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Telemetered Heart Rates of Free-Living Uinta Ground Squirrels in Response to Social Interactions

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TELEMETERED HEART RATES OF FREE-LIVING UINTA GROUND SQUIRRELS IN RESPONSE TO SOCIAL INTERACTIONS

by

Robert L. Ruff

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Wildlife Ecology

Approved:

Major Professor

Committee Member

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Dean of Graduate Studies

UTAH STATE UNIVERSITY
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1971

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Robert L. Ruff

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ABSTRACT

Telemetered Heart Rates of Free-Living Uinta Ground Squirrels in Response to Social Interactions

by

Robert L. Ruff, Doctor of Philosophy

Utah State University, 1971

Major Professor: Dr. Allen W. Stokes
Department: Wildlife Resources

Free-living Uinta ground squirrels (Spermophilus armatus) were instrumented with miniaturized ECG radio-transmitters to measure their short-term and long-term heart rate responses to social interactions. A continuous trapping and direct observation program prior to and during the study provided complete behavioral and life history information for virtually all ground squirrels on the 22-acre study area.

Three broad categories of heart rate information were obtained: responses by squirrels (1) in their burrows, (2) aboveground during social interactions, and (3) aboveground when animals were not fighting and when conspecifics were both absent and present.

Marked changes in the heart rate of ground squirrels occurred even as animals behaved in their burrows and conspecifics were absent. Some changes were caused by motor behaviors and appeared commensurate with different degrees of physical exertion. Others were evident among inactive animals and took the form of diurnal cardiac rhythms which were independent of immediate motor behavior but nonetheless attuned to aboveground activity cycles.

The heart rate of all ground squirrels increased well above burrow baselines when animals behaved aboveground. The greatest elevations occurred during social interactions which ranged from mere threat to physical combat. Combat encounters elicited responses which frequently exceeded 400 beats/minute as compared to burrow and aboveground baselines for inactive animals of 269 and 284 beats/minute, respectively. Threat interactions produced less dramatic increases, but because threat usually lasted longer, it was perhaps as stressful as combat. There were no significant differences between peak responses of dominants and subordinates, initiates and recipients of aggression, or sex and age classes. However, the duration of cardiac response was less for dominants and hence, they apparently experienced less stress than subordinates.

Increases in heart rate, independent of motor behavior and immediate social interactions, were also observed as female ground squirrels roamed within and/or made occasional excursions outside their home ranges. These cardiac changes occurred regardless of the presence or absence of conspecifics in the vicinity. It was concluded that such cardiac acceleration represented chronic response to social interactions and was elicited by spatial factors, specifically spatial familiarity, which acted as conditioned stimuli (previously paired with combat). Such chronic responses were greatest during the initial establishment of territories by females, decreased during territoriality, and increased again following the breakdown of territoriality. So territoriality acted to reduce the magnitude of heart rate response and hence, stress among females.

The mere presence of conspecifics within the immediate vicinity of an instrumented ground squirrel tended to elevate its heart rate. Therefore, even in the absence of overt social interactions, conditions of crowding also contributed towards chronic stress in the population.

The effects upon heart rate with respect to an individual's sex, age, reproductive condition, and its spatial and social relationship with neighboring ground squirrels are also discussed. Finally, the roles which social and non-social factors play in regulating animal numbers on the study are described.

(135 pages)

INTRODUCTION

This investigation comprised an integral part of a broader program designed to determine the roles which behavior and the environment play in regulating the abundance and local distribution of animals in a free-living population of Uinta ground squirrels (Spermophilus armatus). Although some ecologists maintain that social interaction or intraspecific competition is paramount in this regard (Milne, 1957; Nicholson, 1933, 1957; Wynne-Edwards, 1962), others contend that non-social factors of the environment are more important (Andrewartha and Birch, 1954; Lack, 1954, 1966). Still, at least among mammals, social interaction is the one element common to all populations which may elicit an entire gamut of physiological and behavioral responses to influence both reproduction and mortality commensurate with changes in density (Christian, 1963). Therefore, it has the potential to regulate animal numbers and thereby achieve population balance.

The socio-psychological stress which accompanies social interaction appears to be the principle factor responsible for the above physiological and behavioral responses. This has frequently been demonstrated among laboratory populations of small mammals, particularly rodents. As crowding and the rate of social interactions increase, the magnitude of stress and concomittant effects upon reproduction and mortality also increase by way of the pituitary-adrenal-gonadal system. Some animals fail to breed while others breed but produce few or no young (Bruce, (1960a);Calhoun, 1962a; Crew and Mirskaia, 1931; Mykytowycz, 1960; Retzlaff, 1938; Strecker and Emlen, 1953; Terman, 1965). Some animals lose their embryos through resorption or have reduced secretion of prolactin which results in a breakdown of maternal care and a subsequent increase in juvenile mortality (Calhoun, 1962b, 1963; Rosenblatt and Lehrman, 1963; Southwick, 1955b). Dispersal, which often results in increased mortality, may also rise with increasing social strife (Strecker, 1954). In some cases, this heightened mortality and partial or complete suppression of reproduction may be so great as to bring about balance in the population (Clarke, 1955; Southwick, 1955a; Terman, 1965). Furthermore, the effects of crowding on certain behaviors, especially maternal care, may persist for several generations even after crowding has been relieved (Christian and LeMunyan, 1958).

Animals in natural populations apparently respond to social stressors in a similar fashion but the data are inconclusive (Calhoun, 1948; Christian and Davis, 1956; Davis, 1953; Hoffman, 1958; Kalela, 1957). This is largely because animals in the wild are difficult to observe, population and behavioral data are lacking for many species, and most importantly, previous researchers had no means of differentiating between animal responses to social stimuli as opposed to other environmental variables.

Uinta ground squirrels make ideal subjects for this type of study because of their size, trapability, diurnal activity and non-secretive behavior. In addition, complete life history and behavioral records are available for virtually all animals of a known population in northern Utah (Balph and Stokes, 1963;

Burns, 1968; Walker, 1968). And finally, recent advances in bio-electronics now permit certain physiological parameters to be telemetered from free-roaming animals for use as indices of stress. The purpose of the current study was to measure changes in one such parameter, heart rate, as Uinta ground squirrels responded to social interactions and to determine if these measures varied with the level of crowding and the sex, age, reproductive condition and social rank of known individuals.

Previous researchers have used a wide range of physiological measures other than heart rate as indices of response to socially induced stress. These included histological and morphological changes in endocrine glands (Barnett, 1955, 1958; Christian, 1955b, 1956, 1959, 1960; Christian and Davis, 1955, 1956), pathology of the thymicolymphatic system and gastrointestinal tract (Brady, 1958; Chitty et al., 1956; Clarke, 1953), and counts of circulating eosinophils and lymphocytes (Louch, 1956, 1958; Southwick, 1959; Speirs and Meyer, 1949). However, all of these are extremely labile and are probably best used to describe long-term responses to the sum of environmental and social stressors (Christian, 1963; Sayers and Sayers, 1949; Selye, 1956). Furthermore, each necessitates either handling or sacrificing experimental subjects and none provides an accurate instantaneous measure of response.

On the other hand, changes in the heart rate of humans and confined animals have long been used to describe more precisely the magnitude and duration of an individual's psychological or emotional response to specific stressor stimuli (Angermeier, Phelps and Reynolds, 1967; Barger et al., 1956; Belanger and Feldman, 1962; Bond, 1943; Chapman, Fisher and Sproule, 1960; Crow, 1968; Caul and Miller, 1968; Deane, 1961; Deane and Zeaman, 1958; Eisman, 1966; Hahn, Stern and Fehr, 1964; Hodges and Spielberger, 1966; Miller and Caul, 1969; Wilson, 1964). Of particular significance are more recent bio-telemetric studies with small mammals and birds in which heart rate has proven to be an excellent measure of animal response to social interaction, and hence of socially induced stress (Candland, Pack and Matthews, 1967; Candland et al., 1969; Harris and Siegel, 1967). Furthermore, both short-term (acute) and long-term (chronic) responses to social stimuli may be determined with bio-telemetry without disrupting animal behavior, a distinct advantage over the forementioned physiological techniques.

The objectives of the current study were:

1. To establish baseline heart rates relative to non-social behavior of ground squirrels in their burrows and aboveground.

2. To measure the effects of various forms of social interactions upon the heart rate of known individuals.

3. To determine the relationship between heart rate and the sex, age, reproductive condition, and spatial relationship of interacting individuals.

4. To determine if there are short-term or long-term differences in heart rates of ground squirrels which correlate with crowding and levels of aggression in different areas.

Several interpretations are prevalent in the literature with respect to the phenomenon of stress. Selye (1950, 1952, 1955, 1956) considers stress as a state of non-specific tension in an organism which is manifest by tangible morphologic and physiologic changes in various organs. He termed the exogenous factors which induce such a state or response within an animal as "stressors". Starling (1962) asserts "stress is a generic term for any circumstance which tends to disturb an animal from its normal resting equilibrium." Folk (1966) points out that most physiologists customarily view stress as "a condition of the atmospheric environment which provokes a physiological response (a strain)" and thusly speak of stresses and physiological strains. So, the term stress has been used to designate (1) a stimulus, (2) a response, (3) a stimulus-response combination, and (4) a state within an animal which brings about a series of responses.

In an attempt to avoid these disparities, Levitt (1967) defines stress in the following manner:

> 1. A "stress" or "stressful" situation is one containing stimuli or circumstances calculated to arouse anxiety in the individual.
>
> 2. "Under stress" or "stressed" refer to an individual who is faced by, or in the midst of, a stress situation.
>
> 3. A "stress reaction" is an alter~~n~~ation of the individual's condition or performance which comes about presumably as a result of being under stress. (Levitt, 1968, p. 12)

Within this framework, he further defines anxiety as "... a state characterized by a subjective feeling of apprehension and heightened physiological activity" (p. 6), and uses stress and anxiety interchangeably. This essentially is the position adopted in the current study and it also parallels that of

Selye. And because morphologic and physiologic changes accompany emotional stress or anxiety, these presumably allow for quantitative measurements of stress. Among ground squirrels, elevations in heart rate above predetermined baselines during or as a result of social interaction were used as just such measures of stress herein.

GENERAL PROCEDURES

The investigation was conducted on 22 acres of land which encompassed the Utah State University Forestry Field Station located 22 miles northeast of Logan, Utah, at an elevation of 6,300 feet. Predominant vegetation included grassland, sagebrush, and several species of shrubs and trees. Grassland consisted primarily of 2.6 acres of lawn which surrounded a cluster of camp buildings at the Station.

Bio-telemetric phases of this study focused upon the lawn where ground squirrels were plentiful and readily seen from within a building overlooking the area (Figure 1). The latter feature permitted continuous monitoring of ground squirrel responses to environmental and social stimuli without disrupting their activities.

The study area was partitioned into a 40-foot grid system. The location of any event was pinpointed to the nearest 1/10 of a grid section, i.e., within 4 feet. All events were dated in terms of the number of days since the first ground squirrel emerged from hibernation on the study area, hereafter abbreviated DSE.

Nearly all squirrels were captured immediately following their emergence from hibernation and recaptured at least once every 10 days throughout the field season. Animals instrumented with radio-transmitters were captured every 4 to 6 days. Balph (1968) and Walker (1968) have described the techniques

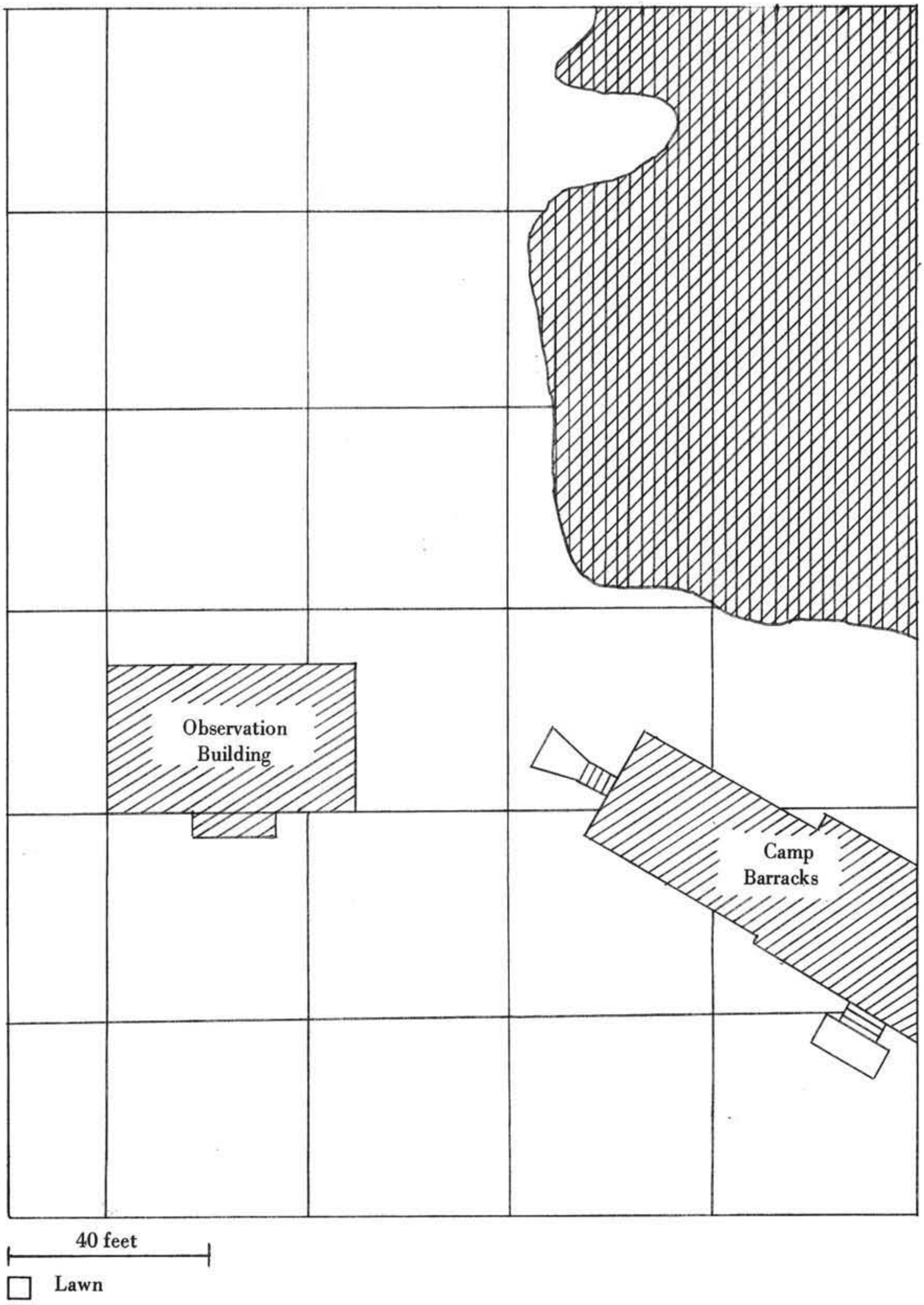

Figure 1. Map of lawn area showing the grid system, camp buildings and vegetation types

of trapping and individually marking ground squirrels. Trapping operations provided the identity, sex, age, weight, and reproductive condition of virtually all animals on the study area.

Observations of ground squirrel behavior were recorded on magnetic tape. Each time an animal changed locations a record was made of its identity, location, activity, time of day and DSE. These "sightings" provided basic information of life-sustaining and maintenance activities, movements and home ranges. As used here, the definition of a home range generally followed that of Burt (1943), "... that area traversed by an animal in its normal activities." Specifically, home ranges of ground squirrels were determined by rounding off a polygon drawn through the outermost points of 90 per cent of the sighted locations for individuals. The remaining 10 per cent of the points, those farthest away from areas of large concentration of points, were arbitrarily omitted because most represented excursions which squirrels occasionally took outside the areas they usually occupied (Burns, 1968).

Records were also made of all observed social encounters. These were used to determine territorial boundaries and the social rank of individuals within the territorial system. A territory was "... any defended area" (Noble, 1939) within the home range of a ground squirrel. An animal was considered territorial only if it "actively defended" a particular area, i.e., it initiated encounters when a transient or neighbor ventured into its domain. Whether the resident won or lost was unimportant so long as it continued in attempts at site defense. Generally however, animals won most of the encounters which they initiated (90 per cent). If a squirrel habitually lost, it deserted its territory and established a residence elsewhere. On occasion, some females were more aggressive and successful in their territorial defense with some neighbors than others. In such instances, a dominant-subordinate relationship developed between individuals and it is in this context that "social rank" is used herein.

With these techniques, complete life history and behavioral data were gathered for virtually all ground squirrels on the study area from 1964 through 1969. These included date and place of birth, size and shape of home ranges and territories, weight changes and seasonal changes in reproductive condition. Such historical records were used in the selection of animals for this study and in the acquisition and analyses of data. More complete descriptions of the study area and techniques have been reported elsewhere (Balph, 1968; Balph and Balph, 1966; Balph and Stokes, 1963; Burns, 1968; Walker, 1968).

In anticipation of the planned field study, pilot experiments were carried out in the field and laboratory. Dummy transmitters, identical in size and weight to those planned for use, were attached to three adult ground squirrels during May and June of 1967. The animals carried the packages for more than 3,500 hours with no adverse behavioral or physiological responses. During the winter of 1968, albino rats in the laboratory were equipped with actual transmitters for 3,000 hours with no ill effects.

A block diagram of the bio-telemetry system is illustrated in Figure 2. The ECG transmitters were factory available units weighing 5.5 grams (batteries included) with case dimensions of 17 X 11 X 25 millimeters. The

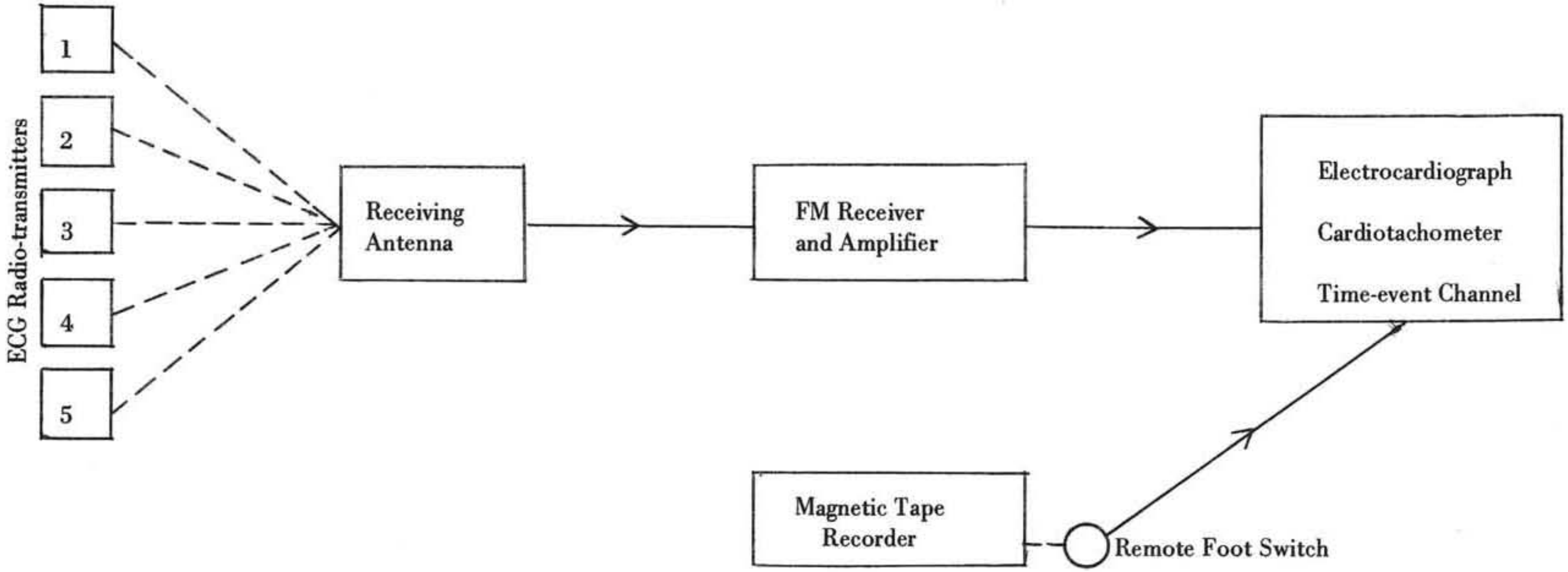

Figure 2. Block diagram of the bio-telemetry system used with ground squirrels

transmitters operated at frequencies ranging between 88-108 MHz. and had a battery life of 100 to 150 hours. Stable transmission range was approximately 100 feet.

Prior to their placement on ground squirrels, transmitters were encapsulated in a form-fitted case constructed from plastic tape, rubberized cement and epoxy. A small door was cut in the case through which batteries were replaced. Various lengths of polyvinyl tape were used to attach the radios to ground squirrels in the form of an adjustable neck collar (Figure 3). The entire assemblage weighed 10 grams and was shockproof and waterproof.

Pure silver ring electrodes were used to detect the electrocardiogram (ECG) potentials. These were implanted subcutaneously on either side of the thoracic cavity. To make the implants, a small incision was opened at the base of a squirrel's chin and fascia were loosened with a dull probe to the sites of implantation. Long surgical needles, connected to the electrodes with nylon thread, were inserted along the probings and exteriorized through the skin. The electrodes were then pulled into place and secured with a knot on the surface of the skin. Teflon-coated wires leading from the electrodes emerged through the chin incision and plugged into the ECG transmitter with connector pins. The wires entered the transmitter case through a small hole which was subsequently sealed with rubberized cement to complete the collar package. After several days, usually at the time of first battery replacements, the electrodes were encapsulated with connective tissue. The external knots which held the electrodes in place were than severed to reduce the chance of outside infection.

Figure 3. Adult female ground squirrel with ECG transmitter and adjustable neck collar. The dark markings on the animal's back and rump are coded symbols used to identify individuals.

Different techniques have been used to instrument small mammals (Longo and Pellegrino, 1967) and birds (Thompson et al., 1968) with equipment identical to that used in this study. However, the methods used here had the advantages of (a) no major surgery, (b) rapid recovery time which in turn prevented the loss of an instrumented animal's territory to neighbors or transients, (c) ease of battery replacement, (d) ease in alternating transmitters from one animal to another while leaving the electrodes and collar intact, and (e) no exposed wires to be chewed or tangled.

Signals from transmitters were monitored with an FM receiver. Both a five-element and dual whip antennas were used to receive the radio signals. The whip antennas were permanent fixtures of the receiver while the five-element Yagi antenna was mounted on a 20-foot tower and could be rotated manually from inside the observation building.

A transducer cable coupled the output of the receiver with a desk model Physiograph-Four[1] recording system. One recording channel displayed ECG waveform while another, a cardiotachometer, presented either "mean heart rate" or "beat by beat intervals" on continuous one millimeter grid paper. A third recording pen was triggered by a time-event channel. By depressing a remote foot switch connected to this channel, graphic recordings of heart rate were synchronized with verbal descriptions of a ground squirrel's overt

---

[1] Trade name of E & M Instrument Company, Inc., Houston, Texas.

behavior as recorded on magnetic tape. A 2.5 kilowatt gasoline generator was used to power all electrical equipment.

Five ground squirrels were instrumented with ECG radio-transmitters in 1968 and eight in 1969. Two animals which were followed in 1968 were re-instrumented in 1969 for short periods. In all, ground squirrels wore operational transmitters for 6,370 hours during the two-year period. The amount of time each individual was instrumented depended upon its date of emergence from hibernation and arrival in the area under telemetric observation, its success in establishing a territory, and its subsequent relationship with neighboring residents.

Heart rates of ground squirrels were monitored in the early morning prior to animal emergence for the day, throughout the day as individuals behaved aboveground or periodically reentered their burrows, and into the evening following their submergence for the day. In this manner, three broad categories of heart rate information were obtained: (1) changes in heart rate among ground squirrels in their burrows, (2) heart rate responses during social interactions, and (3) heart rates of animals aboveground when they were not interacting overtly with conspecifics. The methods of sampling heart rate recordings varied according to animal location, activity and prevalent social conditions. These are discussed separately with each of the above data categories.

RESULTS

General Behavior of Ground Squirrels

The first ground squirrels emerged from hibernation on the study area in late March. Adult males emerged first followed by adult females, yearling females and finally by yearling males. Emergence spanned approximately one month and some overlap in the above sequence occurred. Specific patterns of emergence and probable causes of the phenomena have been reviewed by Walker (1968).

Adult males emerged from hibernation with scrotal testes and were in breeding readiness. The breeding season lasted for about 1 month and during that time, adult males inhabited large areas which overlapped the home burrows of several females and yearling males (Figure 4). They generally formed no lasting attachment to a specific burrow but were active throughout their home ranges and often nested for the night in different burrows. On the other hand, most yearling males emerged with abdominal testes, did not participate in breeding and occupied comparatively small home ranges around a particular burrow. They were nearly always subordinate to adult males.

