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Sociality as a Life-History Tactic of Ground Squirrels

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Summary. Multi-variate analysis of life-history traits of 18 species of burrowing sciurids indicates that reproductive effort is determined by body-size energetics. Other traits, such as age at adult weight reached, age of dispersal, length of time of gestation, were significantly correlated with body size. A principal component analysis suggested that the complex of life-history traits could be reduced to four components: body size (=weight), seasonality, specific reproductive effort, and maturity. The variation in the sociality index was best explained by age of first reproduction and age at adult weight reached. Generally, species are more social when large body size combined with a relatively short growing season is associated with delayed dispersal and occurs in those species typically breeding for the first time at age two or older. Sociality in these species may have evolved through retention of daughters within the maternal home range as a means of continuing reproductive investment beyond weaning.

I. Introduction

Why animals live in groups is a fundamental problem of biology. Although advantages of group living may be tabulated, such listings do not provide a real understanding of the selective pressures leading to group formation (Rubenstein 1978). Alexander (1974) emphasized that the selective forces causing group formation were likely to be few and were primarily predation, exploitation of food, or extreme localization of some resource.

Generally it has not been possible to determine the relative importance of predation or resource exploitation as causes of group formation. Obviously, groups cannot occur unless resources are adequate. Grouping may lead to increased predation pressure (Bertram 1978) and a genetically controlled anti-predator strategy can evolve even though predation does not limit the population (Harvey and Greenwood 1978). In other words, the problem is complicated by the inability to distinguish between anti-predator behavior developing as a consequence of grouping and predation as a cause of grouping. In other words, the increased efficiency of resource exploitation could lead to a group which in turn could invite increased predation. Furthermore, groups could occur in the absence of predation or resource mechanisms. The fitness of an individual is likely to be higher if it can quickly assess the attributes of a particular habitat. A short residence may not be an adequate indicator of long-term fitness. However, the presence of other individuals of that species could indicate that the habitat is suitable and might continue

to be so in the future. Individuals might aggregate because conspecifics are a reliable statistical sampling of habitat suitability. This model assumes that resource competition is not significant, but resource competition and/or predation could subsequently develop. Resource competition might occur only under high population densities, but predation might occur at all densities.

The problem is further complicated by the broad, general use of group. Group is broadly defined as a "set of organisms, belonging to the same species, that remain together for a period of time while interacting with one another to a distinctly greater degree than with other conspecific organisms" (Wilson 1975:585). The great diversity of group function suggests that such a broad definition may obscure the relative selective pressures leading to the formation of a group as part of the life-history tactic of a particular species. Although models describe the role of predation in group formation (e.g., Treisman 1975) or the combined action of predation and resource competition (Rubenstein 1978), these models do not incorporate group formation into the life-history tactics of a species. The consideration of group formation as a life-history tactic incorporates the study of groups more fully into population ecology and suggests mechanisms by which groups are formed.

The purpose of this paper is to examine the role of sociality as a life-history tactic of several genera of the North American Marmotini (*Cynomys*, *Marmota*, *Spermophilus*), typical ground squirrels (Moore 1959). The similarities in the biology of these species reduce or eliminate confounding factors prevalent when species of widely different life histories are compared. All of these species are diurnal, burrowing and characterized by an annual cycle in which reproduction and fattening occur during the homeothermic phase and hibernation or greatly decreased activity occurs during the heterothermic phase (Morrison and Galster 1975). Among these species grouping ranges from solitary dwellers to those forming multi-harem colonies; that is, from those which do not demonstrate sociality to those which do. Sociality is defined as the state of group formation when members of a population of differing sex and age structure share the same space; i.e., have markedly overlapping home ranges, communicate with one another, and whose social interactions include cohesive behaviors.

II. Methods

Life-history traits were obtained for 18 species (Table 1). For five species data were sufficient to treat different geographical populations as separate samples. For all other species, data were combined to provide a mean species estimate. Data were insufficient to include

Table 1. Life history traits of ground squirrels. G=gestation, L=lactation, A=adult, J=juvenile, Y=yearling, T=total. AD=age of dispersal, AAW=age adult weight reached, AFR=age of first reproduction

	Mean body mass (grams)				Mean litter Size	Length of time		Maturity traits			Length of seasons (months)		
	Adult		Juvenile			G	L	AD	AAW	AFR	A	J	T
	Minimum	Hibernation	Weaning	Hibernation									
<i>Spermophilus tridecemlineatus</i>	♂	135	♂	240	8.4	27	31	J	Y	Y	4.5	4.5	7.5
	♀	113	♀	235									
<i>tereticaudus</i>	♂	145	♂	200	6.5	30	30	J	Y	Y	9.0	5.5	9.0
	♀	100	♀	185									
<i>lateralis</i>	♂	155	♂	240	5.2	27	42	J	Y	Y	6.0	4.0	7.0
	♀	130	♀	230									
<i>townsendii</i>	♀	155	♀	230	9.3	24	31	J	Y	Y	4.5	2.0	4.5
<i>beldingi</i>	♂	220	♂	360	6.4	24	26	J	Y	Y	3.0	2.0	4.0
	♀	218	♀	330									
<i>elegans</i>	♂	266	♂	400	6.0	25	31	J	Y	Y	4.5	3.0	5.5
	♀	203	♀	345									
<i>richardsonii</i>	♂	260	♂	350	7.0	25	30	J	Y	Y	4.5	4.5	6.0
	♀	225	♀	300									
<i>armatus</i>	♂	333	♂	596	5.5	24	21	J	Y	Y	3.5	2.5	4.5
	♀	266	♀	440									
<i>franklinii</i> (1)	♂	410	♂	700	6.8	28	31	J	Y	Y	4.0	2.5	5.0
	♀	380	♀	550									
(2)	♂	360	♂	550	9.5	28	31	J	Y	Y	4.5	3.25	5.0
♀	280	♀	430										
<i>columbianus</i>	♂	492	♂	710	4.7	26	28	Y	2	2	2.5	2.25	3.0
	♀	270	♀	390									
<i>beecheyi</i> (1)	♂	650	♂	800	6.25	28	52	J	Y	Y	7.0	8.0	12.0
	♀	500	♀	625									
(2)	♂	600	♂	800	6.1	28	52	J	Y	Y	6.5	8.0	12.0
	♀	420	♀	675									
(3)	♀	500	♀	680	7.0	28	52	J	Y	Y	7.5	8.5	12.0
<i>parryii</i>	♂	700	♂	1,025	6.7	25	28	J	Y	Y	4.5	3.0	5.0
	♀	635	♀	874									
<i>Cynomys leucurus</i> (1)	♂	680	♂	1,500	5.6	30	38	J	Y	Y	4.5	4.0	6.5
	♀	500	♀	1,000									
(2)	♂	800	♂	1,400	5.6	30	31	J	Y	Y	4.5	4.0	6.5
♀	650	♀	1,100										
<i>ludovicianus</i> (1)	♂	600	♂	850	4.6	32	46	Y	Y	2	12.0	8.0	12.0
	♀	500	♀	700									
(2)	♂	600	♂	1,100	4.8	32	46	Y	Y	2	12.0	8.0	12.0
♀	550	♀	1,050										
<i>gunnisoni</i>	♂	720	♂	1,050	4.6	30	35	J	Y	Y	4.5	2.75	5.5
	♀	600	♀	920									
<i>Marmota olympus</i>	♂	1,900	♂	4,200	4.0	30	30	2	3	3	3.5	2.0	4.5
	♀	1,400	♀	3,200									
<i>flaviventris</i>	♂	3,600	♂	4,980	4.2	30	25	Y	3	2	4.5	2.5	5.0
	♀	2,560	♀	3,880									
<i>monax</i> (1)	♂	3,100	♂	5,100	3.6	31	44	J	2	Y	7.0	5.0	8.5
	♀	3,080	♀	4,800									
(2)	♀	2,600	♀	3,900	4.6	31	44	J	2	Y	7.0	5.0	8.5

Sociality Index	Habitat	References
2	Areas of low herbaceous vegetation, fields	Bridgwater 1966, Evans 1951, Foster 1934, Hohn & Marshall 1966, McCarley 1966, Rongstad 1965, Wade 1927
2	Open lawn-like areas with annual grasses and forbs	Drabek 1973, Dunford 1977a, Neal 1965a, b, c Reynolds and Turkowski 1972
1	Rocky meadows, open woodlands	Blake 1972, Cameron 1967, Jameson & Mead 1964, McKeever 1964, Skryja & Clark 1970, Tevis 1955
2	Desert grassland and shrubs	Alcorn 1940
2	Steppe or shrub-steppe	Maxwell and Morton 1975, McKeever 1963, Morton 1975, Morton and Gallup 1975, Morton, Maxwell and Wade 1974, Morton and Tung 1971, Turner 1972
2	Short-grass prairie	Clark 1970a, b, Clark & Denniston 1970
2	Continuous grassy areas, pasture or cropland	Michener 1974, Michener 1977a, Michener 1977b, Michener and Michener 1973, Nellis 1969, Quanstrom 1971, Sheppard 1972, Yeaton 1972
2	Lawn, mixed shrub-grass meadows	Balph and Stokes 1963, Knopf and Balph 1977, Slade and Balph 1974
1	Woodland, field ecotones Grass and forbs	Lyon 1932, Murie 1973, Sowls 1948
1		Iverson and Turner 1972, Turner, Iverson and Severson 1976
4	Grassy meadows, small openings in forested areas	Betts 1976, Kivett, Murie and Steiner 1976, Manville 1959, Michener 1977b, Murie and Harris 1978, Shaw 1925, 1926, Turner 1972
2	Open grassland	Edge 1931, 1934, Evans and Holdenreid 1943, Storer, Evans and Palmer 1944
2	Farm land with herbaceous plants	Tomich 1962
2	Pastures	Fitch 1948
3	Grassy slopes, drained areas	Carl 1971, Galster and Morrison 1975, Kiell and Millar 1978, Mayer 1953, Mayer and Roche 1954, Watton and Keenleyside 1974
3	Grassy areas, medium to tall grasses	Bakko and Brown 1967, Stockard 1929, 1930
3		Tileston and Lechleitner 1966
5	Gentle slopes with short grass and some forbs, overgrazed pasture	Anthony and Foreman 1951, King 1955, Koford 1958, Smith 1958
5		Tileston and Lechleitner 1966
3	Grass, forb, and shrub meadow	Fitzgerald and Lechleitner 1974, Longhurst 1944
4	Subalpine to alpine meadows and talus slopes	Barash 1973
4	Rocky meadows, talus slopes adjoining meadows	Armitage 1974, 1975, Armitage and Downhower 1974, Armitage, Downhower and Svendsen 1976, Svendsen 1974
1	Woodland-meadow edge	Anthony 1962, Bronson 1964, deVos and Gillespie 1960, Snyder 1962, Snyder and Christian 1960, Snyder, Davis and Christian 1961
1		Grizzell 1955, Hoyt and Hoyt 1950

population parameters, such as the intrinsic rate of population growth (r_m), in the analysis. Because body weights of these species are determined by when in the annual cycles the weights are taken, mean weights vary considerably depending on the relative proportions of late summer or early summer animals in the sample. Therefore, all weights were standardized to two points in the annual cycle, minimum weight and weight at time of entering hibernation (maximum weight).

Several indices were calculated from the life-history data. Reproductive index (RI) is the weight of one young at weaning divided by the minimum weight of an adult female. RI is a measure of the relative effort of a female to produce one young. Weaning weight was used rather than birth weight because weaning weight is a better estimate of the total reproductive effort of a herbivorous mammal. Also, birth weights for most species are lacking or are too few to form an adequate sample. Reproductive effort (RE) is the mean litter size times juvenile weight at weaning. RE is an index of the total resources committed to reproduction. RE could be expressed in energetic terms by using growth efficiencies and mass-to-energy conversion values for mammalian tissue (Kilgore and Armitage 1978), but such conversions would merely change the numbers and would not affect the analysis. Specific reproductive effort (SRE) is RE divided by the minimum weight of an adult female and represents the total resources allocated to reproduction in proportion to adult size. SRE also may be calculated as $RI \times \text{mean litter size}$. Both RE and SRE were divided by direct care (gestation + lactation) as a measure of reproductive effort per day and represent rates of reproductive effort. The rate values were highly correlated with their respective measures of reproductive effort ($r > 0.96$). Subsequent multivariate analysis revealed that statistical models using rates of reproductive effort explained less of the variation in life-history traits than RE and SRE. Although the rates were included in the statistical analyses, they were eliminated from the results.

Squirrel species were placed into one of five categories of sociality. Group 1 includes those species that are essentially solitary. Group 2 consists of species that aggregate (form colonies) in favorable habitat, but all members of the colony live individually. In group 3, a male defends a set of females within this territory, but the females live individually. A harem, in which females share burrows, is associated with a territorial male in Group 4. Group 5 consists of species that live in multi-harem colonies. This sociality index is admittedly a first approximation, but the data available do not permit a more refined index.

The life-history traits were subjected to a principal components analysis; RE, SRE, and sociality were analyzed by stepwise regression (Cooley and Lohnes 1971). The four components extracted from the correlation matrix were rotated orthogonally using the varimax method. Only components with an eigenvalue > 1.0 were retained in the model. In the stepwise regression analyses, only those variables with an $F > 4.0$ to enter the model were included. Plots of the independent variables against the residuals were examined for systematic trends. Only three trends warranting transformations of any independent variable were found. These transformations were used in the analyses, but because they proved not to enter the models, they are not presented in the results. All multivariate analyses were performed using the BMDP programs (Dixon 1975). All other statistics followed standard procedures (Sokal and Rohlf 1969).

III. Results and Discussion

1. Patterns of Correlation

There are many significant correlations among the life-history traits (Table 2). For example, minimum weight of females is correlated with nine of the life-history traits of which five are other weight factors or weight was used in their calculations. The traits correlated with hibernation weight are identical to those correlated with minimum weight. This pattern is not surprising because minimum weight and hibernation weight of females are highly correlated. This correlation suggests that all

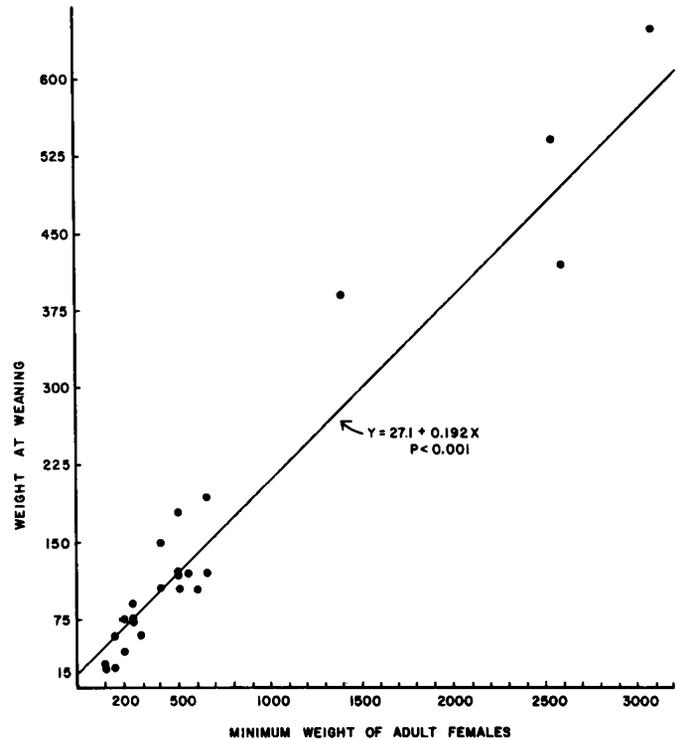


Fig. 1. Weight at weaning (in g) vs minimum weight of adult females (in g)

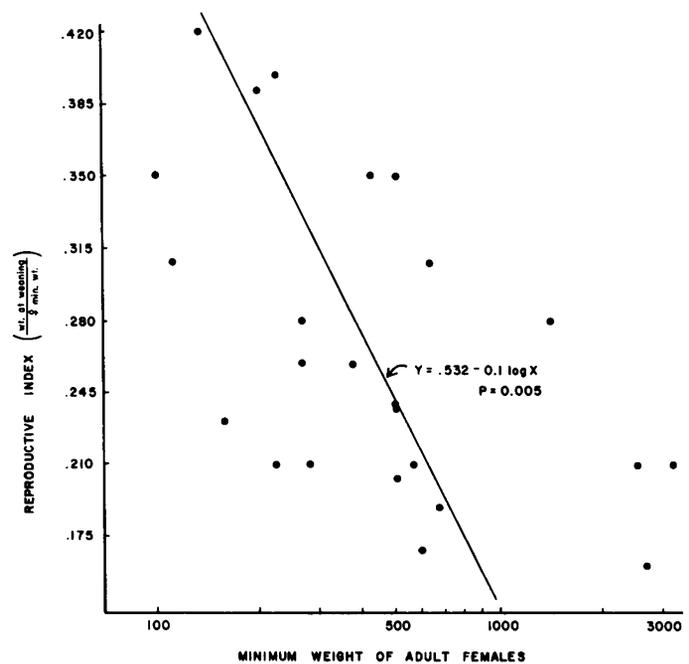


Fig. 2. Reproductive index vs minimum weight of adult females (in g)

of these species gain weight in proportion to their body size and lose it in like proportion during hibernation.

Weight at weaning is directly related to body size (Fig. 1). This relationship is not surprising; larger females produce larger young and litter weight in mammals is directly related to body weight (Blueweiss et al. 1978; Western 1979). By contrast, reproductive index (RI) is negatively correlated with female minimum weight. Larger females produce relatively smaller young (Fig. 2).

Table 2. Correlation matrix of life history traits. Only r values > 0.3 were entered in the table. $N = 24$, $r_{0.05} = 0.404$, $r_{0.01} = 0.515$

	Min. weight ♀♀	Hib. weight ♀♀	Wean. weight	Gest.	Lact.	Age adult weight	Age first repro.	Mean litter size	Repro. index	Repro. effort	Specif. repro. effort	Total active season	Adult active season	Juv. active season	Age of disp.
Minimum weight of adult ♀♀	1.000														
Hibernation weight of adult ♀♀	0.985	1.000													
Weight at weaning	0.974	0.981	1.000												
Period of gestation	0.564	0.587	0.539	1.000											
Period of lactation				0.526	1.000										
Age adult weight reached	0.801	0.861	0.849	0.408		1.000									
Age of first reproduction		0.346	0.326	0.404		0.605	1.000								
Mean litter size	-0.580	-0.609	-0.599	-0.556		-0.512	-0.496	1.000							
Reproductive index	-0.444	-0.410	-0.312	-0.458					1.000						
Reproductive effort	0.943	0.941	0.973	0.507		0.811		-0.497		1.000					
Specific reproductive effort	-0.629	-0.631	-0.551	-0.655		-0.479	-0.427	0.700	0.800	-0.467	1.000				
Total active season				0.455	0.879							1.000			
Adult active season				0.506	0.671							0.851	1.000		
Juvenile active season				0.412	0.865							0.985	0.824	1.000	
Age of dispersal	0.543	0.605	0.564	0.613	0.321	0.638	0.730	-0.670	-0.373	0.489	-0.673				1.000
Sociality index				0.378			0.757	-0.430			-0.371				0.484
Direct care				0.690	0.979						-0.321	0.858	0.694	0.836	0.422

There is a theoretical alternative which none of these species adopted. On a fixed resource budget females could produce more smaller young, rather than fewer larger young, but the size of young seems determined by adult body size rather than by other possible life-history strategies. Weaning weight is directly correlated with gestation (Table 2), but not with lactation. Minimum weight of females also is correlated with gestation, but not with lactation. This pattern suggests that larger females have longer periods of gestation to produce larger young, but that the period of lactation is determined by some other factor.

Lactation is highly correlated and gestation slightly correlated with measures of seasonal activity and direct care. Lactation and direct care are most highly correlated with total active season. Direct care can be estimated from the length of the active season (Fig. 3). Female body size is not correlated with either direct care or any of the measures of seasonal activity. This pattern of correlation suggests that gestation is determined primarily by body size with some modification related to active season whereas lactation is determined by selective factors related to the length of the active season.

Other patterns of correlation could be described at some length. For example, sociality index is not correlated with any measures of body size or active season, but is most highly correlated with age of first reproduction. By contrast, age of dispersal is correlated with weight measures, gestation, age of first reproduction, mean litter size, RE, and SRE. Mean litter size also is correlated with body size, gestation, age of first reproduction, RE, and SRE. Thus, we note many inter-correlations in the correlation matrix which suggests that only a few factors may be involved.

2. Principal Components Analysis

Four principal components explained 89% of the variance among the life-history traits. Component axis I has high loadings

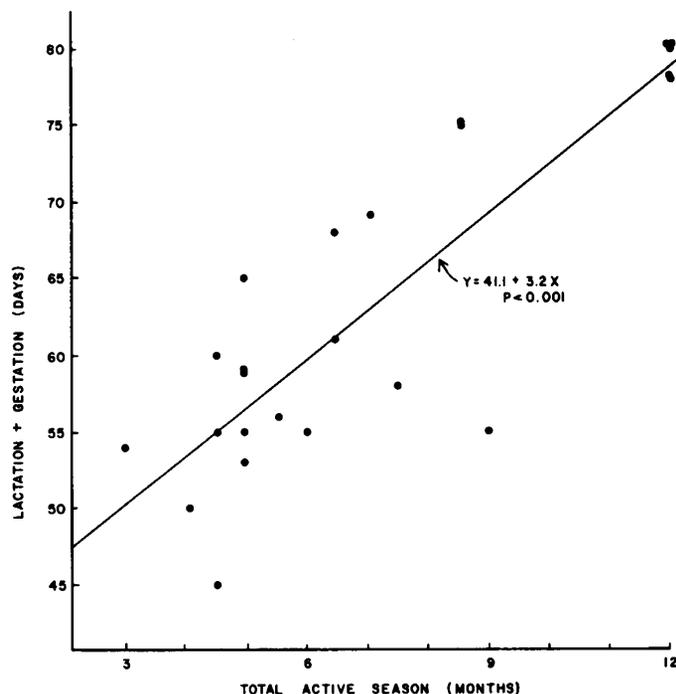


Fig 3. Direct care (lactation+gestation) vs total active season (the total time the species is homeothermal)

for RE, weaning weight, minimum and hibernation weight of females, and age of adult weight (Table 3). All of these variables are measures of or related to measures of body size. Squirrels scoring high on this component are large at weaning, take longer to reach adult weight, and have large reproductive efforts. This

Table 3. Sorted rotated factor loadings from a principal components analysis of the life history traits of 24 populations representing 18 species of ground squirrels. Only loadings $> \pm 0.5$ are included

Life History Traits	I	II	III	IV
Reproductive effort	0.971			
Weaning weight	0.964			
Hibernation weight (females)	0.929			
Minimum weight (females)	0.922			
Age adult weight reached	0.846			
Total active season		0.981		
Juvenile active season		0.970		
Direct care		0.899		
Adult active season		0.874		
Length of gestation		0.525		
Reproductive index			0.916	
Specific reproductive effort			0.852	
Age of first reproduction				0.923
Sociality index				0.888
Age of dispersal				0.650
Litter size				-0.546
VP	6.11	3.96	3.06	2.91
Variance explained	34%	22%	17%	16.2%

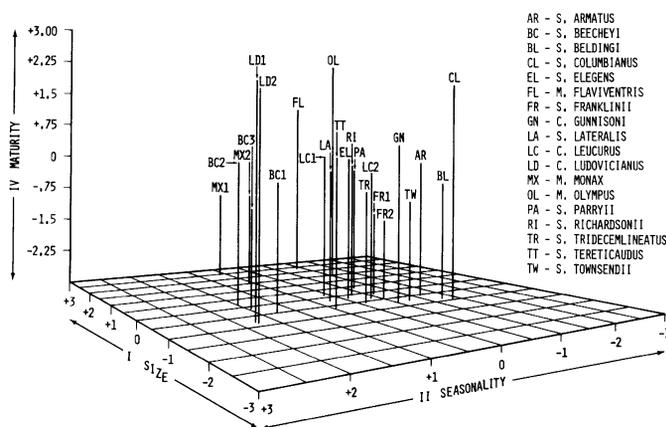


Fig. 4. Three dimensional representation of the position of the 24 squirrel populations representing 18 species on principal components axes I (size), II (seasonality) and IV (maturity). The number following the species abbreviation identifies the population from Table 1

component is interpreted as a general body size (= body weight) factor.

Component axis II has large positive loadings for the three measures of length of activity and direct care. Squirrel populations loading high on this axis have long active seasons and long periods of direct care. This component is interpreted as a seasonality factor. The length of direct maternal care is proportional to the length of the active season.

Reproductive index (RI) and specific reproductive effort (SRE) have high positive loadings on component axis III. Squirrels loading high on this axis have high SRE and high RI. Component III is interpreted as the SRE factor.

The variables age of first reproduction, sociality index, and age of dispersal have high positive loadings on component axis IV. The species loading high on this axis disperse and reproduce for the first time at ages > 1 year and are more social. This component is interpreted as the maturity factor in which life-history traits related to delayed maturity are coupled with sociality.

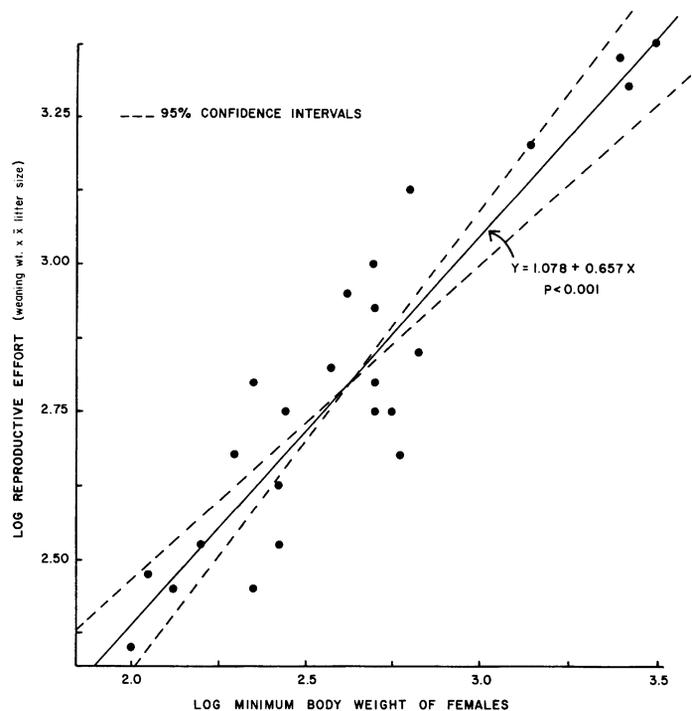


Fig. 5. Reproductive effort as a function of the minimum weight (in g) of adult females. 95% confidence limits are for the regression coefficient

The 24 ground squirrel populations were projected on three principal component axes (Fig. 4). Several patterns are evident in the clustering. All species projecting high into the space of axis IV are highly social and mature as two or three year olds. These species either are relatively large (score high on axis I) with a short active season (score low on axis II), or are medium-sized with a very short active season. *C. ludovicianus*, stands apart from the others by having a long active season (score highest of all species on axis II). *M. monax* stands apart as the only species scoring high on axis I that does not score high on axis IV; it has a long active season (high positive score on axis II). All other species form a large cluster of small to medium sized animals with moderate to long seasonality and early maturity (score low on axis IV) which is coupled with low sociality.

In summary, the complex of life-history traits of these three genera of ground squirrels can be reduced to four components: body size (measured as body weight), seasonality, SRE, and age of maturity.

3. Analysis of Reproductive Effort (RE)

Variation in RE is an important factor in theories of selection strategies (e.g., r and K) which try to explain life-history tactics (Stearns 1976). The correlation matrix revealed very high correlations between RE and several measures of body weight. Based on the correlation coefficients, body weight of adult females ranks as a potentially strong predictor of RE. Therefore, RE was plotted against the minimum adult female weight (Fig. 5). The value of $b=0.75$ for the metabolism:weight curve of mammals (Wilkie 1977) falls within the 95% confidence limits of the RE:W slope. Interestingly, Reinking et al. (1977) calculated $b=0.69$ for the M:W curve of a group of sciurids. The striking similarity between the M:W and RE:W curves suggests that

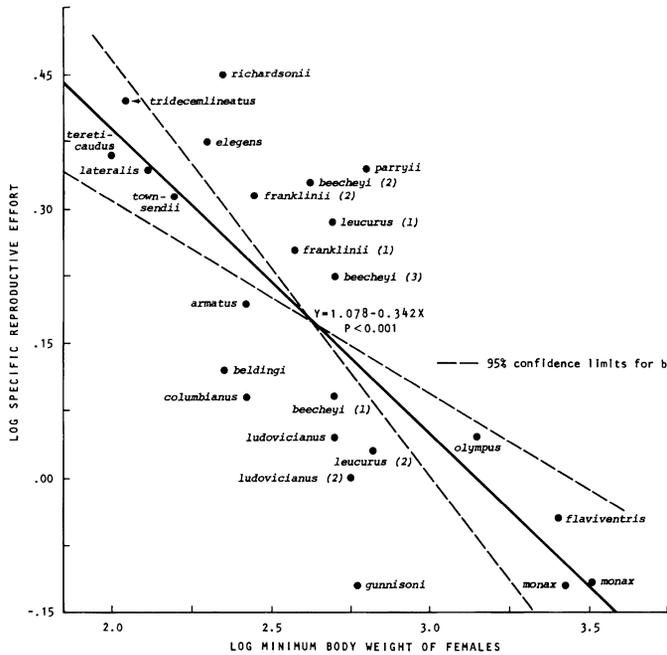


Fig. 6. Specific reproductive effort as a function of the minimum weight (in g) of adult females. The number following a species name refers to the population in Table 1

reproductive effort is a direct consequence of the animal's body-size energetics.

The stepwise regression analysis substantiated the significance of body size as an explanation for the variability in RE. Two variables entered the model, minimum weight of adult females (MWF) and reproductive index (RI). The coefficient of determination, multiple R^2 , was 0.908 which means that 90.8% of the variation in RE can be accounted for by the two independent variables in the following linear regression equation:

$$RE = 55.4 + 0.75 (MWF) + 1283.9 (RI).$$

Hibernation weight of adult females did not enter the model because it did not have a sufficiently high partial correlation with residual RE to enter the model. Also, weaning weight, litter size, and SRE were held out of the model because they are used in the calculation of RE. Although RI is not correlated with RE (Table 2), one might argue that it should be held out of the model because the weight of a young is used in its calculation. If this argument is accepted, age adult weight is reached (AAW) enters the model with a multiple R^2 of 0.898:

$$RE = 189.3 + 0.61 (MWF) + 161.2 (AAW).$$

An 8-step model was developed in which length of adult season, length of juvenile season, age of dispersal, and sociality index entered the model. However, multiple R^2 increased only to 0.927; thus very little additional variance was explained by the additional four life-history traits. In all the models developed MWF alone explained at least 88.9% of the variation, thus testifying to the overwhelming significance of body size as a determinant of RE.

4. Analysis of Specific Reproductive Effort (SRE)

Because SRE is negatively correlated with measures of body size, SRE was plotted against minimum weight of adult females (Fig. 6). Again, the slope of the SRE:W curve is strongly reminis-

cent of the specific M:W curve of mammals. The value of $b = -0.25$ for the M/W:W curve of mammals falls within the 95% confidence limits of the $b = -0.342$ for the SRE:W curve.

RI, litter size, and RE were not used in the stepwise regression model because they were used to calculate SRE. Four variables, age of dispersal (AD), MWF, weaning weight (WW), and sociality (S) entered the model. Multiple R^2 was 0.74; therefore, 74% of the variation in SRE was explained. The model produced the following linear equation:

$$SRE = 2.26 - 0.002 MWF + 0.007 WW - 0.362 AD - 0.170 S.$$

5. Analysis of Sociality

Interestingly, the index of sociality was not significant as a predictor of RE and was the last variable to enter the model predicting SRE. The lack of any correlation between sociality and reproductive effort or measures of body size supports the suggestion that reproductive effort may be determined by size-related energetics and that sociality is a consequence of some other factor or factors. Sociality was most highly correlated with age of first reproduction (AFR), age of dispersal (AD), and litter size (LS) (Table 2).

The stepwise regression analysis substantiated the importance of AFR as a predictor of sociality, but AD and LS did not enter the model. AFR is highly correlated with AD and LS; their partial correlations with sociality index were insignificant. However, after the effects of AFR were removed from the model, age of adult weight (AAW) entered. The multiple R^2 was 0.686; therefore, the two variable model explained 68.6% of the variation in sociality. The variation in sociality is described by the following linear regression equation:

$$Sociality = 0.619 + 2.314 AFR - 0.843 AAW.$$

At first consideration the relationship between AAW and sociality seems inconsistent as it suggests that the later the age of adult weight the less social are the animals. However, this relationship explains some of the variance after the variance explained by AFR was removed. *M. monax*, a large, solitary sciurid with a long active season, heavily weights this variable.

6. Body-Size Energetics and Reproductive Effort

The similarities in the slopes of the regression equations describing the relationship between measures of reproductive effort and body size and metabolism and body size suggest that reproductive effort is determined by weight-specific energetics. Large ground squirrels with small litter sizes could not produce more large young. Presumably they could produce many small young, but selection would operate against such a strategy. The young must become large as soon as possible. Small young would be unlikely to survive hibernation (Armitage et al. 1976). Age at first reproduction is important in determining population growth rate (Cole 1954). Thus, the production of large young is more likely because they will mature at an earlier age and are most likely to survive hibernation. Reaching maturity at an early age is especially important for species that breed only once a year. Even if small-sized young could survive hibernation, they would reproduce at least one year later than the large-sized young and would be at considerable disadvantage in competition for food, burrows, etc.

The production of fewer, larger young probably is not possible. The weight of neonates is tightly scaled to body size (Leutenegger 1976; Blueweiss et al. 1978; Western 1979). A young that is too large would not pass through the birth canal and would

cause its and its mother's deaths. Furthermore, there would be no selection for such large size unless the age of first reproduction could be shortened by a year or some other competitive advantage would accrue (e.g., competition for burrows). It would be impossible for a large sciurid such as *M. flaviventris* to produce a young of sufficient size that it could reproduce as a yearling. Females of this species weigh about 2 kg in the spring of their first reproductive year. If we use the largest growth rate of 22 gm/day for young recorded by Armitage et al. (1976), the young could add about 2.2 kg during a 100 day active season. If 40% of the weight is lost during hibernation, a young must weigh about 1 kg (about 35 times present birth weight) at birth in order to be reproductively mature the next year. Producing slightly larger young may be counter-productive. The energy required to produce larger young would come from producing one less young. For *M. flaviventris*, reducing mean litter size by one could result in individual neonates being about one-third larger. Such a large increase in size probably exceeds the design constraints of the female reproductive system. Unless the competitive advantage accruing to slightly larger young exceeded that of producing an additional young, selection would favor the larger litter size.

Probably the size of young is maximal within the design limits of body size. Males of these species are on the average 1.25 (range: 1.006 to 1.82) times the size of females, but there is no relationship between the relative size of the adult male and the minimum weight of adult females ($r = -0.024$, $p > 0.1$). Sexual dimorphism of this sort is generally attributed to sexual selection in which males compete for females (Ralls 1977). In *S. armatus* (Balph and Stokes 1963), *S. beldingi* (Sherman 1977), *S. richardsonii* (Michener 1979), *S. tridecemlineatus* (McCarley 1966), and *S. tereticaudus* (Dunford 1977a) males are aggressive and may fight during the breeding season, but they do not defend females and may become subordinate to females following breeding. Males of *S. beecheyi* (Owings et al. 1977) defend their home ranges and are associated with several females. Because female dispersion is clumped, males probably defend females as a resource. Male defence of harems occurs in *S. parryii* (Carl 1971), *S. columbianus* (Kivett et al. 1976), *C. ludovicianus* (King 1955), *M. flaviventris* (Armitage 1974) and *M. olympus* (Barash 1973). This trend toward an increased role for dominant males in the social system (Michener 1973a) is not associated with increased sexual dimorphism. The sexual dimorphism may be more closely related to nutrient storage for use during the spring breeding system. Males emerge from hibernation before females (Davis 1976), and in at least some species, the males rely on their fat to carry them through breeding (Shaw 1926; Snyder et al. 1961; Morton 1975). However, the females may also rely on their fat during breeding (Shaw 1926; Galster and Morrison 1975; Morton 1975; Andersen et al. 1976). The larger males have larger absolute amounts of fat which correlates with their earlier emergence and longer period of activity when food is scarce. More female than male *S. beldingi* perished during a spring snowstorm and fewer females reproduced than in normal years (Morton and Sherman 1978). Therefore, selection pressures should produce a body size that will maximize the probability of survival of each sex consistent with its energy needs during hibernation and breeding. Because each sex is favored by large size and because reproductive effort is limited by weight-specific energetics, energy cannot be allocated from females to males to drive a sexual selection system. Counter-selection favoring large females maintains an equilibrium such that sexual dimorphism is small and determined by energetic needs during spring emergence and mating.

Furthermore, the relationship between RE and SRE with body size and the similarities of the regression coefficients relating body size to reproductive effort and metabolism suggests that these species maximize reproductive effort. Why should reproductive effort be maximal? I suggest that survival is highly probabilistic. Maximizing RE maximizes the probability of producing surviving offspring. Therefore, females should reproduce as often as possible within the constraints of producing offspring with the highest fitness while not sacrificing her own fitness. Interestingly, some female *S. tridecemlineatus* produce a second litter in Texas (McCarley 1966); *M. flaviventris* in Colorado produce twice as many young at 2,900 m as those at 3,400 m. Females at 3,400 m rarely reproduce in successive years whereas females at 2,900 m commonly breed every year. Population densities at 3,400 m are as high or higher as those at 2,900 m (Johns and Armitage 1979). If one assumes that intraspecific competition is more intense than interspecific, the production of more young either by second litters or annual breeding can be viewed as maximizing the probability of producing reproductive descendants. In those species with delayed maturity, reproductive maturity generally occurs before adult size is reached. This emphasis on reproducing as early as possible also suggests these species maximize RE. The ability to realize maximum RE may be determined proximally by nutrition. The production of young by high altitude *M. flaviventris* females is correlated with available energy (Andersen et al. 1976). *S. tereticaudus* produce more young in years of good nutrition when winter rains produce more green vegetation (Reynolds and Turkowski 1972). *S. richardsonii* produce larger litters on cropland than on pastures (Sheppard 1972) and *C. ludovicianus* breed as yearlings when food is abundant (Koford 1958).

7. Evolution of Sociality

Sociality occurs in those ground squirrels whose large size associated with a short active season delays reproductive maturity beyond one year of age. Delayed reproductive maturity may be avoided under these conditions if juvenile growth rates are high enough so that squirrels breed as yearlings. *S. parryii*, with the highest juvenile growth rate (Mayer and Roche 1954), seems to be the only species in which rapid growth enables a large spermophile to mature as a yearling. The high growth rate is associated with a daily active period of up to 17 h, in contrast to about 8–10 h in other species. Perhaps this long diurnal period effectively increases the growing season. Thus early maturity is achieved and sociality is absent.

Because individual fitness is enhanced by early reproduction, there must have been strong selection to increase fitness in those individuals with delayed maturity. The association of delayed maturity, large body size relative to the length of the active season, and sociality indicates that selection for large size also required selection for sociality. At least three advantages accrue with larger size. First, some predators are avoided. I have seen *M. flaviventris* easily chase off weasels (*Mustela*). Martin (*Martes*) can also be driven off (Downhower, pers. obs.; Travis, pers. obs.; Waring 1965). Hawks rarely attack adult marmots. Although I frequently see red-tailed hawks flying or perching near marmots and although hawks may nest near marmot colonies, only once in 18 years of observations have I seen a hawk swoop at an adult marmot. Second, a larger animal can utilize a wider array of herbaceous vegetation because gut capacity increases, and the relative amount of protein needed decreases with increasing size (Janis 1976). Third, a larger animal can store more fat (Morrison 1960). Not only is more fat stored,

but it will last longer because of the lower weight-specific metabolism of larger vs. smaller animals. The importance of body size is illustrated by geographic variation in *S. lateralis*. Animals from 2,900 m in Colorado were significantly larger and stored significantly more fat than squirrels from 970 m in Oregon (Blake 1972). There is no way of determining the relative selective pressures of these three advantages, but given the increased efficiency of energy acquisition and use by larger animals, energetics likely had a major role in the evolution of larger size. This evolution requires that larger animals are dominant to smaller ones, a common phenomenon in mammals (Wilson 1975: 293), and that total energy available is sufficient to support the greater absolute energy demands of large animals. For some species, energy available greatly exceeds energy utilization (Kilgore and Armitage 1978), but information on population energetics of ground squirrels is too scanty for general conclusions.

A major characteristic of ground squirrels is that individuals disperse during the active season prior to reaching reproductive maturity (Table 1) in the following spring. This pattern of delayed dispersal is best demonstrated in *Marmota* and is related to increased sociality (Barash 1974). The pattern in marmots suggests that delayed dispersal may be the process leading to sociality. Because the fundamental social unit of the most social of ground squirrels is a male with a harem, sociality could evolve by the selective retention of females in their natal areas. Males of *M. flaviventris* disperse from their natal colonies (Armitage 1974) and males of *S. tridecemlineatus* (McCarley 1966; Rongstad 1965), *S. beecheyi* (Evans and Holdenreid 1943), *S. richardsonii* (Yeaton 1972), *S. beldingi* (Morton et al. 1974), *S. armatus* (Slade and Balph 1974), *S. tereticaudus* (Dunford 1977a) and *M. monax* (Grizzell 1955) either disperse a greater distance, have larger home ranges, or move about more than females. By contrast, females tend to remain near their female parent. For *M. flaviventris*, population growth in a newly established colony occurred by incorporating daughters into the harem (Armitage 1973) and 49% of all harem females in established colonies were born there (Schwartz and Armitage 1980). