an interesting area which has not been reported in the literature. Ms. Wendy Stehling (Student in Biology at ASU) recorded dominance reversals in her work with pairs of non-sibling male mice (personal communication). This agrees with the findings of Pair One since they were the only non-sibling pair tested. Could this reversal be connected to familiarity between the mice? This

study supports an answer of both yes and no. "Yes", in the sense that an unfamiliar, non-sibling pair establish a dominance heirarchy which is subject to greater strain than that formed between familiar, sibling mice. "No", because in this study an individual's social status seems to be a trait, not modified by social experience alone. It may be that dominance reversals occur between individuals with nearly equal social status.

Another question raised by this study, is the ability to predict social status due to the communication of status between the mice? From the data collected during Separation for Pair Three it was found that the criteria used to predict social status were just as reliable whether or not communication was allowed. This indicates that the mice are not able to effectively communicate their status without the ability to contact the other individual. Previous research had concluded that olfaction was the principle means to communicate status. It seems that mice need other types of communication, perhaps tactile, to enhance olfaction in communicating social status.

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APPENDIX A HOUR SCORES

## APPENDIX A

The following pages are lists of the hour scores for each pair of mice used in the research project. Each line of data consists of eight columns of numbers. The first two columns are the hour scores for the "A" mouse. The third and fourth columns are the hour scores for the "B" mouse. The times of day, in hours (01 through 24), are given in the fifth and sixth columns. The days are in the seventh and eighth columns and were numbered to distinguish one day from the next. The following notations are used to indicate where each of the Limited Contact periods begin: LCI - Limited Contact I, LCII - Limited Contact II and LCIII - Limited Contact III.

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## PAIR FOUR

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PAIR FOUR

PAIR FOUR

## PAIR THREE DURING SEPARATION PROCEDURE

## VITA

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