Generally, adult males were aggressive towards all other adult males during the breeding season. However, they did not appear territorial according to the definition offered previously in that they did not exhibit "site defense" *per se*. Instead, their intolerance of other adult males apparently centered

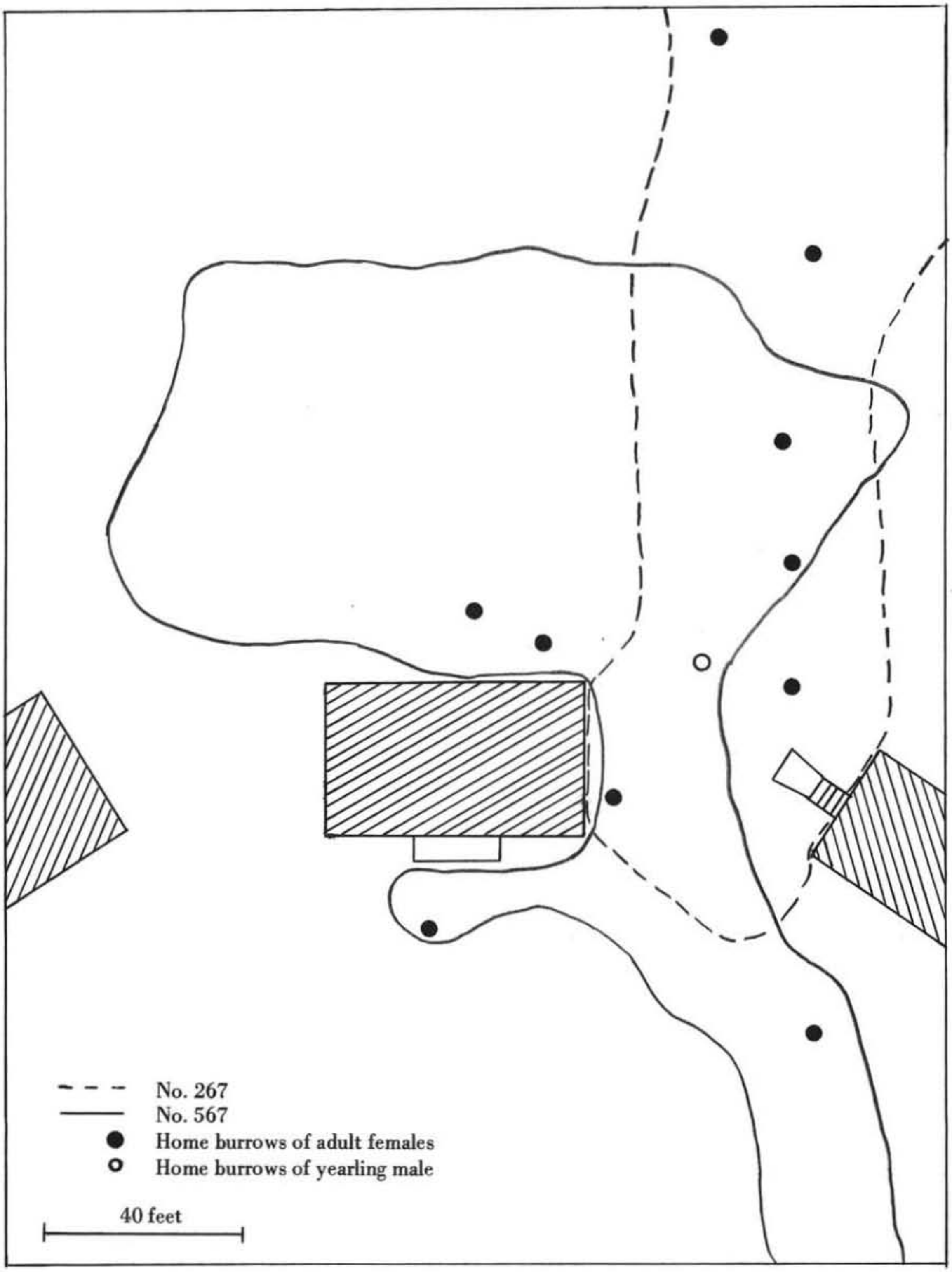

Figure 4. Home ranges of two adult males during the breeding season

about the areas inhabited by females in estrus. As these females were bred, the frequency of interactions between males decreased and the home ranges of neighboring males sometimes overlapped as illustrated in Figure 4. When this occurred, one male was usually dominant over the other. Hence, a social rank was evident but even this changed from time to time during the breeding season.

Females were not aggressive and non-territorial upon their emergence from hibernation. Depending upon snow cover, they either confined activities to the immediate vicinity of their burrows for a few days or made feeding excursions to exposed areas of the lawn. Communal feeding was common at this time and resulted in little conflict except for harassment by adult males.

Most females were bred within a few days of emergence from hibernation. Shortly after conception, each inhabited a relatively small area around a particular burrow (Figure 5). Although some were aggressive throughout their home ranges, most defended a limited area around their burrows. As a result of such territoriality, adult males and most yearling males were forced from the lawn and inhabited small home ranges in surrounding brush or other areas devoid of females.

The lack of overlap between female home ranges as depicted in Figure 5 may create the impression that entire home ranges were in fact territories. Although true in some cases, this was largely the result of the procedures used in this study to establish home range boundaries (see p. ~~8~~ 9). Had all sightings of individual movements been used, more overlap would have been indicated.

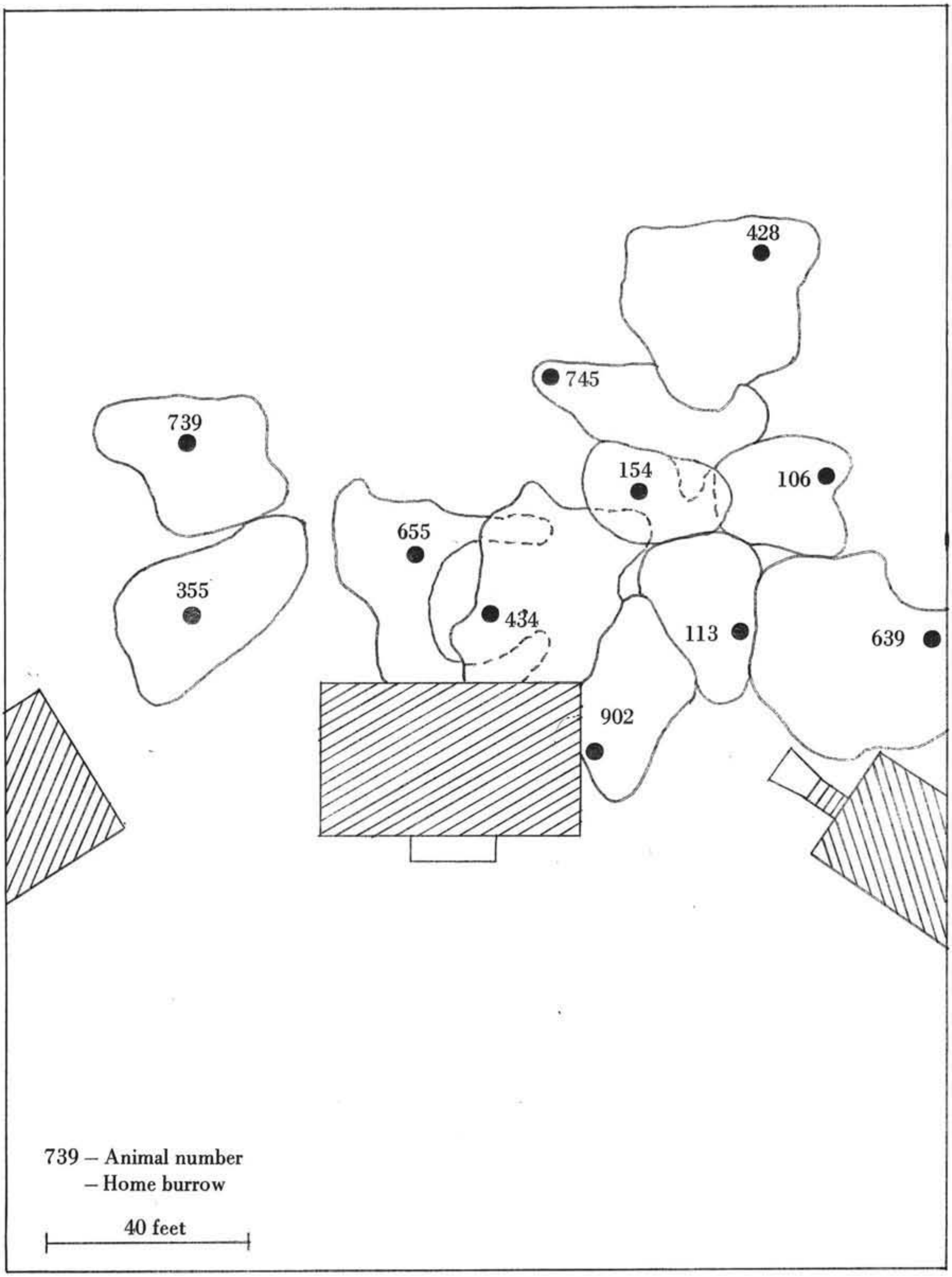

Figure 5. Home ranges of adult females and locations of home burrows during the period from conception through parturition, 1968

Territoriality among females diminished rapidly after parturition and was practically non-existent following the emergence of young from their natal burrows. However, this was a gradual transition as not all females gave birth at the same time. The period of parturition (i.e., from first to last birth) spanned 10 days for instrumented females (Table 1) and approximately two weeks among all females in the population. Parturition was determined by monitoring animals in their burrows when they failed to make routine appearances aboveground, and by subsequent recaptures when they did appear to ascertain changes in weight and condition of mammary glands.

Among three females for which complete reproductive records were obtained, the interval from date of first observed sexual interaction to parturition was 23 days (Table 1). This gestation period is less than the 27-day period calculated previously for Uinta ground squirrels and less than the range of 24 to 30 days reported for other species of the genus <u>Spermophilus</u> (Walker, 1968). It is possible that females in the current study were bred prior to the first observed sexual interactions, thereby making estimates of gestation lower than those reported elsewhere. This was unlikely, and even if it was assumed that females were bred the day they emerged from hibernation, five of seven gave birth 24 to 26 days later. Furthermore, it was known that the other two females were not approached by any males for three (No. 113a) and five (No. 767) days post-emergence, respectively. Hence, it is likely that the gestation period for Uinta ground squirrels is in the range of 23 to 26 days.

Table 1. Dates of emergence from hibernation and reproductive events for instrumented female ground squirrels

Year	Animal number	Date category	Emergence from hibernation	First observed sexual interaction[a]	Parturition	Appearance of young aboveground
1968	113a	Calendar	April 12		May 9	May 31
		DSPE[b]	18		45	67
		DSPE[c]	1		28	50
	428		April 25		May 18	June 10
			31		54	77
			1		24	47
	434		April 14	April 16	May 9	May 31
			20	22	45	67
			1	3	26	48
	655a		April 14	April 15	May 8	May 31
			20	21	44	67
			1	2	25	48
	745		April 26[d]		May 18	June 10
			32		55	77
			1		24	46
1969	95		April 22	April 24	May 17	June 6
			23	25	48	68
			1	3	26	46
	113b		April 13	April 14	(Dispersed)	
			14	15		
			1	2		
	639		April 9			May 27
			10			58
			1			49
	655b		April 16		(Dispersed)	
			17			
			1			
	767		April 11		May 11	June 3
			12		42	65
			1		31	54

[a] Aboveground courtship after which male and female entered burrow, presumably to breed (Balph and Stokes, 1963).

[b] Days since population emergence from hibernation.

[c] Days since individual's emergence from hibernation.

[d] Captured and identified on April 28 but believed to have emerged from hibernation on April 26.

Following the breakdown of territoriality among reproductive females, all ground squirrels continued to defend an individual distance of two to five feet, but this was of little consequence in curtailing animal movements. As a result, all animals expanded their home ranges which they continued to occupy until entering hibernation in mid-summer (Figure 6).

Heart Rate Response to Non-Social Behavior

Before an assessment could be made of the effects of social interactions upon the heart rate of ground squirrels, it was first necessary to determine the degree squirrels responded during non-social behaviors. Of particular importance were changes in heart rate associated with motor activities and diurnal activity patterns since these may become confounded with purely emotional responses to social and other environmental stimuli (Barger et al., 1956; Eisman, 1966; Hahn, Stern and Fehr, 1964; McGrath, 1970). The above measures were obtained by monitoring animals deep in their burrows and as they behaved aboveground at times when they were not involved in overt social interactions.

Burrow Observations

Response to motor behavior

A recording period was begun by triggering the time-event channel on the polygraph when a ground squirrel entered its burrow. This period lasted from 1 to 15 minutes depending upon the duration of the animal's visit and its activity. Heart rate was not measured until a squirrel had been in its burrow

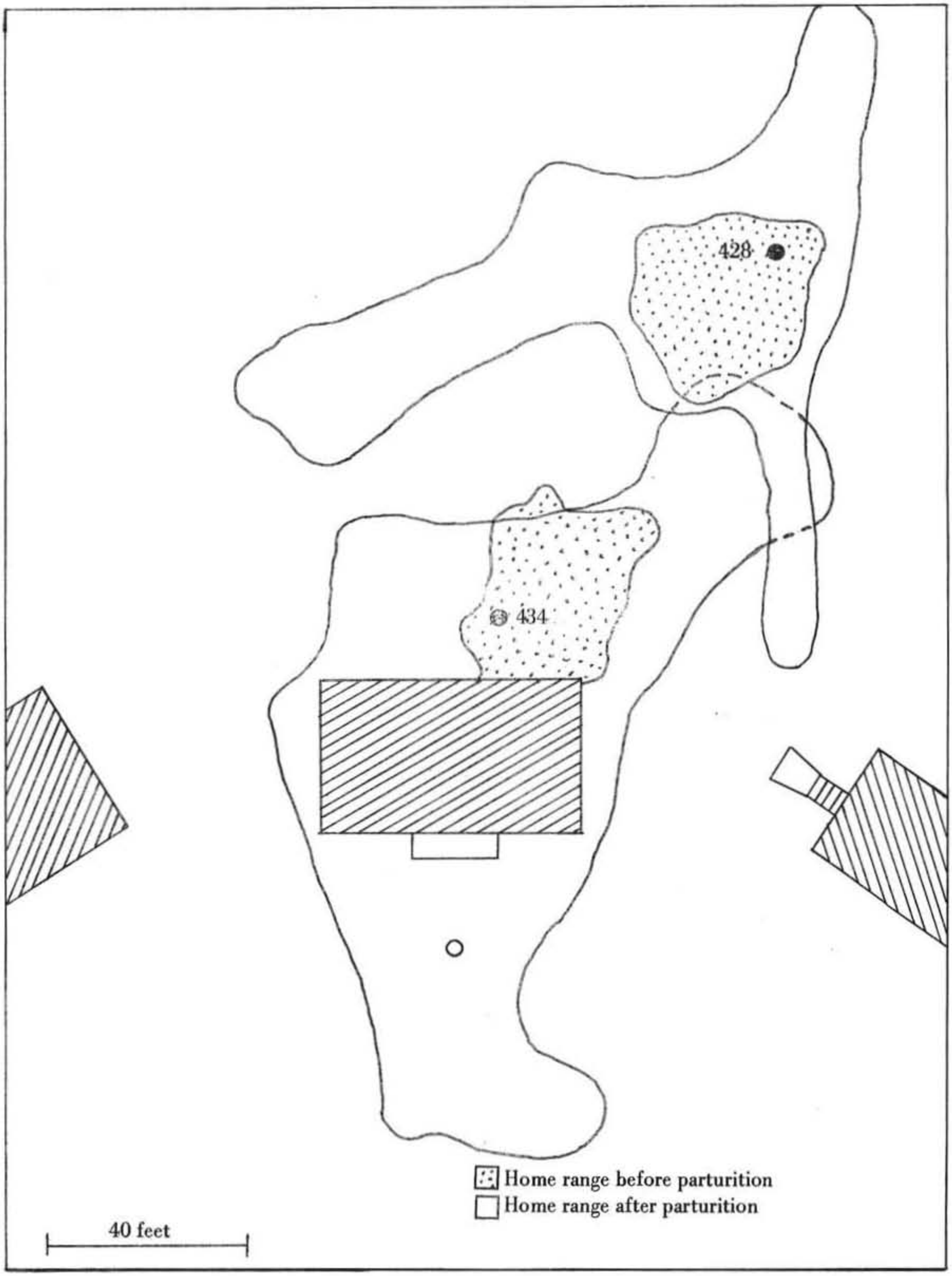

Figure 6. Home ranges of two adult females before and after parturition. No. 434 moved her offspring to alternate burrow (○) after giving birth at home burrow (●).

for at least 1 minute. This procedure allowed heart rate to stabilize in the event the animal was still responding to aboveground stimuli. Measures were then taken once each minute by counting the number of heartbeats within a 3-second interval and each sample represented an individual observation. Counting heartbeats throughout the 3-second interval minimized the influence of transitory fluctuations in heart rate caused by phases of the animal's respiratory cycle (Clynes, 1960; Milnor, 1968; Opton, Rankin and Lazarus, 1966; Westcott and Huttenlocher, 1961; Wood and Obrist, 1964).

Movements by animals in their burrows invariably produced recording artifacts but heartbeat tracings could still be identified. Based upon these recordings, it was apparent that upon entering their burrows some animals traveled directly to the nest cavity where they remained motionless for extended periods, presumably asleep. Others exhibited periods of both activity and inactivity during a recording period and hence, cardiac response to both behaviors were obtained. For purposes of data analysis, an animal was considered "inactive" only if it exhibited no motor behavior for at least 10 seconds prior to the measurement of its heart rate. Changes in heart rate associated with motor behavior had essentially waned within the 10-second interval. When involved in motor behavior, squirrels were considered "active".

A total of 905 observations of heart rate was obtained for ground squirrels in their burrows during both day and night. Of these, 746 and 159 were for inactive and active animals, respectively (Table 2). Characteristic recording artifacts, as compared to those obtained for animals aboveground, indicated

Table 2. Mean heart rates of inactive and active ground squirrels in their burrows

				Daytime (7:00 A.M. – 5:00 P.M.)				Nighttime (5:00 P.M. – 7:00 A.M.)				Change in mean heart rate from day to night (beats/minute)	
				Inactive		Active		Inactive		Active			
Year	Animal number	Sex	Age in years	No. obs.	Mean heart rate	No. obs.	Mean heart rate	No. obs.	Mean heart rate	No. obs.	Mean heart rate	Inact.	Active
1968	113a	F	2	52	266	7	297	11	240	2	248	-26	-49
	428	F	2	25	270	5	268	10	245	1	260	-25	- 8
	434	F	2	92	281	26	286	33	240	7	264	-41	-22
	655a	F	4	87	285	40	303	61	276	14	303	- 9	-27
	745	F	1	7	239	2	300	4	231			- 8	
1969	95	F	1	50	282	8	315	3	285	3	300	3	-15
	113b	F	3	118	244	20	316	5	213	5	268	-31	-48
	267	M	4	22	266	2	311	3	207			-59	
	270	M	1	42	272	3	293	12	244	3	303	-28	10
	639	F	6	35	263			23	237	2	253	-26	
	655b	F	5	12	272	2	272	4	275			0	
	767	F	2	33	281	7	323	2	246			-35	
Totals				575		122		171		37			
Means					269		301		253		284	-24	-23

that activity in the burrows consisted of grooming, arrangement of nest material, moving along burrow passageways and digging. For the population, these motor behaviors elicited a mean increase in heart rate of 12 per cent or approximately 30 beats/minute above that during inactivity. This increase may be attributed primarily to an adaptive response by the cardiovascular system to increased oxygen demands of the body during exercise (Andersen, 1968; Astrand et al., 1964; Bailie et al., 1961; Brouha, 1960; Donald and Shepherd, 1963; Selkurt, 1962).

However, the magnitude of response to motor behavior varied between and within individuals and was not related to sex or age. This suggested other factors were operating. The duration and intensity of physical exertion and the level of arousal before and after exercise were certainly important. Although burrow behavior was not observed directly, some indications of the effects of these variables were provided by comparisons of daytime and nighttime responses.

Eighteen per cent of both daytime and nighttime recordings contained movement artifacts, indicating ground squirrels exhibited motor behavior as frequently at night as during the day. However, the intensity of activity was not comparable during the two periods. Recordings of movement artifacts were nearly always of less magnitude at night and hence, nighttime behavior apparently consisted of deep sleep, restless sleep, grooming and nest repair. Similar behaviors have been observed among captive Arctic ground squirrels (Folk, 1964). During daytime, animal activities were more intense and included digging and moving about burrow passageways. Accordingly, heart rates averaged approximately 24 beats/minute greater for both inactive and active ground squirrels during the day as opposed to night (Table 2).

Diurnal and seasonal rhythms in heart rate

Even while ground squirrels were inactive in their burrows, marked changes in heart rate occurred at different times of day and night. Some of these changes were sudden and brief and may simply have been associated with dreamlike excitement as reported for Arctic ground squirrels and dogs (Folk, 1962). Other more subtle changes indicated additional factors were contributing towards cardiac response. The question was then asked if this latter type of response exhibited any degree of rhythmicity.

It must be emphasized that burrow measurements of heart rate were taken to meet the specific needs of the study (i.e., to establish baseline heart rates) and not to obtain evidence *per se* as to the presence of a physiological rhythm. Heart rates of animals in burrows were simply monitored as time and other project objectives permitted. As a result, a continuous 24-hour record was not obtained for any animal.

Indeed, the daily and seasonal behavior of ground squirrels above and belowground precluded such measures. Early in the season (DSE 1-19), squirrels were aboveground most often during the late morning and early afternoon hours (Figure 7). As the season progressed, animals emerged earlier and were frequently aboveground until late afternoon. This period (DSE 20-39) represented a transition from an acute unimodal to a distinct bimodal activity pattern. By DSE 40-49, a bimodal pattern was evident and extended throughout

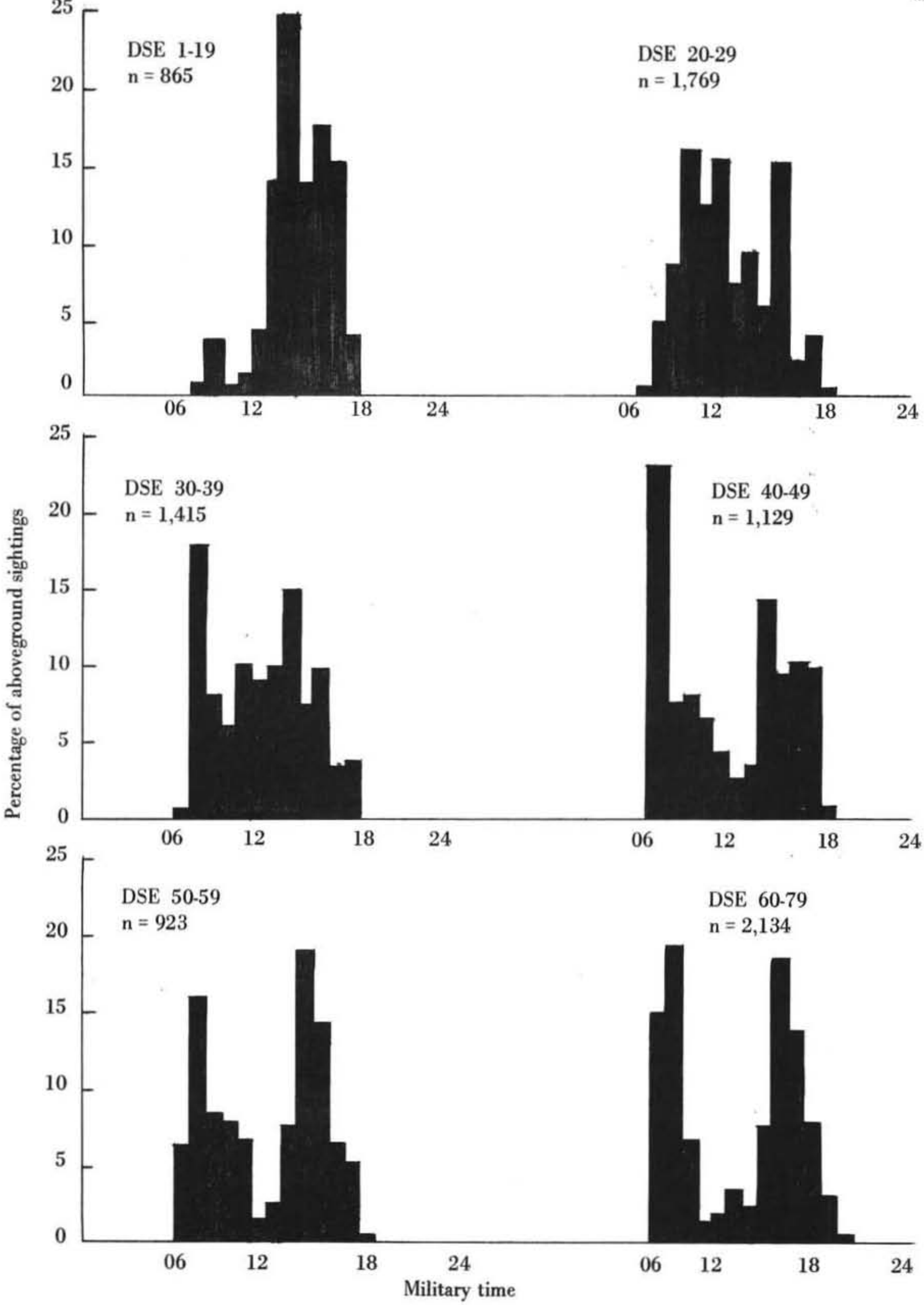

Figure 7. Aboveground activity patterns of ground squirrels related to time of day and season

the remainder of the season. Consequently, heart rate information could not be collected at certain times of day simply because ground squirrels were not in their burrows. Therefore, it was necessary to combine observations within specific DSE intervals to provide a more complete picture of diurnal responses.

Figure 8 illustrates the relationship between heart rate and time of day for two inactive females in their burrows. The values represent hourly means as calculated for the interval DSE 33-74. Heart rate for both animals was lowest between 6:00 a.m. and 7:00 a.m. just prior to their emergence for the day, increased and fluctuated during the day as determined when animals periodically reentered their burrows, and decreased to lower levels when animals submerged for the night.

The above showed that ground squirrels exhibited marked fluctuations in heart rate even as they remained inactive in their burrows. Furthermore, peaks and troughs (Figure 8; a, b, c) of cardiac response indicated the likelihood of seasonal influences. Indeed, this was apparently the case. Heart rate for another female earlier in the season (DSE 14-21) was greatest at midday and coincided with its unimodal aboveground activity pattern at that time (Figure 9). On the other hand, the heart rate of still another female later in the season (DSE 45-74) increased and decreased in accordance with its bimodal activity pattern (Figure 10). If the data for early and late DSE intervals as represented in Figures 9 and 10 are combined, the resultant peaks and troughs roughly coincide with those of Figure 3 which was constructed from both early

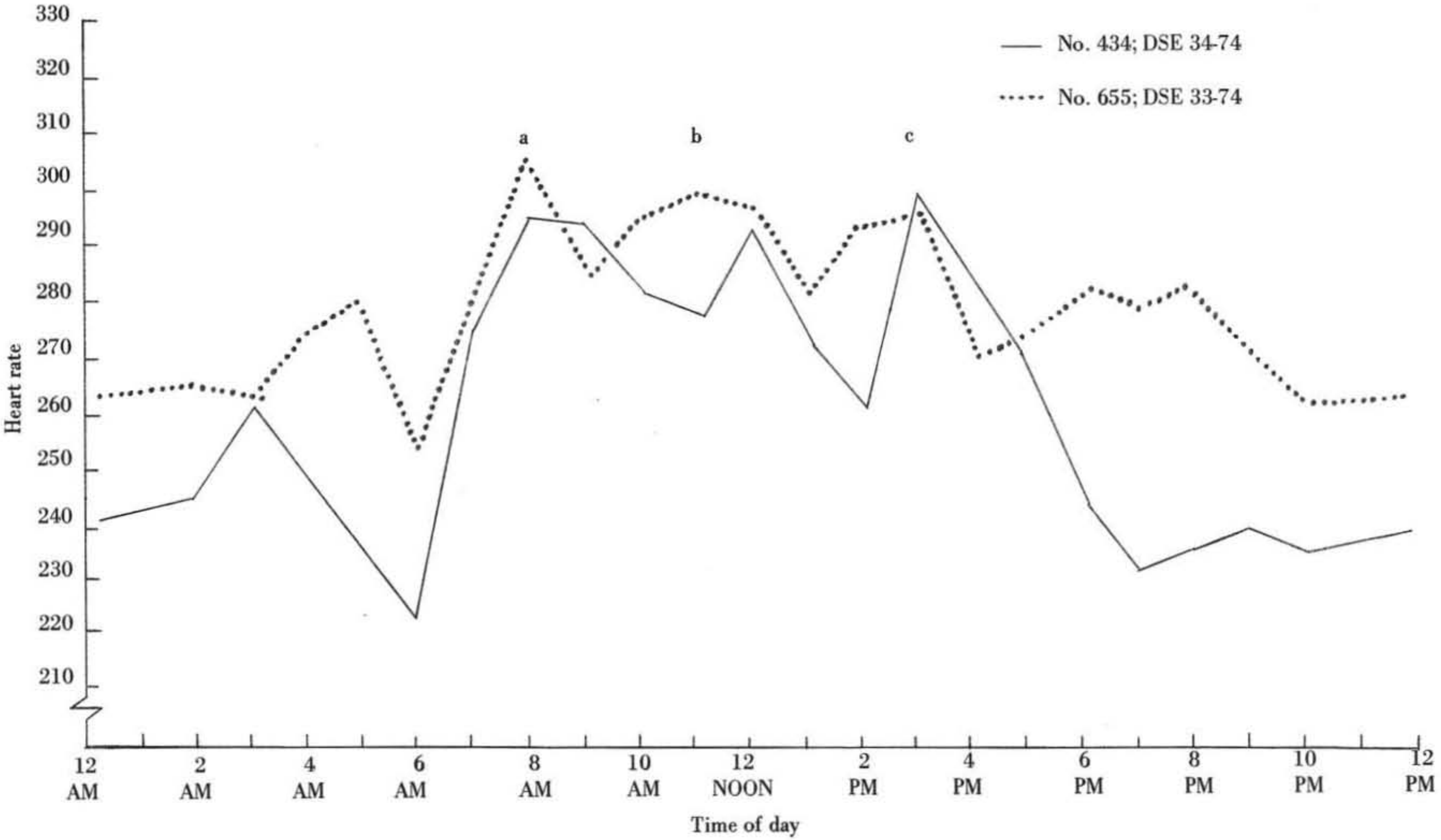

Figure 8. Heart rates of two inactive females in their burrows based upon hourly means for the period DSE 33-74 (see text concerning points a, b, c)

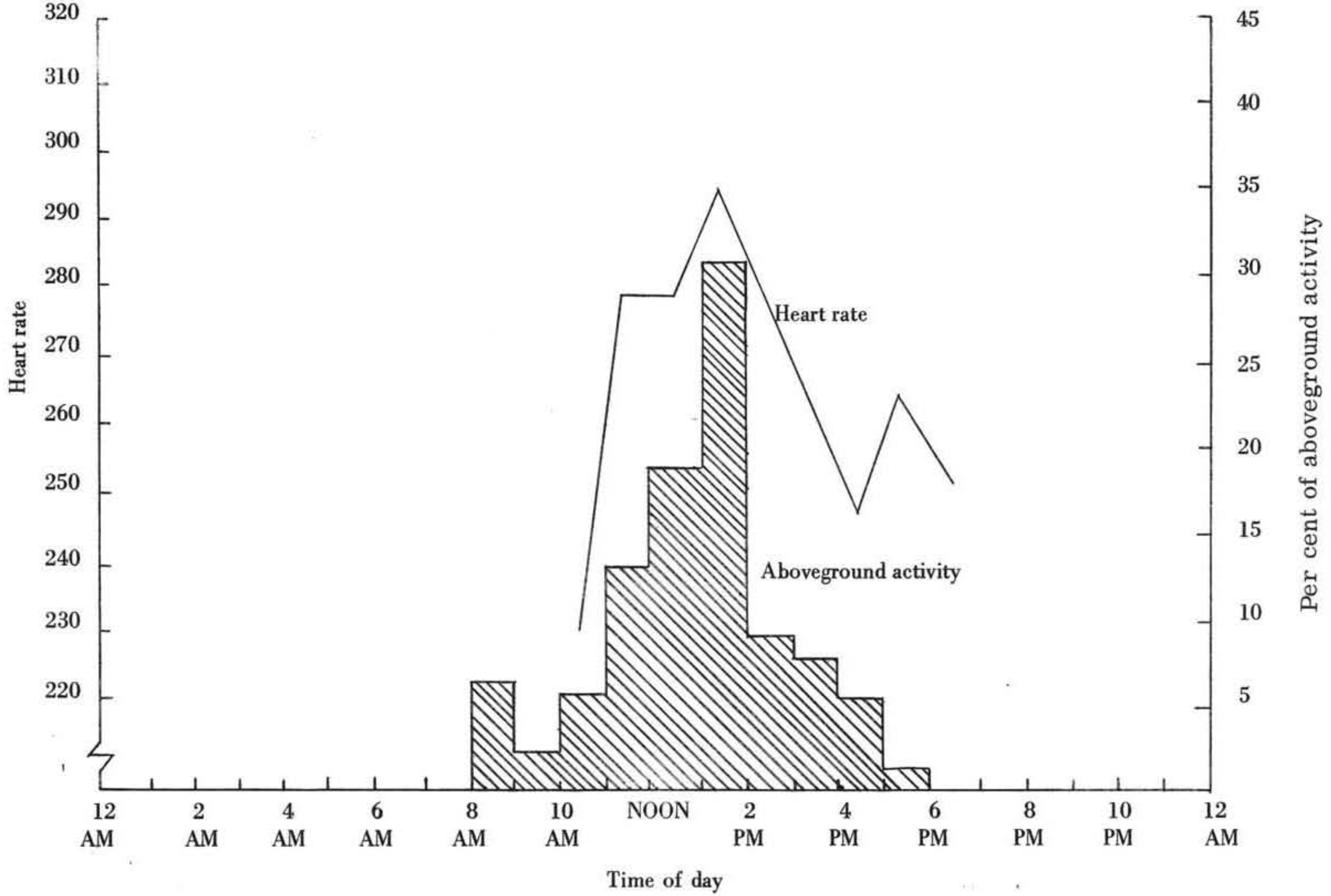

Figure 9. Mean heart rates of an active female ground squirrel in her burrow related to the daily distribution of aboveground activity for DSE 14-21

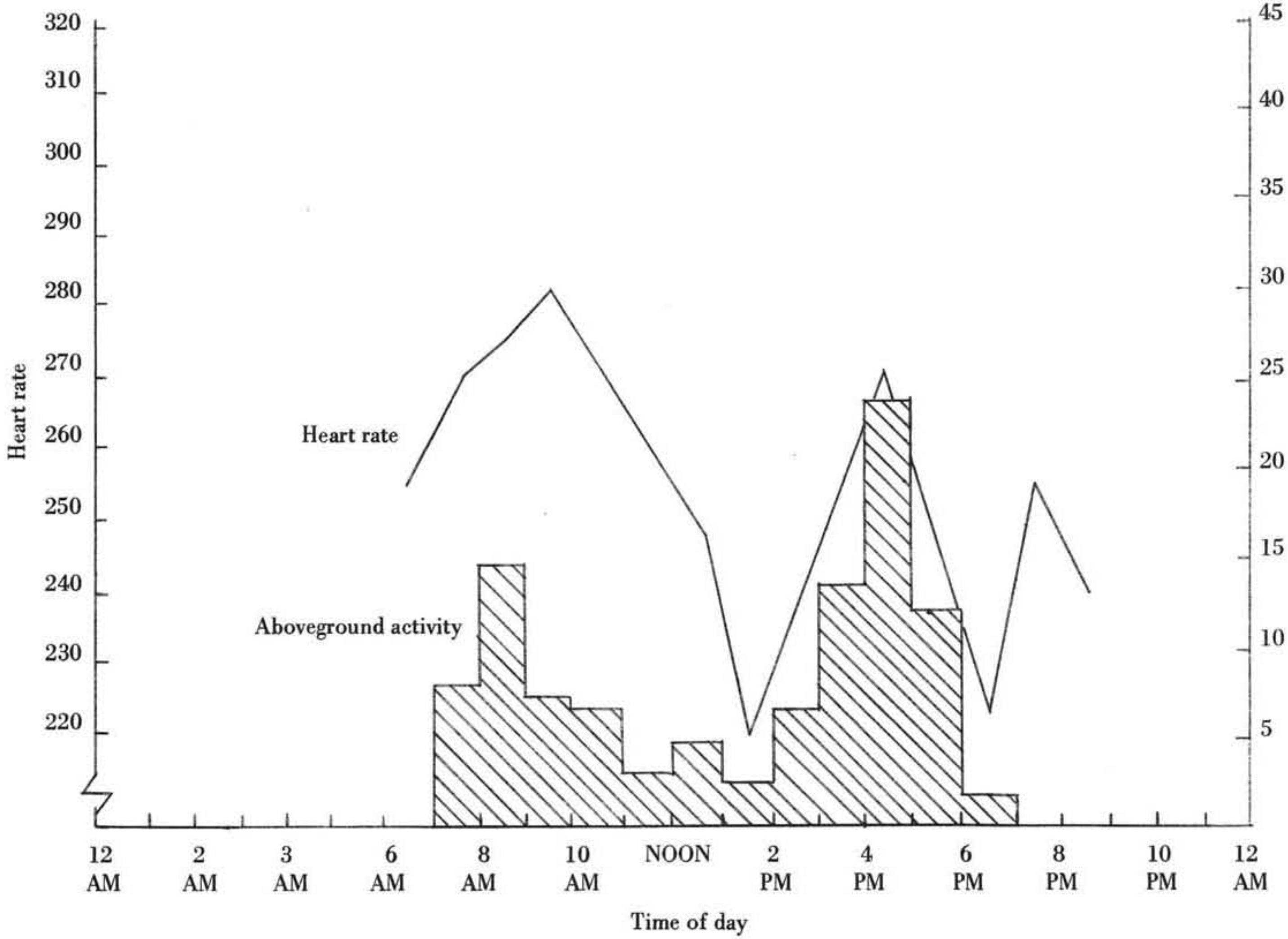

Figure 10. Mean heart rates for an inactive female ground squirrel in her burrow related to the daily distribution of aboveground activity for DSE 45-74

and late seasonal observations. Hence, ground squirrels exhibited both diurnal and seasonal rhythmicity in their heart rates.

Among Arctic ground squirrels exposed to continuous daylight in outdoor pens, Folk (1962) found these animals exhibited daily activity rhythms and their heart rates were nearly always in phase with the motor behaviors. But in the current study, heart rate was measured while animals were in their burrows and not involved in motor behaviors. Even so, diurnal changes in heart rate were evident and coincided with seasonal changes in aboveground activity. This suggested Uinta ground squirrels possessed a physiological rhythm independent of immediate motor behavior, but which nevertheless was influenced by aboveground activity cycles. That is, during periods when ground squirrels were normally active aboveground, they still returned periodically to their burrows to rest. Their heart rate remained elevated indicating a comparatively high level of arousal. Conversely, as they remained in their burrows for extended periods when aboveground activity was usually minimal (i.e., at night or midday during bimodal activity), heart rate decreased and indicated ground squirrels entered deep sleep until their next bout of surface behavior. These seasonal shifts in diurnal activity rhythms are common among many animals (Eibl-Eibesfeldt, 1958; Harker, 1964; Menaker, 1969) and the findings of this study showed that cardiac rhythms may shift in a similar manner.

Aboveground Observations

Response to motor behavior

Exclusive of overt social interactions, motor behavior among ground squirrels aboveground consisted of feeding, moving (locomotor), grooming and gathering of nest material. In contrast, animals sometimes sat motionless in a "down" position on all four legs and exhibited no motor activity. An individual's heart rate was measured by counting the number of heartbeats within a 3-second interval every 10 seconds as ground squirrels exhibited the respective behaviors.

However, except in cases of locomotor behavior, heart rates obtained during the first 10 seconds after an animal changed locations were not considered in the following analyses. This restriction was imposed because preliminary treatments of 1,196 observations taken during this period indicated that responses to subsequent behaviors were influenced by residual effects of the antecedent locomotor behavior. Similarly, heart rates for motionless animals consisted only of measures when subjects had remained inactive for at least 10 seconds. Using these procedures, a total of 5,152 measures of cardiac response to aboveground behaviors was obtained during this study.

As one might expect, the magnitude of cardiac acceleration was related to the apparent effort required by ground squirrels to perform the different motor activities. In general, feeding and grooming elicited the least response above that of motionless animals (Table 3). Moving and gathering

Table 3. Heart rate of ground squirrels aboveground during non-social behaviors

Conditions of crowding[a]	Spatial location of instrumented squirrel[b]	Non-motor Behavior		Motor behavior							
		Motionless		Feeding		Grooming		Moving		Nest gathering	
		No. obs.	Heart rate	No. obs.	Heart rate	No. obs.	Heart rate	No. obs.	Heart rate	No. obs.	Heart rate
Conspecifics absent	Within area of great familiarity	314	285	136	304	24	316	13	340		
	Outside area of great familiarity	929	301	542	318	50	322	100	348	16	367
Conspecifics present	Within area of great familiarity	483	296	395	317	27	334	39	327		
	Outside area of great familiarity	916	312	956	320	55	322	19	341	8	343
TOTALS & MEANS		2642	302	2029	318	156	323	301	341	24	359

[a] Presence or absence of one or more conspecifics within a radius of 40 feet of the instrumented subjects.

[b] Areas of great familiarity were those of FI-5 or greater; areas of low familiarity were those of FI-4 or less as described on page 70.

of nest material were more strenuous and produced a greater rise in heart rate. This increase ranged from 5 per cent (16 beats/minute) for feeding to 19 per cent (57 beats/minute) for nest gathering, and averaged 11 per cent (33 beats/minute) based upon the unweighted means for all motor behaviors. The latter figure was comparable to the 12 per cent (30 beats/minute) increase attributed to motor behavior by animals in their burrows.

Response to spatial factors and crowding

The foregoing data were collected only at those times when ground squirrels were not interacting overtly with one another. Although these were originally construed to be non-social situations, it was recognized that the mere presence of conspecifics could conceivably affect an individual's heart rate. In both rats and humans, the presence of a certain number of conspecifics may actually inhibit heart rate response to "stressful" stimuli (Angermeier et al., 1965, 1967). Conversely, increased crowding among mice may cause a commensurate increase in the degree of certain physiological responses (Christian, Christian, 1955a, 1955b, 1959b; Southwick, 1959).

To determine if either effect operated among ground squirrels, observations were stratified relative to the absence or presence of conspecifics within a radius of 40 feet of instrumented subjects at the time their heart rates were measured. Data in each of these categories were further segregated according to an individual's spatial location since this variable was known to influence the heart rate of captive Uinta ground squirrels (Ruff, unpublished) and albino rats in the laboratory (Black, Fowler and Kimbrell, 1964; Candland, Pack and Matthews, 1967; Snapper et al., 1965; Snowden, Bell and Henderson, 1964).

Individual ground squirrels nearly always exhibited greater heart rates when one or more conspecifics were in the immediate vicinity. The same was true when instrumented animals were outside as opposed to within an area of great familiarity. However, the increase was neither consistent for all behaviors nor statistically significant with regard to population means for the different behaviors (Table 3).

A better appraisal of the effects which spatial factors and the mere presence of conspecifics had upon the heart rate of ground squirrels can be made by consideration of cardiac responses among motionless animals only, thereby eliminating the effects of motor behaviors. In such cases, animals in familiar areas exhibited heart rates which averaged 16 beats/minute less than when individuals behaved in an unfamiliar environment, regardless of conditions of crowding (Table 3). Similarly, heart rates were approximately 11 beats/minute less when animals were alone as opposed to when other squirrels were present. This was true whether the instrumented subject was within or outside an area of great familiarity. Hence, although motor behavior elicited the greatest elevation in heart rate, a ground squirrel's spatial location and conditions of crowding were additional factors which served to enhance or inhibit the degree of cardiac response.

Selection of Baseline Heart Rates

Two heart rate baselines were selected with which to compare responses during social interactions. One baseline of 269 beats/minute was the mean heart rate for inactive ground squirrels in their burrows during daytime. A second baseline of 284 beats/minute was for inactive animals aboveground as they sat motionless in areas of great familiarity when conspecifics were absent within a radius of at least 40 feet.

In essence then, the burrow baseline represented a resting heart rate for animals which were not exposed to any immediate social or environmental stimuli. But upon emerging from their burrows, ground squirrels were faced with the sights, sounds, odors and other changes of their aboveground environment. These contingencies undoubtedly heightened the physiological and emotional arousal of animals and this was reflected in a greater heart rate. Consequently, any further increase could be assigned to the effects of motor activity or additional emotional arousal during social interactions. This was the basic rationale for selecting burrow and aboveground baselines and for subsequent assessments of the effects of non-social and social stimuli upon the heart rate of ground squirrels.

Short-Term Heart Rate Response to Social Interaction

Social interaction among ground squirrels ranged from various forms of mere threat to outright physical combat. Certain types of encounters were brief but intense, and elicited a great rise in heart rate. Others were long and produced more subtle cardiac responses. But in either case, the magnitude and duration of response appeared dependent upon several pre- and post-encounter variables as well as motor activity during the encounters. It was important to determine the effects of these variables to more fully appraise both acute and chronic heart rate response to social interaction.

Changes in Heart Rate During Threat

Threat among ground squirrels consisted of various body postures, movements and calling which obviously served to intimidate conspecifics. Some threats were too subtle or occurred too rapidly for precise correlation with minor fluctuations in heart rate. Instead, threats were grouped into three broad categories: (1) "calling" - two or more squirrels emitted "churr" and "chirp" calls (Balph and Balph, 1966; Balph and Stokes, 1963) while down-slouched (head held low, spinal lordosis and legs flexed beneath the body), upright-slouched (spinal lordosis, sitting on haunches and forelegs held to body), or upright-slouched (trunk extended forward, forelegs extended and hindlegs flexed); (2) "face-off" - two rivals faced each other, their body postures were either down-slouched or down-coiled (head and trunk pressed flat on ground and legs flexed beneath the body), and animals often clattered their teeth and emitted low growling noises or churr and chirp calls; (3) "charge" - a short dash by one animal toward another but which invariably fell short on contact and terminated in a face-off between individuals.

Some types of threat were similar to or formed a continuum with others. Calling bouts were characterized by animals usually calling from an upright position at distances up to 30 feet and calls were emitted throughout the encounter. On the other hand, face-offs generally occurred at distances of less than 6-feet, animals were in a "down" position and calls, if any, were usually confined to the early portion of the encounter. A charge was distinguished from a face-off by the brief dash during the former. Otherwise these encounters were identical.

Since the occurrence of social interactions was generally unpredictable, no particular routine was followed in gathering field information relative to such events. If a situation developed where animals were likely to interact, radio reception was simply switched to those individuals. Heart rate relative to face-offs was measured at 1 and 10 seconds prior to onset of threat. Samples were also obtained at 1, 5 and 10 seconds following onset, and at the time heart rate stabilized following onset. The same measures were made for charges, but with reference to onset and termination of the actual charge component. During calling bouts, heart rate was measured 10 seconds prior to onset of calling and each 10 seconds from onset to termination of the bouts. All measures consisted of mean heart rates determined for one-second intervals.

Figure 11 illustrates changes in heart rate among ground squirrels during various types of threat. Preliminary treatments indicated no significant differences regarding sex and age or initiates and recipients of aggression. Therefore, the response curves were constructed from mean values for all animals during the

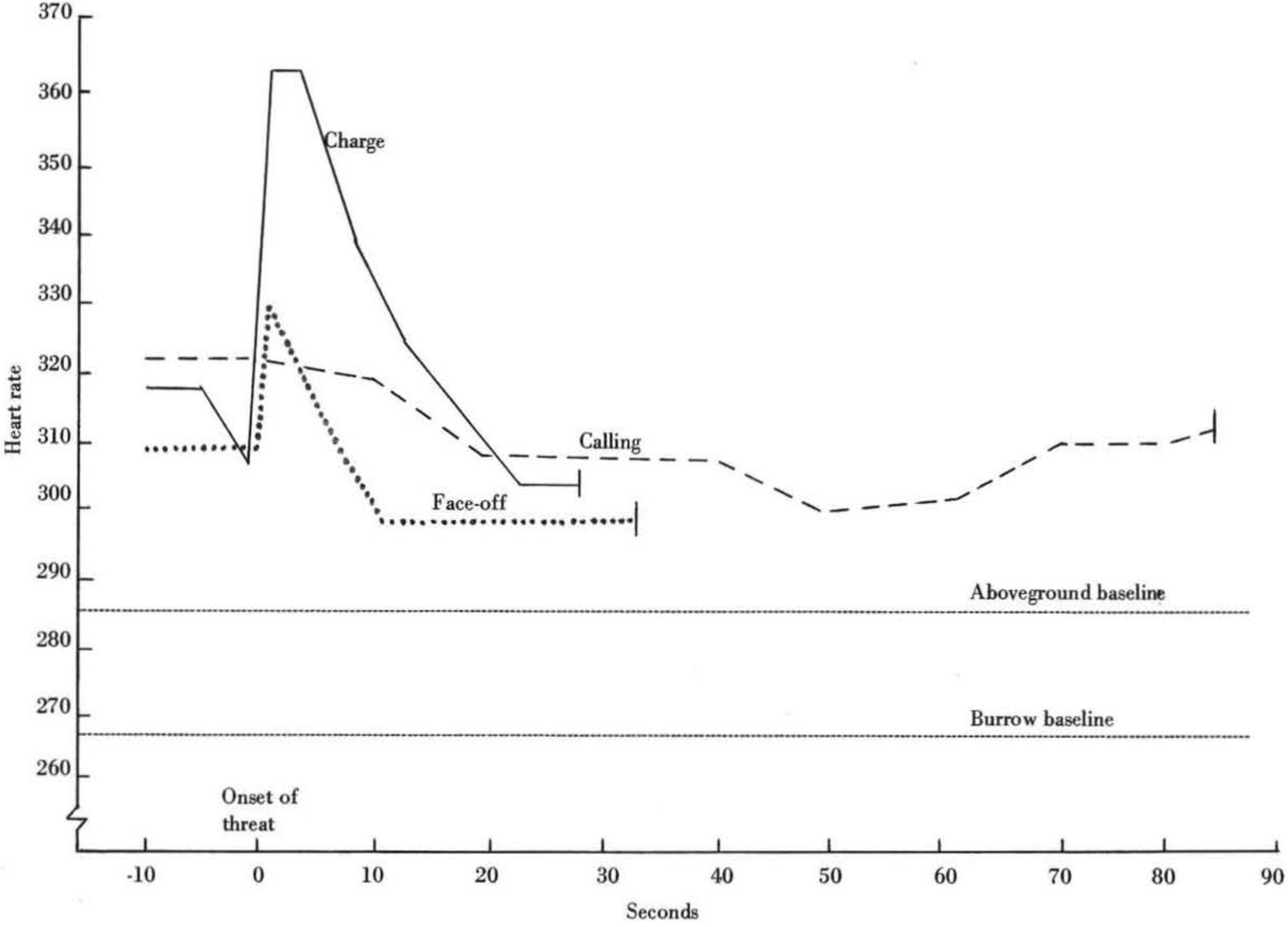

Figure 11. Heart rate response of ground squirrels to threat

different types of encounters. Charges elicited the greatest response which averaged 364 beats/minute as compared to 329 beats/minute for face-offs and 321 beats/minute for calling bouts. Mean maximum response for charges was significantly greater than those of face-offs (t = 2.263, 28 d.f.) and calling bouts (t = 3.706, 35 d.f.), but means of the latter two encounter types were not significantly different (t = 0.945, 49 d.f.)

Maximum response to all threat interactions was usually attained within one or two seconds of threat onset. Harris and Siegel (1967) observed a similar rapid acceleration in the heart rate of game cocks during threat encounters, and Bond (1943) noted that dogs usually attained maximum cardiac response with 3 to 5 seconds following a loud noise. Bond further showed that hormonal agents alone could not elicit such a rapid response although adrenaline did serve to maintain an elevated heart rate. Hence, the rapid increase in the heart rate of ground squirrels during this study was obviously the result of neural stimulation rather than a reaction to hormonal agents or to motor activity.

The duration of threat encounters averaged 83 seconds for calling bouts, 33 seconds for face-offs and 28 seconds for charges. The mean of calling bouts was significantly greater than either face-offs (t = 5.738, 54 d.f.) or charges (t = 4.443, 44 d.f.), but those of face-offs and charges were not significantly different (t = 0.942, 24 d.f.). Yet heart rate usually waned and stabilized before threats terminated. Consequently, the period of elevated heart rate or the duration of response averaged just 20 seconds for charges and 11 seconds for face-offs.

This period of response could not be determined for calling bouts because heart rate showed no rapid acceleration and subsequent waning.

The motor component of charge interactions was not the sole factor responsible for greater heart rate during charges as opposed to other forms of threat. Even motionless recipients of charge threat exhibited a mean maximum response of 437 beats/minute as compared to 329 and 321 beats/ minute for motionless animals in face-offs and calling bouts, respectively. Hence, anxiety was apparently heightened during all types of threat but more so during charges. Still, the anxiety was short-lived and largely waned before interactions ceased.

The above observations appeared related to results of human studies. When human subjects were warned they were to receive a mild electric shock; marked cardiac acceleration occurred, for subjects had no way of knowing how "mild" the shock would be. Having received the shock once and when threatened later with the same shock, humans had lower heart rates than on the first threat trial. Accordingly, Deane and Zeaman (1958) reported:

> Loosely speaking, Ss (subjects) are relieved at discovering the shock is no worse than it is. This notion ... requires the auxiliary postulate that strong anxiety produces cardiac acceleration, and weak anxiety a deceleration, an assumption for which there is some independent evidence. Zeaman and Wegner (1947) found that Ss giving larger unconditioned responses to shock tended to give accelerative cardiac CRs, while those with smaller shock URs tended towards the decelerative type of CR. (Deane and Zeaman, 1958, p. 106)

This may have been the case with ground squirrels. At the onset of face-offs and especially charges, anxiety was comparatively high as animals may have expected a "shock" (combat) of unknown intensity. But once the interactions were in progress, some characteristic motor patterns may have signaled both animals that combat was not forthcoming. Hence, they may have been "relieved" that the stimulus was no stronger than it was. Consequently, their heart rates declined and stabilized even while threat continued.

Heart rate response to calling did not show an initial acceleration followed by waning. In fact, heart rate was less following the onset of calling than during antecedent behavior. This was largely because motor behavior often preceded calling and acted to increase heart rate. But during calling, animals were motionless and their heart rate declined. Still, it remained well above burrow and aboveground baselines. So did the heart rate of ground squirrels during other forms of threat. Therefore, although only face-offs and charges elicited an acute cardiac response, the elevated heart rates which accompanied all types of threat indicated chronic response to social interaction as well.

Changes in Heart Rate During Combat

Three general forms of combat occurred among ground squirrels: (1) "contact" - body contact with biting and wrestling, but no chase by the dominant as the subordinate escaped or remained: (2) "chase" - pursuit by a dominant and escape by a subordinate; (3) "contact-chase" - either order of these components, but usually consisted of contact followed by chase. Combat was often followed by threat postures and calling. However, such behaviors were considered integral components of combat interactions and were not included in previous analysis of threat conflicts.

Intensive motor activity produced recording artifacts which made it difficult to obtain accurate counts of heartbeats during actual combat. Instead, the number of heartbeats within a 1-second interval immediately following combat was used as a measure of maximum response to an interaction. Otherwise, heart rate sampling procedures were the same as described previously for "charge" threats.

Figure 12 illustrates changes in heart rate among ground squirrels during different forms of combat. The values represent means for 40 contact-chase, 23 chase and 21 contact encounters without regard to the sex and age of combatants or initiates and recipients of aggression. These latter variables generally had little effect but exceptions will be discussed in detail later.

Contact-chase interactions elicited a mean maximum heart rate of 397 beats/minute as compared to 384 beats/minute for chase and 356 beats/minute for contact. Responses to contact-chase and chase were both significantly greater than contact ($t = 4.794$, 55 d.f., and $t = 2.564$, 41 d.f., respectively), but not significantly different from one another ($t = 1.576$, 56 d.f.). All forms of combat elicited a significant increase in heart rate above baseline and antecedent measures.

The duration of combat averaged 6.1 seconds for contact-chase, 3.9 seconds for chase and 2.2 seconds for contact. All were significantly different from each other. Furthermore, the sum of means for contact and chase (6.1 seconds) exactly equalled that of contact-chase, indicating the duration of combat components were remarkably constant regardless of encounter type.

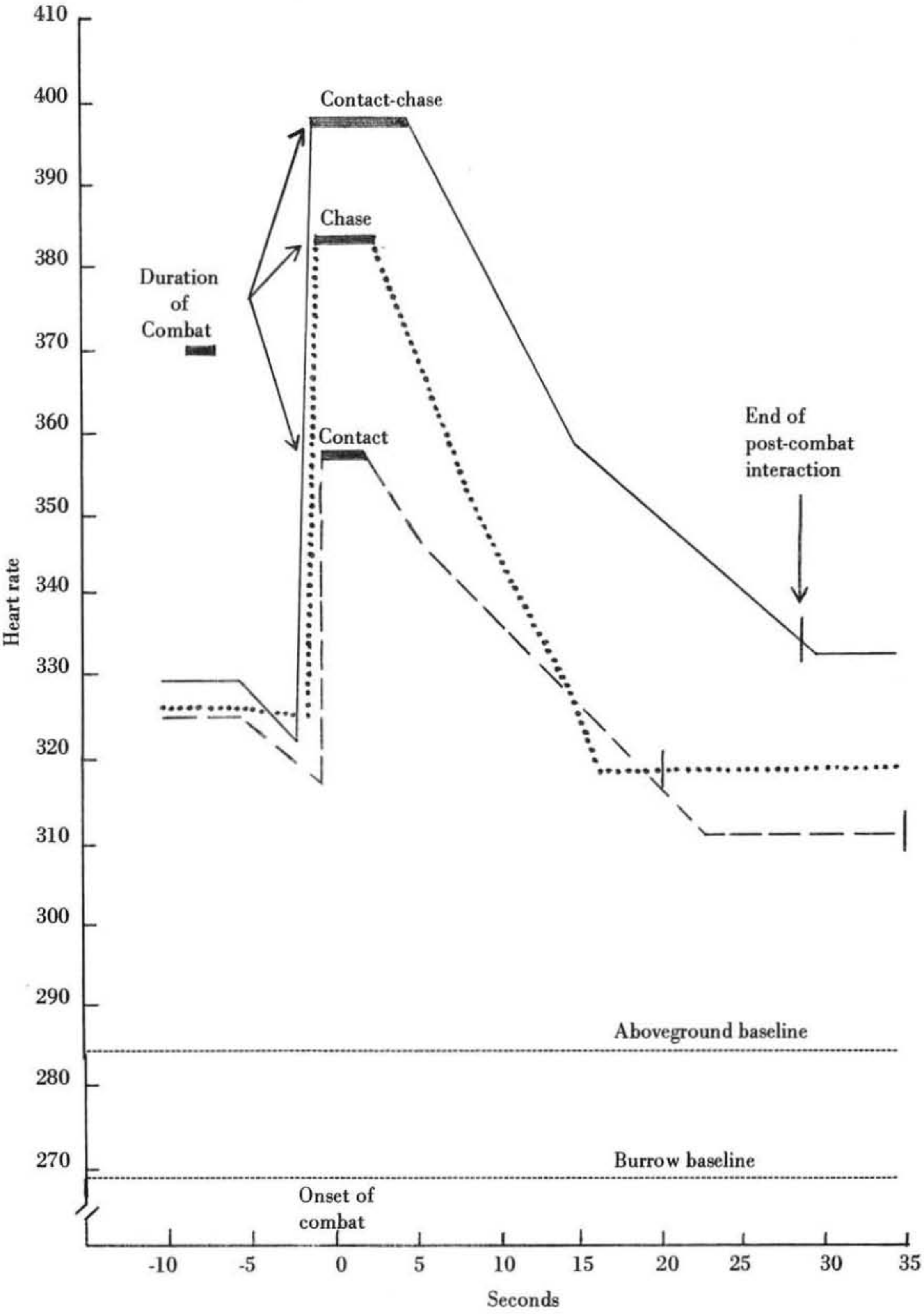

Figure 12. Heart rate response of ground squirrels to combat

Combat was often followed by various forms of threat such as calling and face-offs. At other times, animals simply remained motionless and peered intently at each other. Occasionally one or both would feed and groom but they continually watched each other until the distance between them exceeded approximately 10 feet. Therefore, although the squirrels did not necessarily display overt threat, some interaction was evident. Accordingly, the time animals remained within 10 feet following combat was used as an interval of post-combat interaction. This averaged 34 seconds for contact, 23 seconds for contact-chase and 17 seconds for chase. Only the means of contact and chase were significantly different (t = 2.238, 27 d.f.), but the duration of post-combat interaction was generally less following encounters having components of chase. This was because chase tended to separate ground squirrels in space and thus reduced the opportunity for continued interaction at close quarters.

The duration of acute cardiac response, the period of elevated heart rate from onset of combat to time of stabilization, averaged 31 seconds for contact-chase, 23 seconds for contact and 17 seconds for chase. Only the means of contact-chase and chase were significantly different (t = 4.430, 39 d.f.). Hence, the foregoing indicated that contact-chase encounters were the most intense forms of combat, elicited the greatest elevation in heart rate, produced the longest period of cardiac response, and therefore, were the most stressful of all forms of combat.

As illustrated in Figure 12, ground squirrels frequently exhibited cardiac deceleration one second prior to actual combat. This also occurred during charge threats (Figure 11). In cases of combat, this decrease was evident most often prior to encounters having contact as a component. Heart rate decreased an average of 21 beats/minute in 59 per cent of contact-chase and contact interactions, but declined just 12 beats/minute in only 42 per cent of chase encounters. In the remainder of combat interactions, heart rate increased or did not change. Prior to charge threat, heart rate decreased 11 beats/minute 75 per cent of the time.

The above findings closely parallel those of human studies. Among subjects in which anxiety was induced experimentally by warning signals of electric shock-to-come, heart rate sometimes increased (Lacey and Smith, 1954) and sometimes it decreased (Deane, 1961; Deane and Zeaman, 1958; Notterman, Schoenfeld and Bersh, 1952) prior to onset of shock. In other tests with humans (Zeaman and Wegner, 1954) and laboratory rats (McCleary, 1954), both effects were observed in different subjects under the same experimental conditions. Consequently, much disagreement exists among researchers as to the significance of such tachycardia and bradycardia (Graham and Clifton, 1966; Lacey, 1959; Lacey and Lacey, 1958a; Sokolov, 1960, 1963a, 1963b). But following a series of trials in which human subjects (S) were verbally instructed when to expect shock, Deane (1961) offered the following interpretation.

> The groups that were told when to expect shock showed ... a pronounced deceleration at the time shock was expected. Both acceleration and deceleration occurred in the group that never received shock. It was speculated that these two cardiac effects may be unlearned responses associated with what may be called anxiety

> and fear. When S expects a noxious stimulus of unknown strength a state of anxiety with its associated response of cardiac acceleration is aroused, and in addition if S expects the noxious stimulus at a particular instant in time a state of fear with its associated response of cardiac deceleration is aroused immediately prior to and during the time the stimulus is expected. (Deane, 1961, p. 493)

If indeed animals experience different emotions, then the above may apply to the changes in heart rate which were observed among ground squirrels. Intraspecific combat must certainly be considered a noxious stimulus, especially those forms having components of body contact with biting and wrestling. Prior to such encounters, ground squirrels exhibited greater and more frequent bradycardia than during interactions consisting only of chase. Accordingly, this indicated that animals "feared" contact more than chase. But then the question may be asked, how did rivals perceive an encounter would involve contact even before combat began?

The overt behavior of individuals immediately preceding combat suggested a possible mechanism. Chase nearly always occurred just after a subordinate turned to move away from a dominant. This initial escape response may have signaled the dominant contact was not forthcoming. By the same token, the subordinate anticipated escape rather than contact. Consequently, both rivals in chase situations only infrequently exhibited cardiac deceleration and this was usually of low magnitude. However, when a subordinate did not turn in an avoidance or escape response, both animals conceivably expected contact. This also would apply to charge threat. Hence, the heart rate of interactants declined more often and to a greater degree than prior to chase.

Previous social contact among ground squirrels also appeared to influence cardiac deceleration. When encounters were the first between individuals, heart rate decreased just prior to interactions only 12 per cent of the time while remaining unchanged 44 per cent and increasing 44 per cent of the time. But if combatants had met previously, their heart rate decelerated in 77 per cent of the cases while remaining unchanged 16 per cent and increasing 7 per cent of the time. These differences may also be explained according to Deane's (1961) interpretations. If animals had not interacted aggressively before, perhaps neither expected combat or anticipated it as a noxious stimulus of unknown strength. In the first case, heart rate would remain unchanged. In the latter it would accelerate as the result of anxiety. But in cases where rivals had met previously, either in disputes over territories or individual distances, a state of "fear" of impending combat and its associated response of cardiac deceleration would result.

Ultimately, the direction of cardiac response may depend entirely upon a species' "definition" (Ax, 1964) or "cognitive appraisal" (Lazarus and Opton, 1966) of a stressful or anxiety-evoking situation. And even within a species, a stimulus may serve as a stressor for one animal but not another. Therefore, individual differences and prior conditioning also play important roles in effecting changes in heart rate (Hodges and Spielberger, 1966; Lacey, 1950).

On the other hand, some researchers have contended that the direction of cardiac response in itself may not be a reliable indicator of anxiety or fear among animals. Poor correlations have frequently been found between heart rate and other autonomic measures of a subject's psychological or emotional state (Clemens, 1957; Lacey and Lacey, 1958b; Lewinsohn, 1956; Malmo and Davis, 1956; Wenger, 1942, 1948). However, more recent evidence has shown these poor correlations resulted largely from differences in experimental procedures methods of data analyses (Lazarus, Speisman and Mordkoff, 1963).

Additional evidence was gathered during the current study which strongly suggested cardiac deceleration was indeed indicative of fear among ground squirrels. At times when ground squirrels were held captive in traps, their heart rates never declined so long as they were not approached by humans. On the contrary, heart rates remained greatly elevated as the animals fought the traps in an effort to free themselves. But if a human approached a trap, the heart rates of captive animals declined. This bradycardia was especially evident when a hand was extended as if to grasp an animal. In such cases, the heart rates of ground squirrels often decreased 100 beats/minute within two or three seconds. Because instrumented animals were handled, marked, had their toes clipped and experienced minor surgery upon initial capture, it was logical to assume that prior experiences of capture and handling could serve as conditioned stimuli to elicit a few response on subsequent occasions. That heart rate decreased markedly on these occasions supported Deane's (1961) hypothesis of bidirectional cardiac responses associated with anxiety and fear.

Factors Affecting Maximum Heart Rate During Social Interactions

The preceding response curves represented mean heart rates for all instrumented ground squirrels during social interactions. Associated with these means was a degree of variance caused by changes in motor behavior and emotionality before, during and after the encounters. Because maximum cardiac response to social interactions has been used most commonly as an indicator of socially induced stress, an attempt was made to distinguish between the motor and emotional stimuli which elicited this response.

Maximum heart rate tended to be greater the longer the duration of motor activity which accompanied combat during an interaction (Figure 13). This initially suggested that maximum response was dependent primarily upon motor activity rather than rodent emotionality. However, heart rates recorded during combat lasting only one or two seconds often approached or exceeded those obtained when combat periods were much longer. Hence, heightened emotional arousal also contributed towards cardiac acceleration in cases of combat just as with threat which involved no motor activity.

Regardless of the duration or type of encouter, heart rates among ground squirrels seldom exceeded a level of approximately 420 beats/minute. Evidence will be presented later which indicated this was some kind of physiological ceiling to cardiac acceleration regardless of stimulus intensity. Perhaps this was the reason contact-chase interactions elicited only an insignificant elevation in heart rate above that of chase, even though the duration and intensity of the former represented the sum of contact and chase interactions.

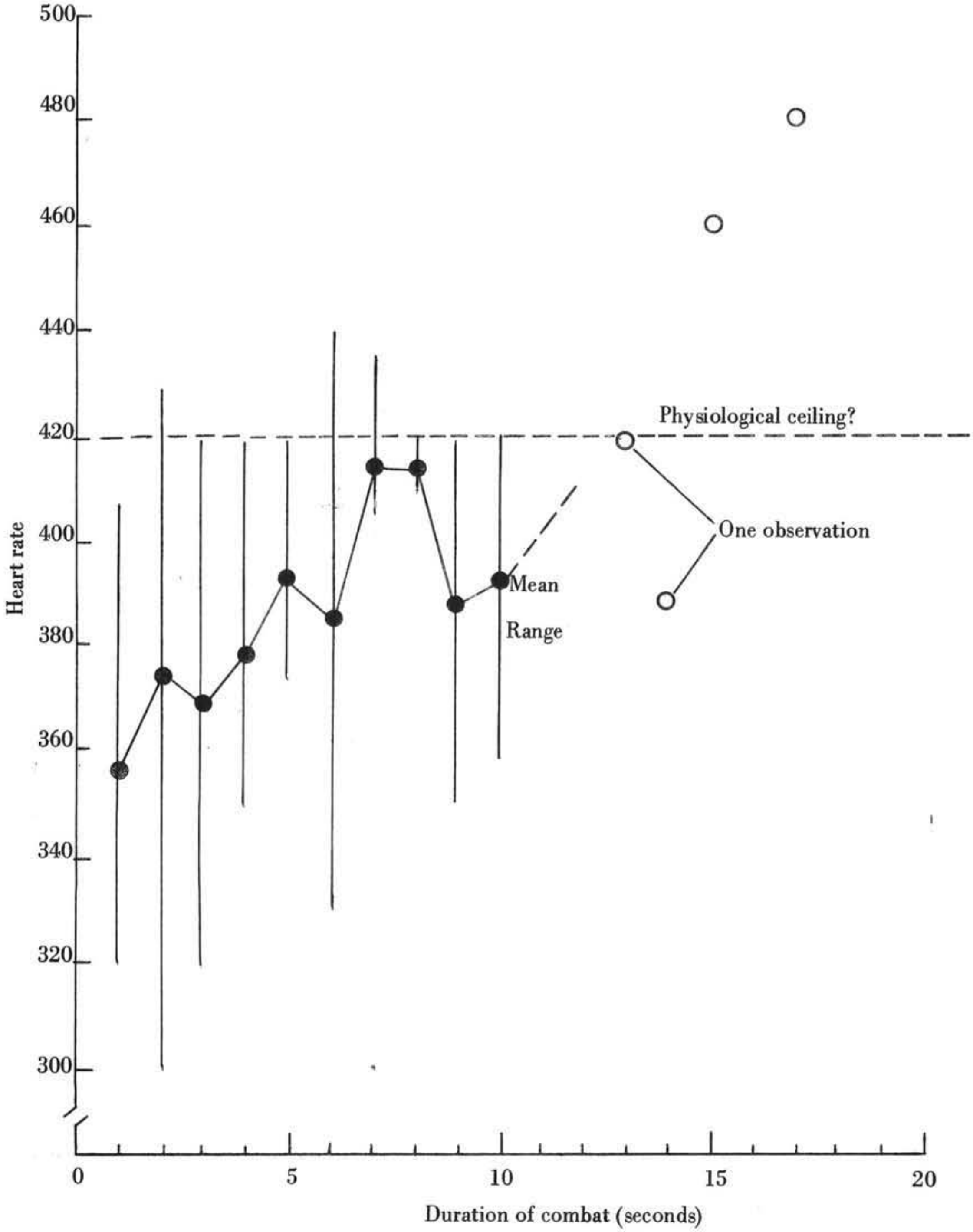

Figure 13. Relationship between maximum heart rate response and duration of combat during social interactions

The apparent cause of social interaction also affected maximum response. Generally, the heart rate of a ground squirrel was greater when the animal defended its territory rather than an individual distance (Figure 14). Similarly, the heart rate was greater when an animal encroached upon the territory rather than the individual distance of another. Although these differences were not statistically significant, similar U-shaped response patterns were evident for all forms of encounters and this indicated maximum response was at least partially a function of the above variables. Data for calling bouts and charges were excluded as results pertained only to the defense or invasion of territories.

The spatial relationship of interacting ground squirrels also affected their heart rates. Regardless of encounter type, mean maximum response was greater when an individual defended its territory against an immediate neighbor (abutting home ranges) as opposed to another resident of the study area (Figure 15). Again, data for charges and calling bouts were not included as all pertained to interactions with immediate neighbors. The above relationship was not unexpected. The further ground squirrels roamed from their territories, the more often they lost encounters (Burns, 1968). This increasing subordinace with distance from territory was manifest by characteristic motor patterns which other residents undoubtedly recognized (Ewer, 1968). As a result, defenders exhibited less emotional arousal and expended less effort when expelling such intruders in contrast to immediate neighbors.

The foregoing was true with the exception of chase interactions. In such cases, the heart rate of an animal was similar whether it defended its territory

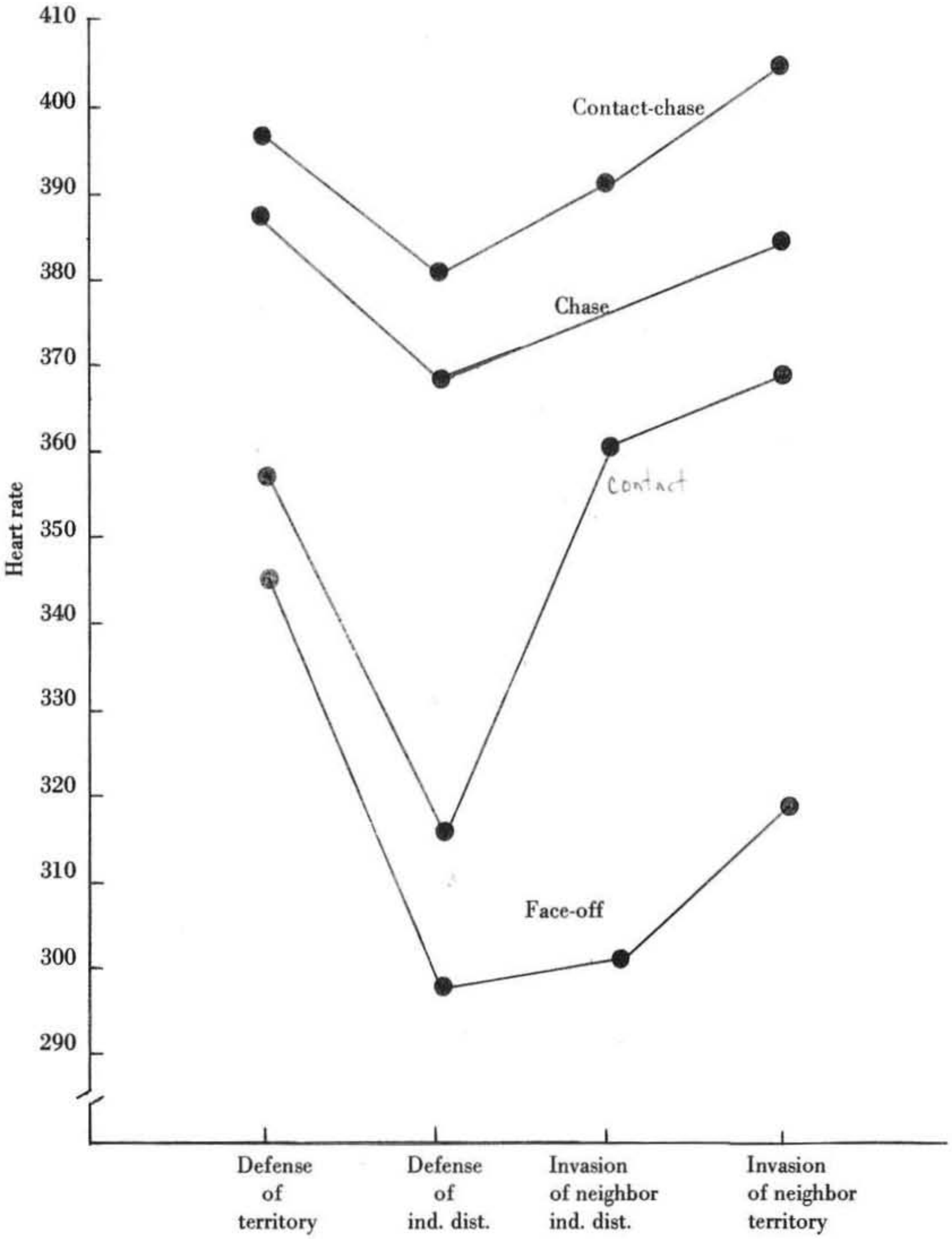

Figure 14. Effects of cause of social interaction upon heart rate

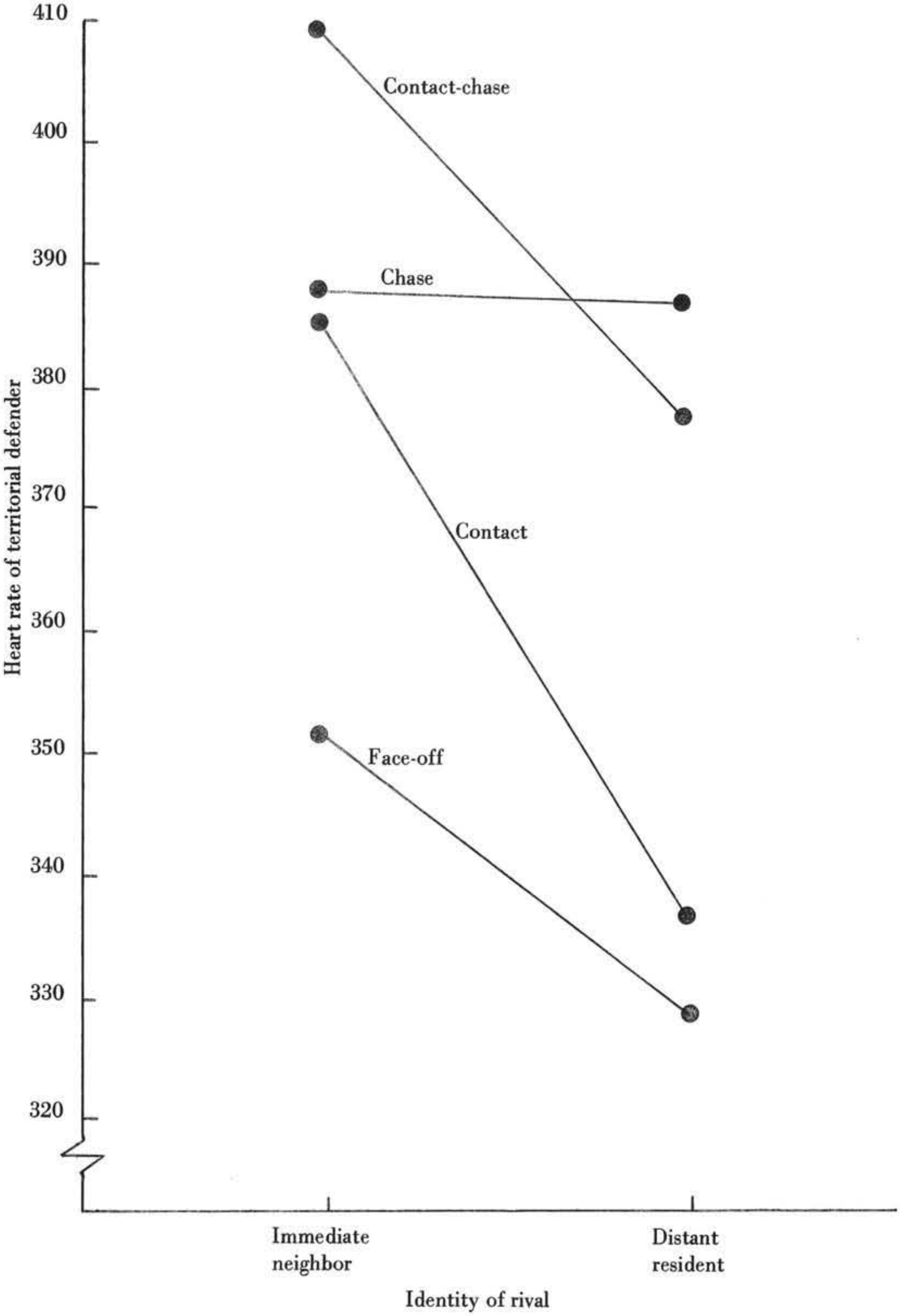

Figure 15. Effects of spatial relationship of combatants upon the heart rate of territorial ground squirrels

against a neighbor or more distant resident. This was because all intruders were chased approximately the same distance, to the edge of the defender's territory. So because physical exertion was comparable in the respective situations, so was the individual's heart rate. That this did not occur in contact-chase interactions was apparently related to the contact component prior to chase. Contact with transients was usually more brief than with immediate neighbors. The intensity of the interaction also appeared less because transients were not aggressive in unfamiliar surroundings and usually attempted escape soon after contact. As a result, the heart rate of ground squirrels during contact-chase interactions with distant residents was less than with immediate neighbors and less than in chase only situations.

The sex and age of combatants had no significant effect upon short-term cardiac responses to social interactions. Neither were there differences between initiates and recipients of aggression (Table 4) or winners and losers of the encounters (Table 5). However, the effects of motor and locomotor behavior upon heart rate during social encounters may have masked emotional contingencies. For example, initiates of charge threats had a greater heart rate than recipients. But initiates also exhibited locomotor behavior during a charge whereas recipients simply sat motionless. This added locomotor behavior unquestionably contributed towards the differential response by rivals in such situations.

Table 4. Differences between heart rates of initiates and recipients of aggression

Encounter type	Mean maximum heart rate of initiates of aggression	Mean maximum heart rate of recipients of aggression	Difference (beats/min.)	Level of confidence
Contact-chase	394	405	11	.70
Chase	383	383	0	--
Contact	346	367	21	.80
Charge	374	347	-27	.60
Face-Off	334	315	-19	.70
Calling bout	317	330	13	.70

Table 5. Effects of outcome of social interactions upon the heart rate of ground squirrels

Encounter type	Mean maximum heart rate of dominant	Mean maximum heart rate of subordinate	Difference (beats/min.)	Level of confidence
Contact-chase	396	408	12	.70
Chase	384	385	1	--
Contact	342	357	15	.70

Factors Affecting the Waning of Heart Rate Following Social Interactions

With the exception of calling bouts, all forms of social interactions among ground squirrels elicited a pronounced acceleration of heart rate which was followed by a period of slower deceleration. This latter waning response may also be used as an indicator of the severity of socially induced stress. Presumably, the lesser the rate or greater the duration of waning, the greater the stress.

As illustrated previously in Figures 11 and 12, the rate and duration of waning varied between encounter types. Differences also occurred within a specific type of encounter and these were largely contingent upon animal behavior during the waning period. For example, all forms of combat were followed by either threat interaction, motor activities or motionless behavior. If ground squirrels continued to interact or exhibited motor behavior during the waning period, their heart rates invariably waned more slowly and stabilized at higher levels than if animals remained motionless. This relationship is illustrated in detail for contact-chase interaction in Figure 16, but it also applied to all forms of combat (Table 6). Such differences did not occur during threat because ground squirrels interacted continuously and did not display motor or motionless behaviors.

During the waning period, interacting ground squirrels were immobile just as were "motionless" animals. The only difference was the display of an overt threat posture or calling by the former. Hence, differences in the waning response

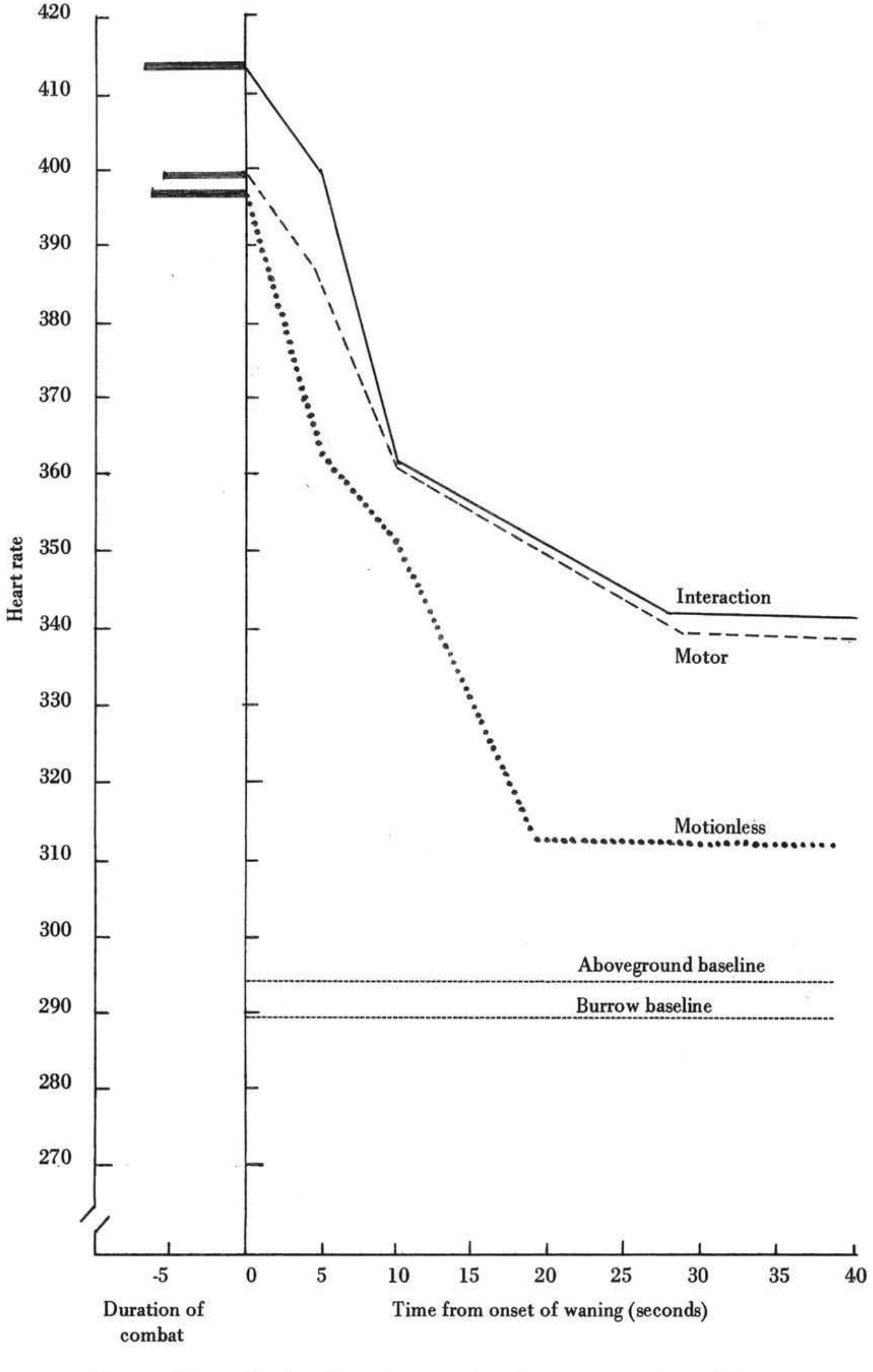

Figure 16. Effects of post-combat behavior on rate and duration of waning of heart rate

Table 6. Measures of the cardiac waning response to social interactions

Encounter type	Behavior during waning	Mean heart rate at onset of waning	Mean heart rate at stabilization	Mean duration of waning (sec)	Mean rate of waning (beats/min/sec)
Contact-chase	Interaction	413	343	27.4	2.6
	Motor	399	340	30.0	2.0
	Motionless	397	313	18.5	4.5
Contact	Interaction	406	342	34.0	1.9
	Motor	345	303	26.3	1.6
	Motionless	334	301	14.9	2.2
Chase	Interaction	390	350	12.3	3.3
	Motor	369	320	16.5	3.0
	Motionless	376	299	14.4	5.3
Charge	Interaction (only)	364	305	20.1	2.9
Face-off	Interaction (only)	329	300	11.0	2.7

may be attributed solely to differences in rodent emotionality relative to the various behaviors.

The rate of cardiac waning associated with the respective post-combat behaviors was least for contact and greatest for chase interactions (Table 6).

This was probably because ground squirrels remained within one or two feet of each other following contact and were in violation of each other's individual distance. Anxiety was undoubtedly heightened and the rate of cardiac waning slowed. In cases of threat, spacing between animals increased as did the rate of waning. Following chase, ground squirrels were separated by 10 to 20 feet and the rate of waning for any post-chase behavior was greater than for similar behaviors which followed other types of encounters.

Whether an animal won or lost an encounter, or whether it was the initiate or recipient of aggression seemed to have little effect upon the rate and duration of cardiac waning. However, the post-combat behavior of interactants did vary according to encounter outcome. Winners of encounters engaged in post-combat threat only 11 per cent of the time, but rather, they exhibited motor behavior or sat motionless 25 per cent and 64 per cent of the time, respectively. Conversely, losers seldom sat motionless (11 per cent) but interacted (44 per cent) or exhibited motor behavior (44 per cent). If combat interactions resulted in a stand-off or no decision, animals continued to threaten each other after combat in 75 per cent of such cases or sat motionless 25 per cent of the time. Because heart rate invariably waned more rapidly when individuals sat motionless, indicating little emotional arousal, dominant ground squirrels apparently experienced less stress during interactions than subordinates. This was also probably true of initiates of aggression since ground squirrels were dominant in about 90 per cent of the encounters which they initiated.

Following the waning period, the level at which heart rate stabilized was primarily dependent upon two factors: the type of post-combat behavior exhibited by a ground squirrel and the animal's spatial location on the study area. Effects of the former variable were illustrated previously in Figures 11, 12, and 16. But it was also noted that when a ground squirrel returned to the center of its territory or to its home burrow following social interactions, its heart rate waned more rapidly and stabilized at a lower level than when it did not. Later, if an animal returned to areas where it had previously experienced social conflicts, its heart rate again increased even in the absence of conspecifics. Hence, spatial factors (previously paired with combat or threat) served as conditioned stimuli and elicited marked changes in the heart rate of ground squirrels. The precise magnitude and duration of these chronic responses to social interactions are discussed in detail in a subsequent section.

Physiological Limitations of Cardiac Response to Social Interactions

In the preceding account, the magnitude and duration of cardiac response to social interactions were used as measures of anxiety and hence, of socially induced stress. Part of the increased heart rate exhibited by fighting ground squirrels was caused by motor behavior. Heightened emotionality was also indicated because an animal's heart rate frequently increased too rapidly and to a level which was not commensurate with associated physical exertion. In addition, response to these variables appeared regulated in part by physiological limitations of the heart to respond.

For example, most forms of interactions elicited a significant increase in heart rate above that of pre-encounter levels (Table 7). But contact-chase encounters produced a change of 67 beats/minute which was just 9 beats/minute greater than the change of 58 beats/minute for chase. Yet contact-chase was actually a combination of contact and chase interactions, respectively, both in duration of combat and intensity. Therefore, one might have expected an increase equal to the sum of changes associated with contact and chase, i.e., 89 beats/minute. This did not occur and so some kind of physiological factor was apparently damping cardiac acceleration at higher rates of response.

In fact, most autonomic responses, including heart rate, are governed in part by what has become known as the "law of initial value" or LIV. Originally defined by Wilder (1962), the LIV states that the magnitude of physiological response to a stimulus is related to the pre-stimulus level according to the following rule: Given a standard does of stimulus and a standard period of measurement, the response, defined as the change from initial (pre-stimulus) level, will tend to be smaller when the initial level is higher. The physiological reasons for this phenomenon have been described by Lacey (1956) and Hord, Johnson and Lubin (1964). Basically, the LIV is a product of the dual innervation of the heart. When the sympathetic branch of the autonomic nervous system is stimulated, heart rate accelerates. This acceleration is counteracted by parasympathetic influences which exert an increased braking action the greater the heart rate. Finally, a physiological ceiling may be reached where heart rate no longer increases regardless of stimulus intensity.

Table 7. Change in heart rate during social encounters as compared to pre-encounter levels

Encounter type	Mean heart rate prior to encounter	Maximum mean heart rate during combat	Increase (beats/min)	"t" and degrees of freedom	Level of confidence
Combat					
Contact-chase	330	397	67	8.675 (66 d.f.)	.9995
Chase	326	384	58	5.602 (39 d.f.)	.9995
Contact	325	356	31	2.890 (36 d.f.)	.975
Threat					
Charge	318	364	46	2.962 (14 d.f.)	.975
Face-off	310	329	19	1.536 (34 d.f.)	.80
Calling-bout	324	321	-3	-0.472 (52 d.f.)	N.S.

To determine whether the LIV operated among ground squirrels, pre-encounter (pre-stimulus level) heart rates were plotted against maximum response (stress level) for different types of combat interactions. The regression of stress levels on pre-stimulus levels was then computed with the equation $Y = a + bX$. Using this method, if the LIV holds, b is less than unity (Bridger and Reiser, 1959). Furthermore, the requirement of the LIV of "a standard dose of stimulus" was approximated by using only those encounters which had combat components of five seconds or less.

As shown in Figure 17 for contact-chase interactions, the LIV held only to a point. Bridger and Reiser referred to this point at which the regression line crosses the line of equality as the cross-over point (P). For values above P, that which Wilder (1962) termed a "paradoxical" reaction occurs, i.e., a decrease in heart rate rather than an increase when a stimulus is presented. The computed cross-over point for contact-chase interactions was 425 beats/minute, a value nearly identical to the 420 beats/minute which was the suspected physiological ceiling referred to in Figure 13. Although comparable data were lacking for other forms of combat, P in all cases was less than 500 beats/minute and this indicated maximum response to social interactions was physiologically restricted within the range of 420 to 500 beats/minute.

It should be clear then that the <u>magnitude</u> of change in heart rate from pre-stimulus to stress levels is not in itself a suitable measure of stress response. For because of the LIV, an encounter in which heart rate increased only 20 beats/minute from 400 to 420 beats/minute could nonetheless be as stressful as one effecting a rise of 75 beats/minute from 300 to 375 beats/minute. Similarly, measures of maximum response may reveal only relative differences in socially mediated stress as discussed previously for different forms of combat. The increased damping by the parasympathetic nervous system upon heart rate at higher response levels certainly must be considered in such absolute

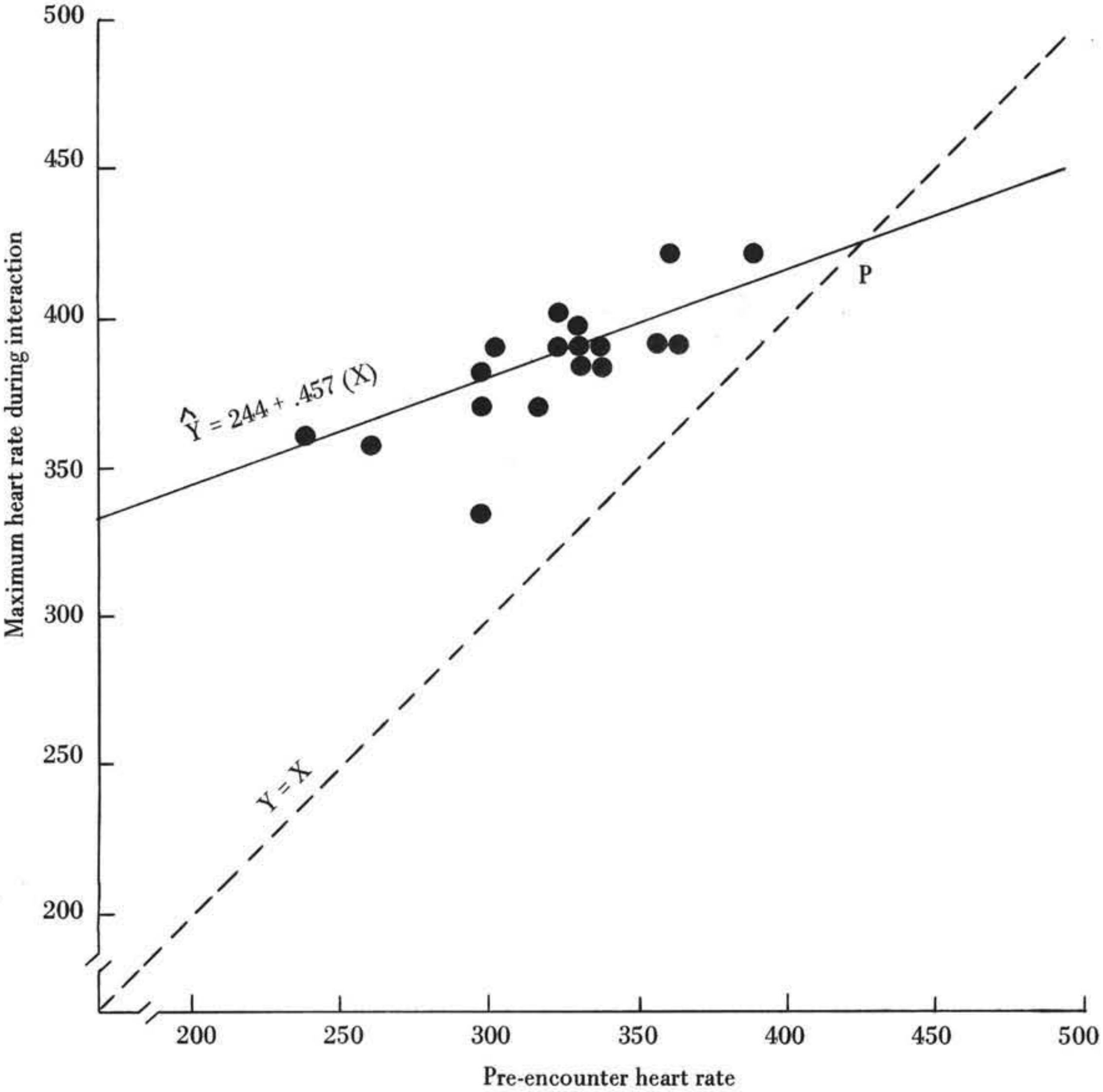

Figure 17. Relationship of pre-encounter heart rate to maximum response during contact-chase interactions

comparisons. Still, because some types of encounters elicit responses which are consistently and significantly greater than others, it follows they are the more stressful. The question which remains then is simply one of degree.

Long-term Heart Rate Response to Social Interactions

It has been shown that ground squirrels exhibited marked short-term changes in heart rate during social interactions. Some of these changes were caused by motor activities but others were indicative of heightened emotional arousal. Furthermore, this anxiety apparently persisted long after social interaction as heart rate remained elevated even after an encounter had ceased. The precise degree of this heart rate elevation was largely dependent upon an animal's location on the study area. So spatial factors, previously paired with combat and threat, acted as conditioned stimuli to elicit chronic responses to social interaction.

Therefore, the next questions asked were which spatial factors were most important in causing cardiac acceleration and to what extent were responses influenced by various degrees of crowding and an animal's sex, age, and reproductive condition? To answer these questions, data were placed into two categories: (1) Heart rate responses by ground squirrels as animals behaved aboveground alone, i.e., during non-social situations, and (2) responses as ground squirrels behaved in the presence of conspecifics, but only at those times when individuals were not interacting overtly. Data in the first category were used to determine which spatial factors were most important in eliciting changes in heart rate, and the degree these changes were influenced by a ground squirrel's sex, age, reproductive condition and relationship with neighboring animals. The second category was used to determine the effects of crowding and the mere presence of conspecifics upon the heart rate of known individuals.

Heart Rate During Non-Social Situations

Non-social situations were defined as those times when no other ground squirrels were within sight or within 40 feet of the instrumented subjects. The 40-foot limit was established when field observations indicated ground squirrels did not respond overtly or physiologically to the mere presence of other animals beyond that distance.

A recording period was begun each time an animal changed locations. Heart rate was not measured for the first 10 seconds following an individual's arrival at a new location. This procedure allowed heart rate to wane and stabilize in the event the animal was responding to antecedent locomotor behavior. Heart rate was then measured every 10 seconds by counting the number of heartbeats within a three-second interval. The sex, age, reproductive condition, overt behavior and spatial location of the instrumented ground squirrel were recorded simultaneously with each of the above measures.

Only heart rates of "motionless" animals (down on all four legs and not moving) were used to determine emotional response to spatial factors and hence, as indicators of long-term or chronic response to social interactions. In this way, the effects of motor behavior upon heart rate were not considered. A ground squirrel was considered motionless only if it had remained so for at least 10 seconds prior to the measurement of its heart rate.

Spatial factors as conditioned stimuli

At the outset of this investigation, I recognized that several spatial factors could elicit changes in the heart rate of ground squirrels. An important objective of the study was to select the one which was most important, functioned similarly for all individuals, and could be measured throughout the year. These restrictions were essential in order to determine individual and seasonal variations in cardiac response.

I had originally thought that heart rate would rise as an animal moved farther from its home burrow because the probability of social interaction should also increase accordingly. Indeed, this was generally true. However, the precise effects of "distance from home burrow" depended upon the location of the burrow within a ground squirrel's home range and its relationship to the home ranges of neighboring animals. For example, a burrow was sometimes located on the periphery of a home range. If the resident took a short excursion outside its home range but near the burrow, its heart rate was greater than if the animal was farther from the burrow but within its home range. In addition, seasonal variations in heart rate response to this variable were not measurable because adult males and some females used several different burrows during the course of the field season.

Next, I postulated heart rate would be less when an animal was within its own home range and territory as opposed to those of neighbors. Again, this was generally the case. However, ground squirrels were territorial only at certain times and some never exhibited territoriality. Furthermore, an individual's territory was overlapped by its home range and the home ranges of all animals overlapped extensively following the breakdown of territoriality. Therefore, heart rate response to these spatial variables were often confounded and could be measured only seasonally.

These disparities lead me to suspect that an animal's familiarity with certain locations was the primary cause of changes in heart rate. Accordingly, I calculated a "familiarity index" (FI) for every location visited by an animal and this was done each time a squirrel changed locations. The indices were simply percentage expressions of the total number of sightings for that individual since its emergence from hibernation which fell within a 12-foot square encompassing the animal's location. An index of "1" indicated an animal spent 5 per cent of its time at the location; "2", that it spent 10 per cent, and so on by 5 per cent increments to an index of "9" which indicated an animal spent 45 per cent of its time there. Seldom however did a ground squirrel spend 30 per cent or more of its time in such a small area. Sightings were made continuously throughout the field season and familiarity indices were updated each day to account for changes in the frequency of visits to each location. Thus, an animal's familiarity with portions of the study area was also a measurable variable throughout the year.

Figure 18 illustrates the relationship between heart rate and spatial familiarity for nine females throughout the field season. All responded to

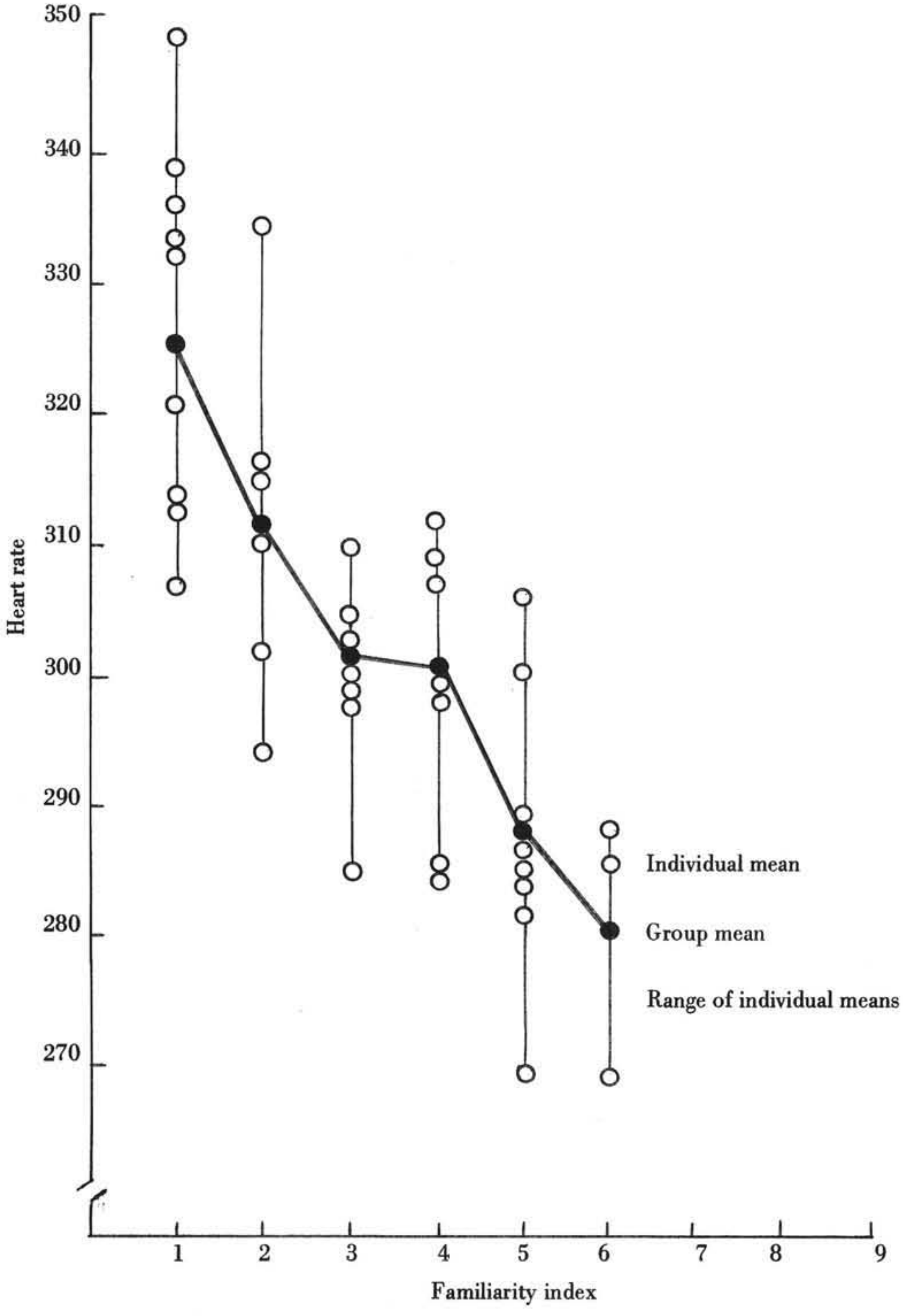

Figure 18. Relationship of heart rate and spatial familiarity for nine females throughout the field season (after Raff 1971)

increasing familiarity with a decrease in heart rate. For any individual, heart rate in areas of low familiarity (FI-1) was significantly greater than in areas of high familiarity (FI-5 or greater). Males reacted somewhat differently and are treated separately in another section.

In essence, spatial familiarity was contingent upon prior social experiences and conditioning among ground squirrels. Animals tended to visit areas which possessed "pleasant" and lacked noxious stimuli, and avoided areas with opposite qualities. In fact, spatial familiarity *per se* may simply have reflected the overt responses of animals to the probability of exposure to noxious stimuli such as attack by conspecifics or predators, and the lack of food and cover. In the current study, social interaction was undoubtedly the single most important noxious stimulus and hence, spatial familiarity was largely a product of it. For these reasons, spatial familiarity was used almost exclusively as the independent variable in determining chronic heart rate responses to social interaction.

Responses by females

Onset and establishment of territoriality

Females were non-territorial upon their emergence from hibernation although all defended an individual distance of two to five feet. Heart rate information was collected for only three females during this pre-territorial period. These data were difficult to obtain because females were bred the same day or within a few days of emergence and they became territorial shortly thereafter.

One female, No. 113, was captured and instrumented within a few hours of emergence and before she had been bred. For two days (DSE 14-15) she co-existed peacefully in a small area with several other non-territorial females. When she was aboveground alone, her heart rate increased from a mean of 278 beats/minute in areas of greatest familiarity to 310 beats/minute in those of least familiarity (Figure 19; DSE 14-15). It should be noted however that great familiarity was not attained for any area as the animal was aboveground only a short time and activities were quite dispersed. For the most part, the difference of 32 beats/minute probably reflected the animal's response to environmental novelty as she moved from one location to another. This may be likened to the increase in heart rate of laboratory rats when animals were removed from their home cages and placed into strange or novel environments (Black, Fowler and Kimbrell, 1964; Candland, Pack and Matthews, 1967; Ruff, unpublished; Snapper et al., 1965; Snowden, Bell and Henderson, 1964). To a lesser extent, the changes in heart rate may also have represented chronic responses to prior disputes over individual distances which occurred at different locations.

Several neighboring females showed signs of territoriality for the first time on DSE 17. Aggression was intense with more encounters consisting of combat at this time than during any other (Burns, 1968). Upon emerging from her burrow the morning of DSE 17, No. 113 was attacked repeatedly although she herself exhibited no aggression. Thereafter, even when aboveground alone, she appeared very anxious and her heart rate fluctuated between means of 346 to 379 beats/minute in areas of greatest and least familiarity, respectively (Figure 19;

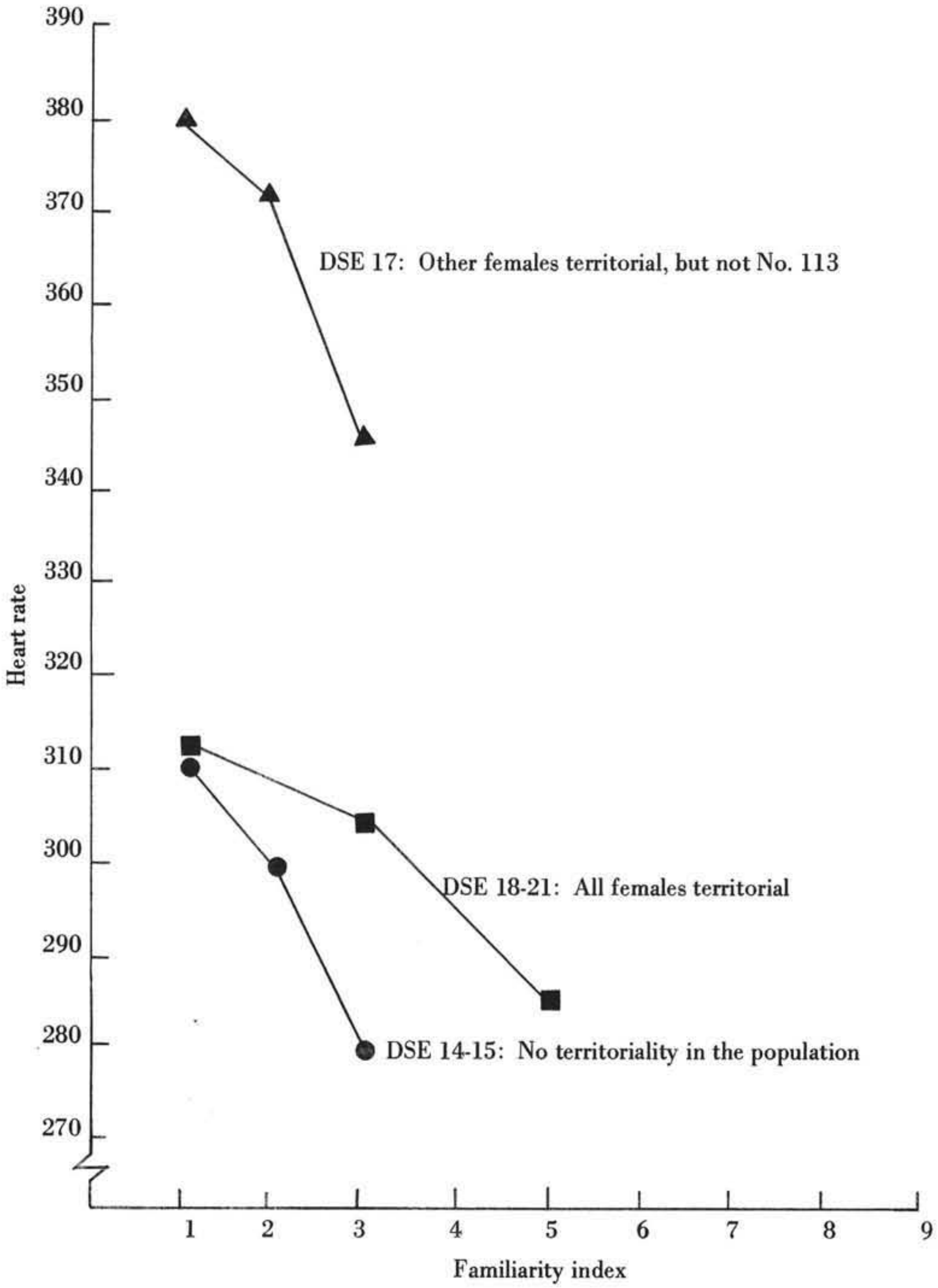

Figure 19. Changes in the heart rate of female No. 113 before, during, and after territoriality in the population

DSE 17). The difference of 33 beats/minute was nearly identical to that of DSE 14-15, but now responses were elevated an average of 70 beats/minute in all areas regardless of familiarity. This elevation suggested No. 113 anticipated attack wherever she wandered as territories were in a state of flux. Even areas of high familiarity around her home burrow were not a safe refuge. Similar accelerations in heart rate reflecting anticipation of noxious stimuli, including combat, have been reported for domestic fowl (Candland et al., 1969), laboratory rats (Stern and Word, 1962), monkeys (Banks, Miller and Ogawa, 1966; Miller and Caul, 1969) and humans (Fuhrer, 1964; Jenks and Deane, 1963; Kanfer, 1958; Lacey and Smith, 1954; Obrist, Wood and Perez-Reyes, 1965; Schachter, 1957; Zeaman, Deane and Wegner, 1954; Zeaman and Wegner, 1957).

Another female, No. 655a, was instrumented 10 days after her emergence from hibernation and at a time when other females in the vicinity had just emerged and were beginning to establish territories. Although No. 655 had been bred for some time, she previously had not displayed territoriality because the area simply lacked conspecifics with which she could interact. Unlike No. 113, she exhibited no change in heart rate with changes in spatial familiarity. Apparently, she had been aboveground long enough that responses to environmental novelty had waned. Instead, No. 655's heart rate remained elevated at approximately 310 beats/minute at all locations. This was about 25 beats/minute more than her aboveground baseline as determined a few days later when territoriality was manifest in the population. So again, a period of territorial flux was accompanied by a rise in heart rate indicating heightened anxiety.

Female No. 767 was also instrumented on the 10th day following her emergence from hibernation. But unlike either of the two previous animals, she emerged in an area isolated from other ground squirrels. Prior to and during the establishment of territories by others in the population, No. 767 had little or no social contact with other residents. Her heart rate ranged from a mean of 283 beats/minute at FI-5 to 296 beats/minute at FI-1, or a difference of just 13 beats/minute. Hence, this animal exhibited only minor changes in heart rate as she moved from one location to another, apparently because she had never been punished for such movements. The cardiac acceleration which did occur was associated largely with FI-1, areas visited only rarely, and thusly may have been the usual response to environmental novelty.

Several important conclusions were drawn on the basis of the foregoing observations. First, environmental novelty may elicit marked increases in heart rate of ground squirrels during the first few days following their emergence from hibernation. This response wanes quickly because ground squirrels generally restrict their activities to small areas. Indeed, they must within the confines of a territorial system. But if territoriality is not manifest, and if certain animals (i.e., 767) range widely, then environmental novelty may continue to elicit at least minor changes in heart rate. Second, for an animal without a territory, the period of initial onset and establishment of territories is especially stressful. And third, this stress is evident even in the absence of conspecifics and it persists long after overt social interactions. Next, an attempt was made to determine the effects which territoriality had upon the heart rate of ground squirrels.

Heart rate during territoriality

Shortly after conception and through parturition, females occupied a particular burrow and were generally intolerant of their neighbors. Home ranges were small and all or portions of these areas were defended against intruders. Once the territories were fixed, females usually did not encroach upon those of their neighbors. In fact, even home ranges seldom overlapped and except in one instance, territories were mutually exclusive units.

The effects of territoriality upon heart rate may be characterized best through a continued appraisal of responses by female No. 113. She became aggressive on DSE 18, just 2 days after being bred, and established territory in the midst of other territorial females. While she was territorial, her heart rate ranged between means of 285 and 311 beats/minute in areas of greatest and least familiarity, respectively (Figure 19; DSE 18-21). These responses were slightly greater than those before territoriality (DSE 14-15) but significantly less than when other females were just beginning to establish territories (DES 17). So, territoriality acted to reduce the magnitude of response and hence, the degree of stress which accompanied the first appearance of aggression in the population.

No. 113's heart rate was comparable to those of all other territorial females (Figure 20). For such animals, areas of least familiarity elicited

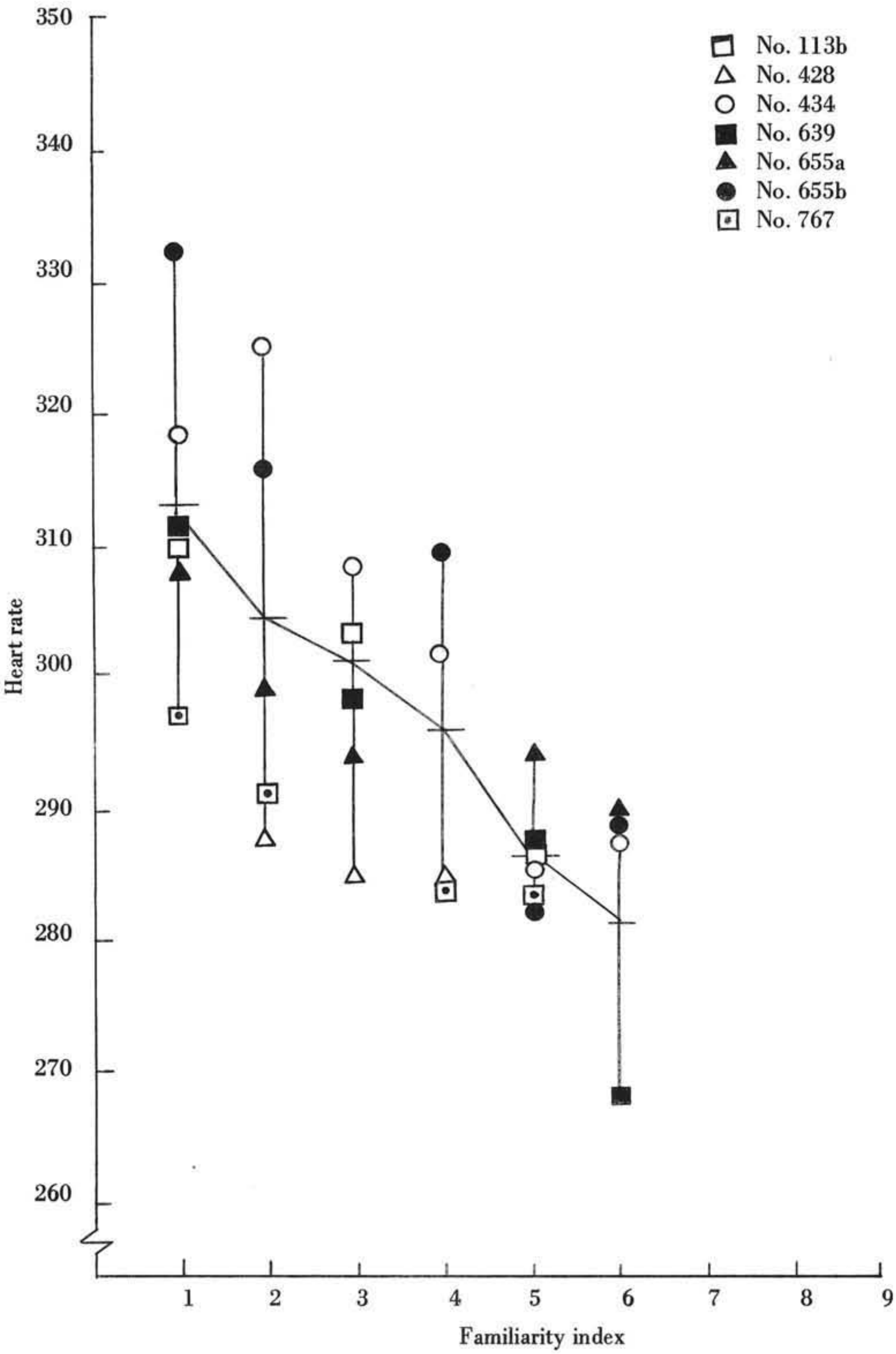

Figure 20. Mean heart rates of territorial females related to spatial familiarity

mean heart rates which ranged from 296 to 332 beats/minute. Minimum or baseline rates for each animal in areas of greatest familiarity were less variable with five of six in the range of 281 to 289 beats/minute and the other at 267 beats/minute. So most ground squirrels had comparable heart rates when they were undisturbed and in areas of great familiarity. On the other hand, individual responses to decreasing familiarity varied both in rate and magnitude. This suggested factors other than spatial familiarity *per se* also influenced cardiac response and these are discussed in a subsequent section.

Effects of breakdown of territoriality upon heart rate

Territoriality by individual females diminished rapidly following parturition. All animals continued to defend an individual distance of two to five feet but this behavior was of little consequence in curtailing animal movements. As a result, ground squirrels expanded their home ranges in all directions where they were not thwarted by females which were still territorial.

Following the breakdown of territoriality, females continued to respond to spatial familiarity but heart rates were greater than during territoriality. This relationship is illustrated in Figure 21 for three females. In areas of low familiarity (FI-1, 2), heart rates for all animals were significantly different and averaged 24 beats/minute greater after as compared to during territoriality. Areas of high to moderate familiarity (FI-3, 4, 5, 6) elicited an average increase of 12 beats/minute.

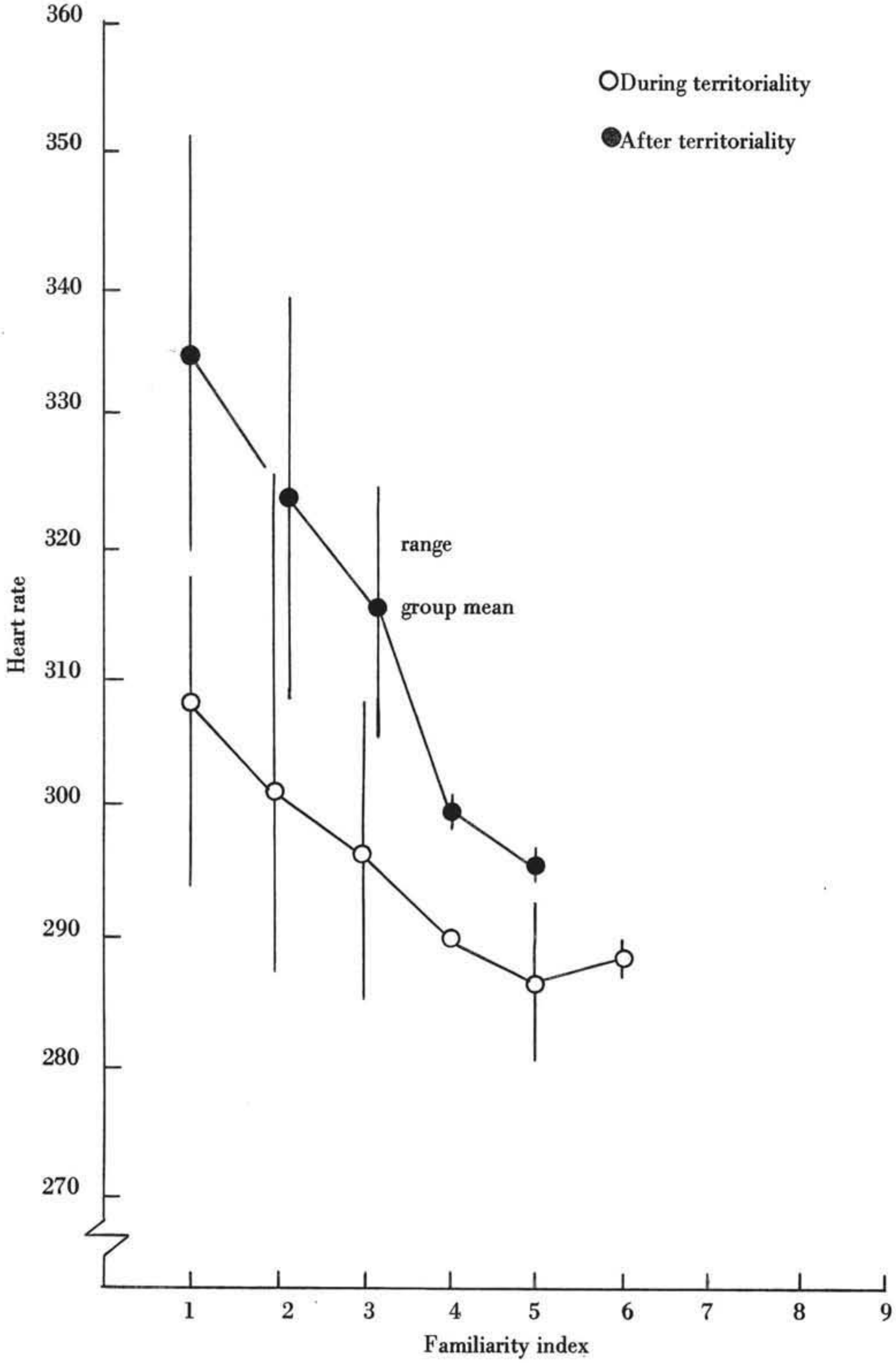

Figure 21. Differences in heart rate response to spatial familiarity during and after territoriality

Part of this increase may have resulted from changes in the size, configuration and location of an animal's home range and its relationship to those of neighboring ground squirrels during and after territoriality. Specific effects of these variables are discussed in the following section. But the anticipation of attack in areas of low familiarity may have also elicited a response. The question was then asked, if ground squirrels were not territorial, why should animals anticipate attack? This was because not all females gave birth at the same time. Parturition for the population spanned several weeks. Therefore, as animals moved into unfamiliar areas, a resident female might suddenly emerge from a burrow and defend against such encroachment. It is tenable that ground squirrels were anxious of such behavior and their heart rate increased accordingly. Similar responses were noted in domestic fowl when birds were placed into situations where they had previously experienced combat. The chickens responded with an increase in heart rate even though they could not see their combatants (Candland et al., 1969).

Hence, the interpretation that territorial behavior acted to reduce the magnitude of heart rate response to spatial factors is supported by observations following the breakdown of territoriality. It is also supported by results pertaining to an individual which loses or deserts its territory as described below.

After four days of successfully maintaining a territory, female No. 113 suddenly left her residence on DSE 21 and spent the night in another burrow 100 feet away. Upon emerging the morning of DSE 22, she became involved in a series of social encounters with a nearby territorial female. Subsequently, when No. 113 was aboveground alone, her heart rate averaged 328 beats/minute. This was greater than any of her responses while she was territorial. Later in the morning, she began to move back towards her old burrow. While she traveled through unfamiliar areas, her heart rate averaged 354 beats/minute. Upon arriving at her old residence, she was chased from the area by another territorial female and was neither seen nor trapped again. Nevertheless, No. 113's heart rate was greatly elevated when she did not occupy a territory, and approached that during the stressful period of onset and establishment of territories by other females.

Effects of size, configuration and location of home ranges upon heart rate

Although all females exhibited a decrease in heart rate with increasing spatial familiarity, the rate (slope) and magnitude of response varied between individuals during both territorial and non-territorial periods. Therefore, factors other than territoriality operated to enhance or suppress cardiac response.

One such factor was the location of a ground squirrel's home range and its spatial relationship to those of other animals. During territoriality, if a female ground squirrel was isolated or if its home range abutted or overlapped that of one conspecific, her heart rate changed only slightly as she moved from familiar to unfamiliar areas (Table 8). The magnitude of response was greater if a female's home range abutted those of several neighbors. And if an

Table 8. Effects of spatial relationship of home ranges upon the heart rate of female ground squirrels

Reproductive period	Animal number	Number of home ranges of conspecifics which abutted or overlapped the home range of an instrumented female		Increase in heart rate when instrumented female moved from familiar to unfamiliar locations (beats/minute)	
		Abutted	Overlapped		
During territoriality	767	0	0	13	12[1]
	428	1	0	2	
	655a	0	1	20	
	113b	3	0	32	38[2]
	639	4	0	44	
	434	1	2	41	56[3]
	655b	1	2	51	
	95	2	2	76	
After territoriality	428	1	3	20	
	767	1	3	34	
	113b	1	4	35	
	655a	2	7	43	
	434	2	7	66	

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[1] Mean heart rate of females whose home ranges abutted or overlapped the home range of none or only one other female.

[2] Mean heart rate of females whose home ranges abutted more than one other female.

[3] Mean heart rate of females whose home ranges both abutted and overlapped those of other females.

individual's home range both overlapped and abutted those of several neighbors, the animal exhibited the greatest increase in heart rate with decreasing spatial familiarity.

The above relationship may be explained in the following manner. Squirrels that lived in relative isolation experienced little social interaction with the onset and establishment of territoriality in the population. Therefore, as they moved from familiar to unfamiliar areas, females exhibited little anxiety apparently because they had never been threatened or punished for such movements. But if a ground squirrel's home range abutted those of several neighbors, then anxiety increased for wherever the animal moved the probability of social interaction also increased. However, because home range boundaries only abutted one another, this indicated animals recognized the domains of others and thereby assured a measure of social stability. If home ranges both abutted and overlapped those of neighbors, this suggested lack of organization in the social system and prompted heightened anxiety and greater heart rates.

The size and internal configuration of home ranges may have also influenced cardiac response to spatial familiarity. Females that occupied small home ranges responded the least to decreasing familiarity. This was not unexpected for regardless of where such females roamed within their home ranges, they were always close to areas of great familiarity. Conversely, animals with large home ranges were often far from their centers of activity and heart rate increased accordingly. Indeed, this may partially explain the higher heart rates which were recorded following the breakdown of territoriality and the subsequent expansion in the size of home ranges. Still, at least among females, it should be clear that the location, size, shape and internal configuration of an animal's home range were largely products of prior social interactions. So although preceding results have related heart rate to spatial familiarity and other spatial factors, these factors were actually conditioned stimuli which served to elicit chronic cardiac responses to social interactions.

Responses by males

Heart rate of yearling males

Yearling males usually emerged from hibernation without scrotal testes and participated little in breeding activities. Most were forced from the lawn by territorial females and, like adult males after breeding, occupied burrows away from females. But in 1969, yearling male No. 270 did emerge with scrotal testes and rather fortuitously became a resident of the lawn where I was working. He was the only yearling male during the two years of this study to do so.

On DSE 22, No. 270 moved into the burrow system which was vacated by female No. 113 on DSE 21. At the time, territorial boundaries of neighboring females were fixed and these animals were still honoring the boundaries established earlier by No. 113, and so there was a small vacuum. Otherwise, it is unlikely that the yearling male could have acquired a residence in the midst of such aggressive females.

The behavior of No. 270 was somewhat reminiscent of territorial females. For several days, he defended a small territory around his burrow against all intruders. Thereafter, he generally tolerated females, but if conflicts did arise, the yearling male was invariably dominant in the "territory" around his burrow. Still, much of the remainer of his home range was overlapped by the ranges of neighboring females (Figure 22).

During the interval DSE 22-38, which roughly coincided with the conception to parturition or strong territorial period for females, No. 270's heart rate was elevated whenever he visited those portions of his home range shared by others. It was much lower in that small area around the burrow where No. 270 was dominant and where other animals rarely intruded (Figure 23).

On DSE 38, he moved more than 100 feet to another burrow where he remained permanently. Territoriality in the population had diminished considerably and No. 270's home range was frequented by several animals. His heart rate at this time was greater for all indices of familiarity as compared to measures obtained during the interval DSE 22-38 (Figure 23). Two factors may have caused this. First, No. 270's new home range was larger than his original one. When he visited areas of low familiarity in the larger home ranges, he was farther from highly familiar areas and heart rate increased accordingly. But this alone did not explain differences in heart rate which occurred even in areas of high familiarity. Hence, heightened anxiety because of visits by surrounding squirrels probably contributed towards No. 270's cardiac acceleration in all areas of his home range.

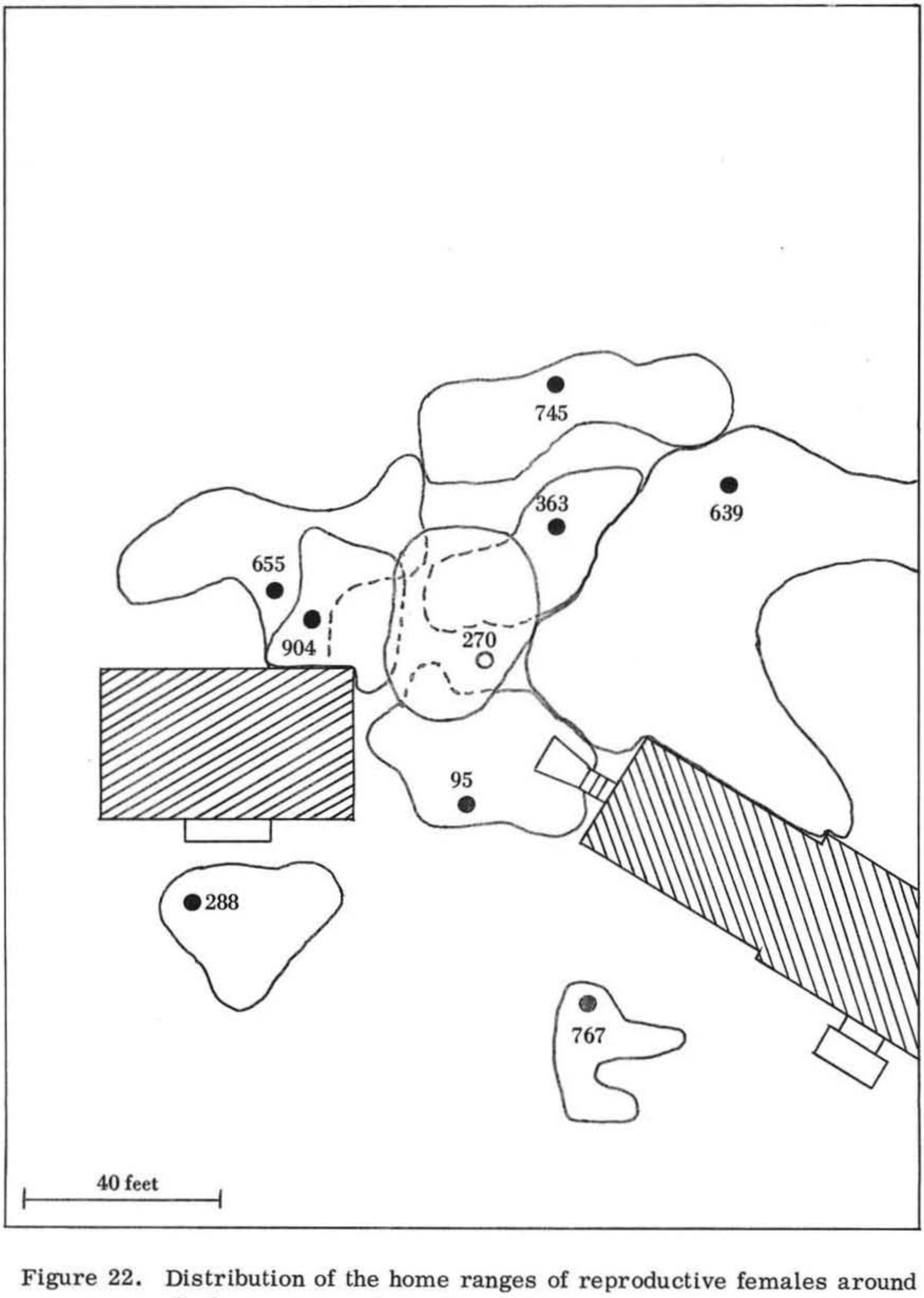

Figure 22. Distribution of the home ranges of reproductive females around the home range of yearling male No. 270 in 1969

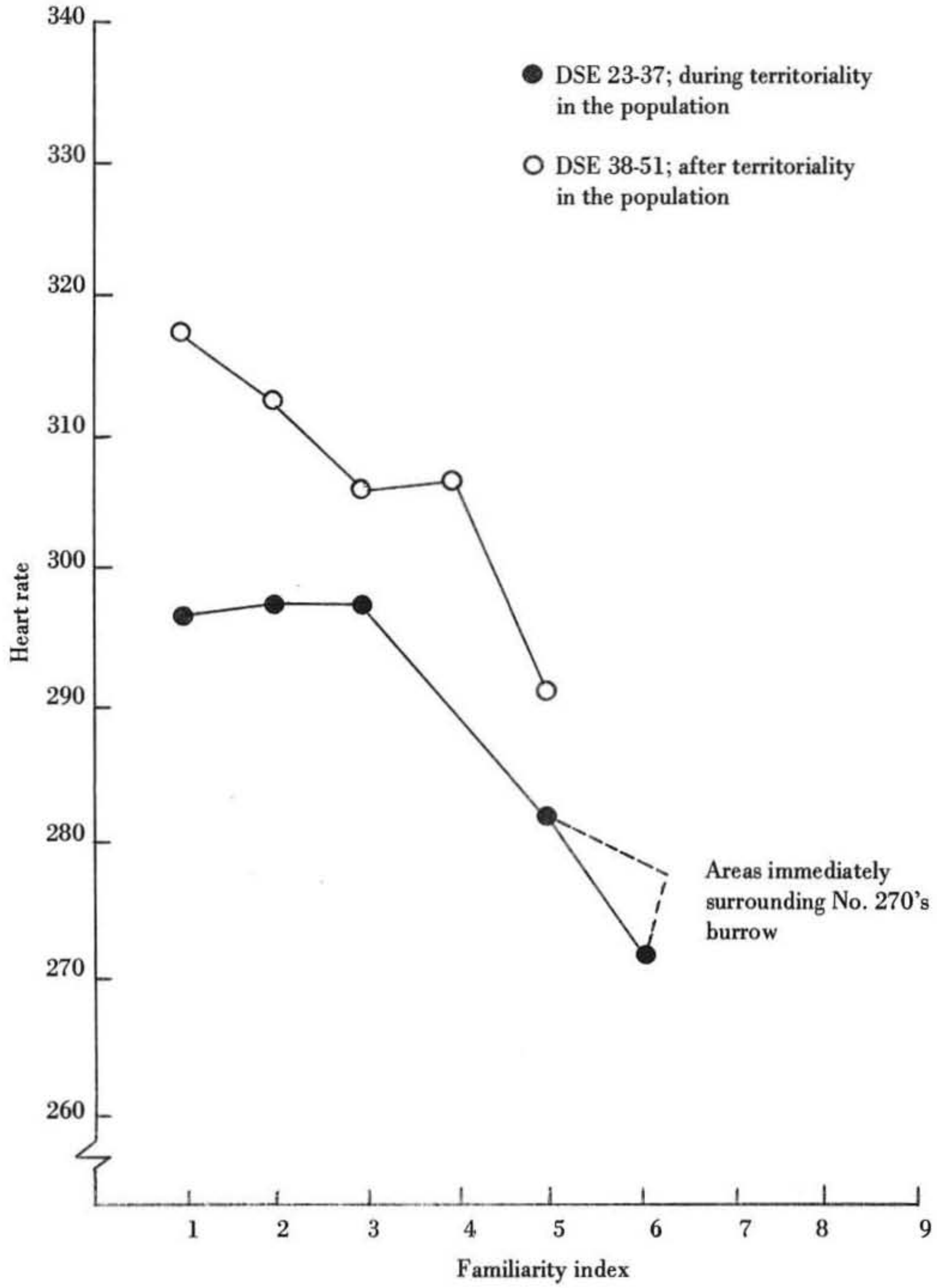

Figure 23. Mean heart rate of yearling male No. 270 related to spatial familiarity before and after territoriality

Heart rate of adult males

Adult males emerged from hibernation in breeding readiness and were aggressive towards all other males. During the breeding season, they inhabited large areas which encompassed the home ranges of several females. Following the breeding season, adult males were excluded from the lawn by territorial females and led rather uneventful lives in areas away from females until the breakdown of territoriality. Consequently, adult males were only instrumented during the relatively short breeding period.

Adult males were less attached to specific burrows than females and so seldom gained great familiarity with different locations as did females. Furthermore, the heart rate of adult males showed no functional response to spatial familiarity (Figure 24). Instead, the heart rate of both males was lowest at FI-3. This index was associated with a specific area which was visited by each male in the absence of the other. The area was located on an embankment which afforded the males a commanding view of the lawn, and more significantly, a view of the home burrows of several females which were or had recently been in estrus. The embankment was also laced with a network of burrows and so provided animals with ample escape cover. Hence, certain physical characteristics of the environment may be more important than familiarity *per se* with regard to eliciting changes in heart rate among males.

In fact, one might expect males to have higher heart rates in areas of great familiarity during the breeding season. This is because males spent much of their time near the home burrows of females, and thusly became the most familiar with such areas. But in doing so, males were vulnerable to sudden

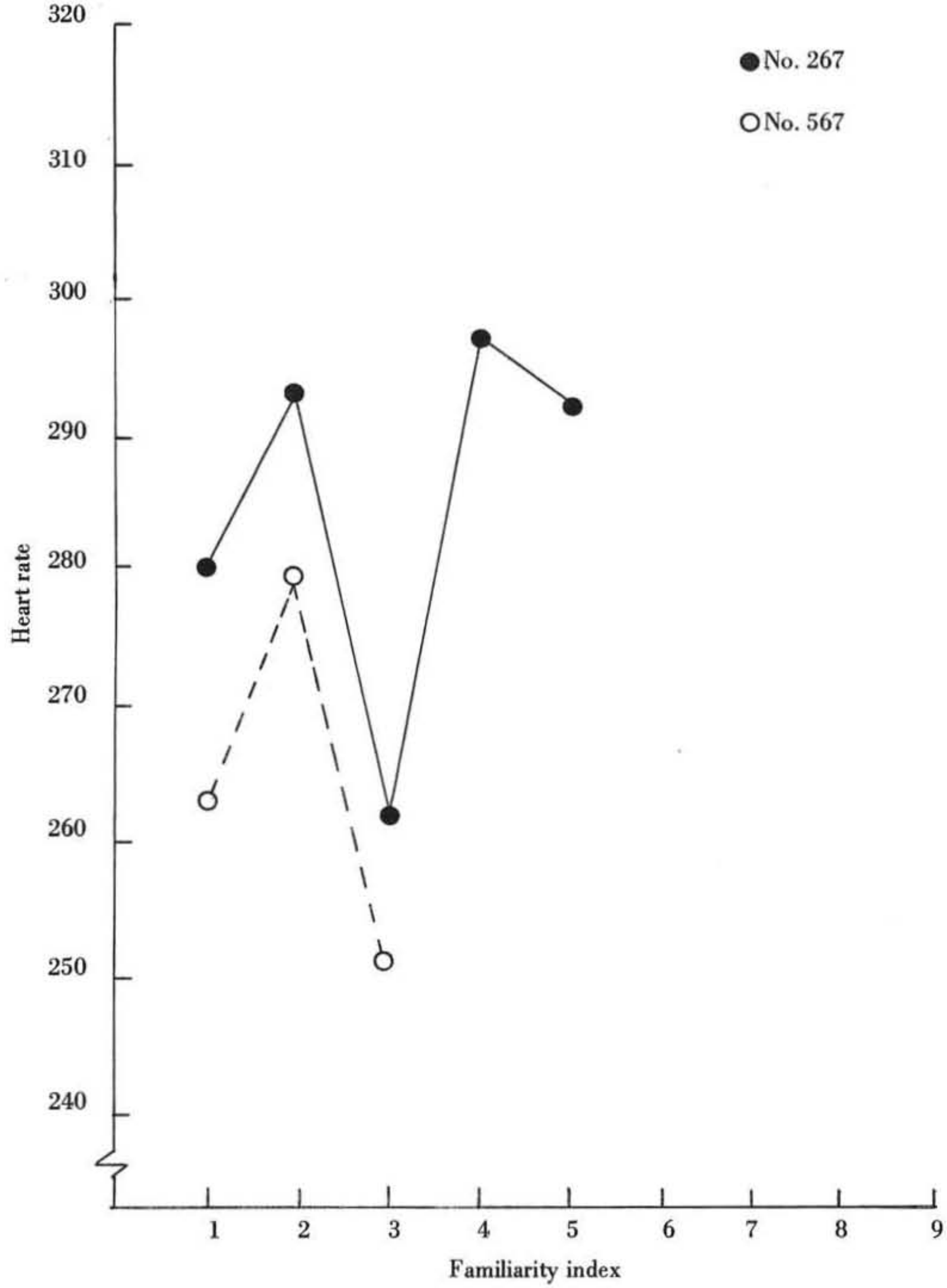

Figure 24. Heart rates of two adult males related to spatial familiarity during the breeding season

attacks by females which had been bred previously and then became territorial or by females defending an individual distance. Therefore, even when females were not aboveground, perhaps males still anticipated such attacks when within a female's home range and this was reflected in a greater heart rate.

Two additional features of the data in Figure 24 merit comment. First, the heart rates of adult males were generally less than those of females. In itself, this suggested adult males were operating under less stress than females. But because the magnitude of change in heart rate at different familiarity indices was comparable between the sexes, it was more likely that the lower heart rates of males were physiological in origin. Secondly, the heart rate of the dominant male (No. 567) was less than that of the subordinate (No. 267) for any familiarity index. If this was not simply an individual difference of a physiological nature, then perhaps dominant males did not experience the degree of stress as subordinates when moving about the study area.

Effects of Crowding Upon Heart Rate

The preceding measures of chronic responses to social interactions were taken when instrumented subjects were aboveground alone and therefore, under no immediate social stimulation. But as noted previously, the mere presence of conspecifics may also affect heart rate in some mammals. To determine if such effects operated among ground squirrels, heart rate information was gathered at times when conspecifics were present but not interacting overtly. These situations essentially represented transitory periods of crowding.

Response by females

A recording period was begun each time an instrumented animal changed locations. If during this period a neighboring animal also changed its position, a new recording period was begun. Heart rate and spatial factors were then measured in the same manner as described previously for non-social situations. In addition, records were made of (1) the number of conspecifics within 40 feet of the instrumented ground squirrel, (2) distance to nearest animal, and the (3) sex, (4) age, (5) activity, and (6) direction of movement of the nearest animal.

Figure 25 illustrates the changes in heart rate of instrumented ground squirrels when one or more conspecifics were aboveground within a radius of 40 feet, or in other words, during temporary crowding. The values represent means for all females during the designated time intervals.

There was no significant relationship between heart rate and the number of animals within 40 feet of the instrumented subject. Nor did the sex, age, activity and direction of movement of the nearest animal affect a female's heart rate. For some individuals, heart rate increased as the distance to nearest animal decreased, but this relationship was neither consistent nor significant for the population of instrumented ground squirrels. So apparently, no single agent was responsible for cardiac acceleration during crowding. Rather, all

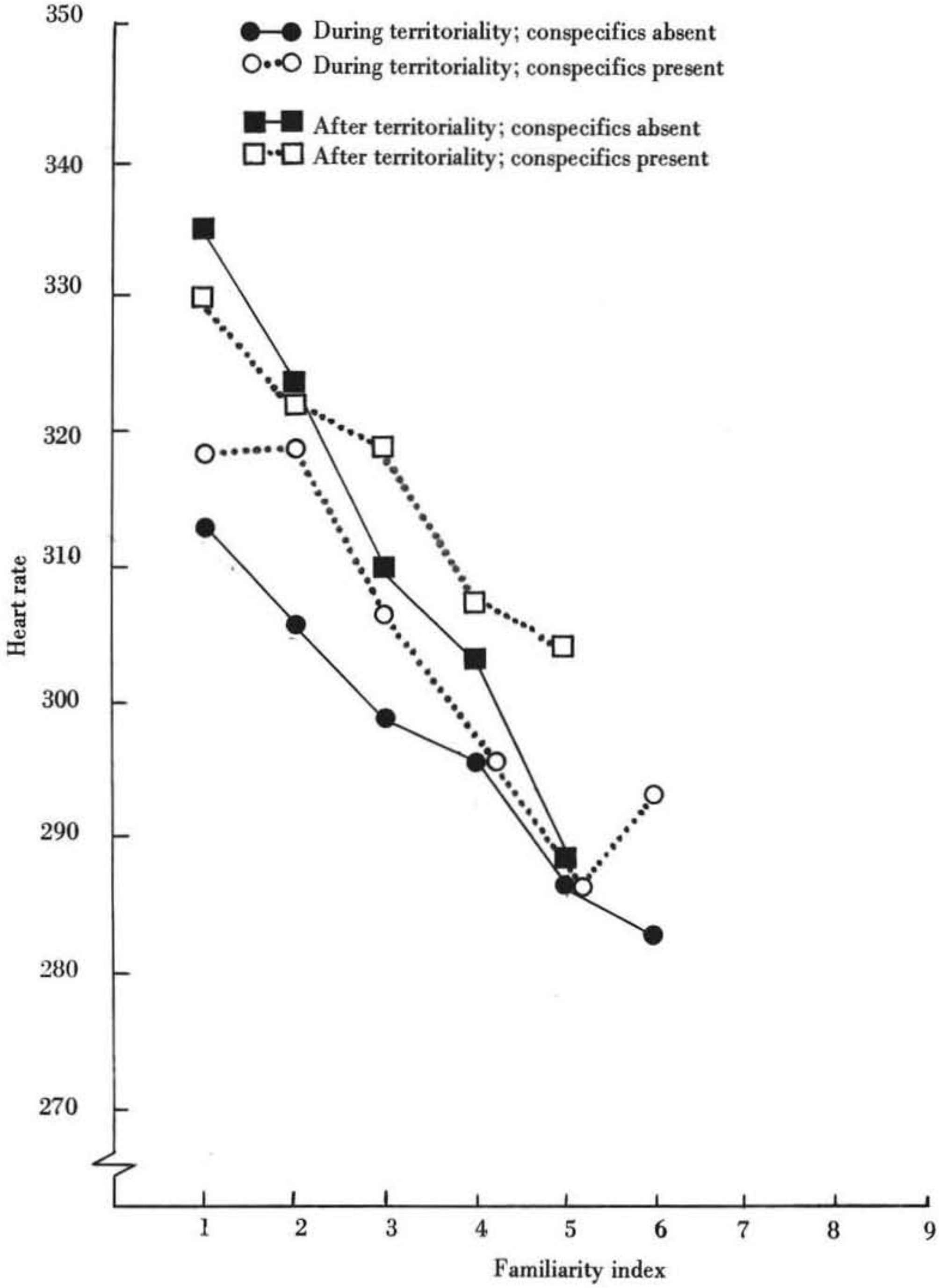

Figure 25. Effects of crowding upon the heart rate of female ground squirrels during and after territoriality

the above variables in combination tended to elevate an animal's heart rate above that during non-social situations.

This increase in heart rate during territoriality averaged 9 beats/minute in less familiar areas (FI-1, 2, 3) and just 3 beats/minute in areas of greater familiarity (FI-4, 5, 6). After the breakdown of territoriality, this relationship was nearly reversed. Females exhibited heart rates in unfamiliar areas (FI-1, 2) which averaged 3 beats/minute less when animals were crowded as compared to 9 beats/minute greater when they were in more familiar areas (FI-3, 4, 5) and crowded (Figure 25).

Although the above mean differences were not significant, several aspects of these data merit additional comment. During territoriality, one would not expect the mere presence of conspecifics to increase a ground squirrel's heart rate so long as the instrumented animal was near or within its territory (FI-4, 5, 6). Such an individual would be on familiar ground in an area seldom trespassed by neighbors. So there would be little need for the animal to exhibit heightened anxiety with crowding in these situations. But when ground squirrels ventured into less familiar areas, they usually decreased their distance to neighbors and thereby increased the probability of attack. Consequently, their heart rates increased.

After the breakdown of territoriality, animals could wander about less familiar areas without being anxious. Their comparatively lower heart rates reflected this. But when a ground squirrel was within areas of great familiarity or its prior territory, areas which it previously defended against encroachment and where its young were still found, one might expect cardiac acceleration with crowding. And indeed, this was generally the case.

Responses by males

Adult males were instrumented only during the breeding season. During this time, they responded to the mere presence of conspecifics with heart rates which averaged 12 beats/ minute greater at all locations as compared to non-social situations. The greater elevations in heart rate occurred in areas of greatest familiarity, in other words, those areas inhabited by females. Yet this was not unexpected as males should exhibit great anxiety in areas where females were aboveground and likely to attack with minimal provocation. And the sexual arousal of the males may also have contributed towards response in other areas where females were not yet territorial.

Yearling male No. 270 responded less than adult males to the mere presence of other ground squirrels. His heart rate averaged just 6 beats/ minute greater with crowding during territoriality. After the breakdown of territoriality, No. 270 moved to an area away from females. Too few observations were obtained while conspecifics were present for a critical analysis, but in general, the male responded little. So No. 270 behaved in much the same manner as females during territoriality and his heart rate was also similar. The major difference was that the yearling male's heart rate remained elevated in nearly all locations except those immediately adjacent to his burrow. The heart rate of females usually responded in a more linear fashion with

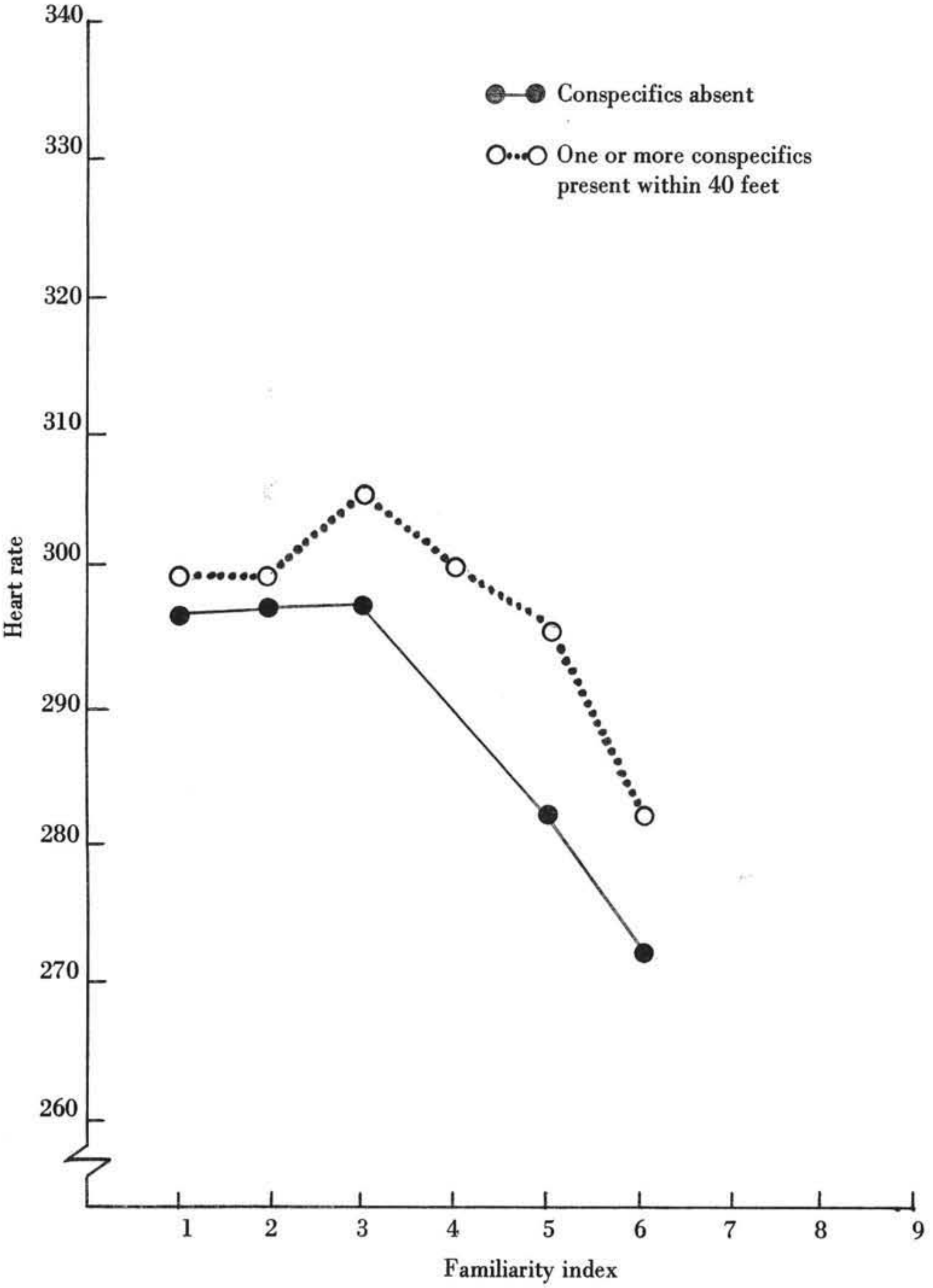

Figure 26. Effects of crowding upon the heart rate of a yearling male during territoriality

decreasing spatial familiarity. Hence, yearling males in the midst of territorial females may experience greater stress at this time than their female counterparts.

DISCUSSION

The heart rate of ground squirrels fluctuates markedly as animals behave aboveground or in their burrows. Some of the fluctuations are the result of physical exertion accompanying motor activities, but others occur in the absence of such behavior and therefore indicate heightened emotional "arousal" (Duffy, 1957) or "anxiety" (Appley and Trumbull, 1967; Levitt, 1967). It is previsely this emotionality, which may elicit widespread behavioral and physiological responses in animals and effect demographic changes in populations, to which this study is addressed.

Skaggs (1926) and Cannon (1929) long ago recognized the many bodily changes which occur in mammals in response to a wide range of social stimuli. Some changes represent short-term adaptations which serve to mobilize body reserves to meet a particular emergency and together, these have been termed the "Emergency" or "Flight or Fight Syndrome." Under repeated emergencies, humans may develop long-term adaptations which also lead to various pathologic conditions and materially reduce an individual's chances of survival. Collectively, such responses constitute the "General Adaptation Syndrome" (Selye, 1950). Strikingly, this syndrome may be elicited by an entire gamut of stimuli with little resultant differences in the form or magnitude of physiologic or pathologic responses.

Christian (1950) then extended Selye's findings to wild animals and suggested they might account for the increase and decrease in density of mammal populations. Subsequent studies with freely-growing populations of small mammals in the laboratory indicate such a phenomenon is indeed operative (reviewed by Christian, 1963). Both reproduction and mortality are apparently influenced by behavioral and psycho-physiological responses in animals which increase with crowding. Various reproductive functions are partially or completely suppressed. Population mortality may rise through several means, including dispersal. In some cases, these effects on population parameters may be commensurate with density and bring about population balance.

Similar behavioral and physiological responses occur among free-living Uinta ground squirrels. Some inhibition of reproduction results from strong territorial behavior by females which excludes some animals from the better breeding habitat on the lawn. Litter size is smaller among adult females which reside off as opposed to on the lawn (Walker, 1968). Then among those females that gain nesting sites on the study area, some fail to breed while others breed but produce no young. This also lowers productivity.

Population mortality on the other hand is largely a result of dispersal, although a few animals may die in their burrows over winter or are taken by predators. This dispersal occurs in two stages. First, a large number of juveniles born into the population each year disappear prior to hibernation. Of an annual mean of 485 young, only 140 emerge on the study area the following spring. Second, many yearlings as well as adults disperse from the area in spring shortly after their emergence from hibernation. A mean of 133 females may emerge each spring but only 95 remain through the breeding seasons.

Burns (1968) and Walker (1968) concluded most of these demographic changes are products of emotional stress among ground squirrels which increases with density, mediated by rising rates of social interaction. Results of the current telemetry study indicate this is largely the case. However, the precise effects of social interaction and animal emotionality upon population numbers is also attuned to spring climatic conditions (Walker, 1968). When early spring temperatures are mild, ground squirrels emerge from hibernation in a fairly distinct sequence; adult males emerge first followed by adult females, yearling females, and finally, by yearling males with each group preceding the other by about one week. Adult females are bred within a few days of emergence and become territorial shortly thereafter. Hence, by the time yearling females emerge, adults have already secured the prime breeding sites and exhibit much aggression.

This period of initial establishment of territories is especially stressful for those animals without a territory. Social interactions are more frequent, of greater intensity and elicit greater elevations in heart rate than at any other time. Furthermore, these interactions induce chronic stress which is manifest by cardiac acceleration at different locations even when conspecifics are absent. Therefore, it is not surprising that late-emerging yearling and adult females attempt to escape this stress and seek burrows in less crowded breeding areas. Fewer females occupy larger territories on the lawn and litter size of adult females in non-lawn areas is smaller. Hence, these two factors may lower productivity in early springs. Although litter size may be a function of poorer nutrition of females at non-lawn sites (Christian, 1959b; Lutwak-Mann, 1958), it may also be a result of social stress which animals experienced previously on the lawn before moving to non-lawn areas (Christian, 1956, 1959a).

On the other hand, the emotional stress of social interactions appears less for those females which emerge early and successfully establish themselves on the lawn. This is because they have gained "familiarity" with the area which in turn affords them a psychological edge over later-emerging intruders (Ewer, 1968). Their heart rates wane more rapidly following interactions and they also experience less chronic stress in the absence of conspecifics than their counterparts. Again, this reduced stress alone may account for the larger litter size of females on the lawn.

When spring weather is cold, emergence from hibernation is more synchronous. When this occurs, adult and yearling females tend to emerge simultaneously and compete for the better breeding sites on an equal basis. As indicated by heart rates, no animal is afforded a psychological edge by having gained familiarity with an area prior to a neighbor. Consequently, more females gain territories on the lawn than in early springs. And because litter size is also greater for lawn residents, productivity is also enhanced in late springs (Walker, 1968).

The late summer dispersal of juveniles also appears socially mediated (Burns, 1968). If results from older animals apply to juveniles, it is understandable that such dispersal should occur. The frequency and intensity of social interactions reach another peak in the summer among juveniles just as in the spring for adults. In fact, this period may be comparatively more stressful for interactions. First, during an agonistic encounter, juveniles have no avenue of escape from the stress of social interaction. Adults may simply return to their own territory or home burrow. Juveniles cannot although they may assume a subordinate position and thereby reduce the intensity and perhaps frequency of attack. Still, the duration of response is probably more than among adults. Second, even when juveniles are not involved in agonistic behavior, they are still continually crowded into a single burrow. And as shown for adults, crowding tends to elevate heart rate and so, stress. The one means juveniles have of avoiding this stress is by dispersing, and this they do.

The role of burrows in reducing both acute and chronic stress to social interaction was repeatedly observed during the current study. As Brown and Roy (1943) observed for Richardson's ground squirrel (*S. richardsonii*), Unita ground squirrels do not share their burrows with conspecifics except while rearing young or in cases of extreme danger. Therefore, animals are not exposed to social stimuli while in their burrows but may sleep, rest quietly or display various motor behaviors such as digging or grooming. With each of these activities, heart rate rises and falls in accordance with the degree of immediate physical exertion or physiological arousal resulting from prior aboveground activities. In this regard, their behavior and the nature of cardiac response is similar to that of Arctic ground squirrels (Folk, 1963, 1964a, 1964b) and several other species of small mammals (Essler and Folk, 1961, 1962;

Essler, Folk and Adamson, 1961). But the important point is that burrows offer ground squirrels a safe refuge from both environmental and social stressors as indicated by the rapid waning of heart rate when they enter their burrows. This feature of wild animal ecology, the opportunity for escape from social stressors in particular, may be an important consideration when comparing behavioral and physiological results obtained from confined as opposed to free-living animals.

For example, Candland et al. (1969) measured the heart rate of domestic chickens as individuals fought in a small arena. Dominant birds had greater heart rates than subordinates during combat. This relationship between social rank and heart rate was not evident among ground squirrels and in fact, dominants tended to have lower heart rates than subordinates. However, a significant difference between the two studies is that the chickens had no way to escape battle even if they wanted. So the continued presence of the subordinate, and the fact it was forced to fight and could not escape, may have enraged the dominant bird even more. In other words, the aggressive drive of the dominant was not dissipated by escape of the subordinate (McBride, 1964). Among wild animals, a subordinate would have escaped, thereby relieving its own anxiety as well as that of the dominant. And so it is significant that once the chickens were separated by a wire screen after combat, the heart rate of the dominant waned more rapidly than that of the subordinate. This same phenomenon occurred among ground squirrels and indicated dominants probably experienced less stress than subordinates as a result of agonistic behavior.

A most important aspect of the study with ground squirrels is that of elevated heart rates among animals even in the absence of conspecifics. This indicates such animals experience chronic stress as a result of prior social interaction at certain locations which they apparently remember. Such conditioning prompts animals to be alert and cautious much like California ground squirrels when they venture into unfamiliar areas (Fitch, 1948). But usually, ground squirrels tend to avoid places where they previously experienced social conflict and subsequently center their activities in areas of least probability of attack. This behavior is similar to that of vagrant shrews (Sorex vagrans) which also space themselves and their areas of activity as a function of their frequency of contact with stranger (Eisenberg, 1964).

Such behavior and associated cardiac response is expected among territorial species. Indeed, animals must react in this manner if the integrity of a territorial system is to be maintained. In this regard, Uinta ground squirrels fit well into the concept of "social force fields" as put forth by McBride (1964). This "force" appears to be a function of:

> a. the social position of the dominant;
> b. the social position of the subordinate;
> c. the difference in the social positions;
> d. the frequency of agonistic contact between the pair;
> e. the size of the group.
> The relative agonistic contact frequency is the operational component of the function (McBride, 1964, pp. 87-88).

Hence, through social interactions in the early stages of territoriality or social heirarchy there may be considerable fighting. This combat is gradually reduced as a consequence of learning and conditioning, and social organizations are manifest. And within such an organization, an individual's reaction to other animals or their territories may take the form of a sliding scale. As residents move outward, they meet the repelling force of neighbors and lose the familiarity of home. These forces are felt even when conspecifics are not present to thwart certain movements. Although this is probably a result of prior conditioning, other factors such as scent in the area may tend to reinforce conditioning and thusly serve to heighten anxiety and elevate heart rate.

From the foregoing, it is apparent that emotionality is dependent upon a host of factors such as early experience and learning (Goldman, 1965; Weininger, 1954), sex and reproductive condition, and perhaps, genetic make-up (Adolph, 1968). These influences are reflected in an animal's heart rate which proves to be a good measure of both short-term and long-term response to stressors (Findley and Brady, 1969). And there is evidence that changes in heart rate, which are controlled by the autonomic nervous system, may also be correlated with endocrine responses that have traditionally been used as indices of stress (Brady, 1967; Smith, 1965). And finally, as suggested by Goldstein et al. (1966), the stimuli associated with reward or punishment situations may be more decisive with respect to eliciting changes in heart rate than the actual reward or punishment. Consequently, chronic anxiety stemming from social interactions may be more important in terms of stress loads among ground squirrels than the more acute but short-lived responses associated with agonistic behaviors.

SUMMARY AND CONCLUSIONS

This study was an attempt to measure the degree of socially mediated stress which operated in a free-living population of Uinta ground squirrels in northern Utah. The study was conducted during the springs of 1968 and 1969 with known individuals in a population which had been under intensive observation since 1964. The underlying objective of this and a larger parent investigation was to determine the roles which social behavior and organization play in regulating the abundance and distribution of animals in the population.

The specific objectives of the study were:

1. To establish baseline heart rates relative to non-social behavior of ground squirrels in their burrows and aboveground.

2. To measure the effects of various forms of social interactions upon the heart rate of known individuals.

3. To determine the relationship between heart rate and the sex, age, reproductive condition, and spatial relationship of interacting individuals.

4. To determine if there are short-term or long-term differences in heart rates of ground squirrels which correlate with crowding and levels of aggression in different areas.

All ground squirrels in the population were marked as a result of continuous trapping on the study area. Repeated observations of the movements and overt behavior of animals were made to determine the size, shape, and location of home ranges and territories. Known individuals were equipped with miniaturized radio-transmitters to measure their cardiac response to social interactions ranging from mere threat to physical combat. Instrumented subjects were also monitored while deep in their burrows and as they exhibited various motor behavior aboveground. The latter measures were used to describe changes in heart rate associated with non-social behaviors and as baselines to determine the precise influence of social interactions upon heart rate.

Significant results of the investigation may be summarized as follows:

1. Marked changes in the heart rate of ground squirrels occurred as animals behaved aboveground and in their burrows. Some changes were caused by motor behavior but others were indicative of heightened emotional arousal or anxiety.

2. Animals in their burrows either slept, rested quietly while awake, or exhibited various motor behaviors. In general, heart rates appeared commensurate with the degree of physical exertion associated with the different activities.

3. But even as ground squirrels remained inactive in their burrows, either sleeping or resting, heart rate increased and decreased at different times of day. These diurnal rhythms were in phase with aboveground activity cycles and hence, were probably a product of heightened physiological arousal which accompanied antecedent aboveground behavior.

4. Upon emerging from their burrows, ground squirrels either sat motionless, exhibited various forms of motor and locomotor behavior, or

became involved in social interactions which ranged from mere threat to physical combat.

5. All types of threat elicited increases in heart rate which were significantly greater than either burrow or aboveground baselines, but only charge-threat caused a significant elevation in rate above that of antecedent behavior.

6. Calling bouts produced the least increase in heart rate, but because the duration of this type of threat was approximately three times greater than others, they were perhaps as stressful or more so.

7. Combat interactions elicited the greatest elevation in heart rate of any behavior. In all cases, responses were significantly greater than antecedent or baseline heart rates.

8. The prior spatial and social relationships of ground squirrels, duration of combat, and motivation for combat were all factors which tended to enhance or inhibit cardiac response to social interaction. Interactions with immediate neighbors elicited greater heart rates among resident animals than did similar interactions with more distant residents of the study area or transients. Heart rate also tended to be greater when ground squirrels defended their territories as opposed to an individual distance. This was also true regarding invasion of another animal's territory or individual distance by the instrumented female.

9. The duration of heart rate response to social interaction was largely dependent upon post-combat behaviors. Responses were longer and heart rate

was greater if animals continued to threaten or displayed motor behaviors following combat than if they simply sat motionless.

10. So because dominant animals nearly always sat motionless after combat, whereas subordinates continued to interact or displayed motor behaviors, dominants presumably experienced less stress than subordinates.

11. In all cases, the duration of social interaction and concomittant responses were relatively short-lived and hence, may not have been as stressful as indicated by the overt behavior of interactants.

12. Responses to agonistic encounters were regulated in part by physiological restraints on the heart which tended to dampen further cardiac acceleration the higher the pre-interaction heart rate. So the magnitude of change in heart rate caused by social encounters was not as good a measure as maximum response regarding the "stressfulness" of a situation.

13. The heart rate of female ground squirrels varied from one location to another even though animals sat perfectly motionless and no other conspecifics were aboveground to elicit differential responses. Spatial factors, previously paired with social interactions, apparently acted as conditioned stimuli to elicit these conditioned responses to social interactions and produced chronic stress.

14. In support of this, it was found that females showed little or no change in heart rate with changes in spatial location before aggression or territoriality was manifest in the population. During the initial establishment of territories, significant responses did occur and often approached those of

agonistic encounters. These decreased in magnitude during territoriality but increased again following the breakdown of territorial behavior.

15. The latter was probably a consequence of increased anticipation of attack by ground squirrels at all locations because territorial boundaries were in a state of flux and individuals could not recognize the precise domain of others. Hence, territoriality acted to reduce heart rate and hence, stress for territorial animals.

16. The spatial relationship of ground squirrels influenced their cardiac responses to changes in location. Those animals in crowded areas and having a history of much aggression responded more than isolated or uncrowded ground squirrels.

17. All else being equal or nearly so, animals with small home ranges responded less to unfamiliar areas within their range than did conspecifics with larger home ranges. This was apparently because animals in the former instance were always relatively closer to their territories or other areas of high familiarity in which they were dominant.

18. The mere presence of conspecifics tended to elevate the heart rate of females at all locations. However, the number of animals in the vicinity and their sex, age, activity and direction of movement had no significant influence as individual agents upon heart rate of ground squirrels. Rather, all these variables acting in combination served to heighten anxiety and associated heart rates.

19. Yearling males responded acutely and chronically to social interactions in the same manner as females. Yet, only the heart rate of one such animal was measured and this was done as he exhibited territoriality. Since the majority of yearling males are not territorial, these results were interpreted only in the light of the animal's overt behavior without emphasis upon sex and age.

20. Adult males also responded acutely to agonistic encounters similar to conspecifics. However, they exhibited no changes in heart rate with changes in spatial familiarity per se during the breeding season. Therefore, they did not respond chronically to social interactions. Had this been the case, such heightened anxiety as males approached females may have curtailed reproduction. So the lack of chronic response may have adaptive value.

In general, heart rate proved to be an excellent measure of both short-term and long-term responses to social interaction, and hence of stress. Still, the magnitude and duration of response depended upon such things as the sex, age, reproductive condition, history of prior experiences and conditioning, and the spatial and social relationship of individuals in the population. In this regard, increased crowding in itself and even the rate and overt intensity of social interactions may not be reliable indicators of the severity of population stress. These measures only provide information relative to short-term or acute stress. It is likely that only certain physiological parameters as heart rate can be used to reflect the important phenomenon of chronic stress.

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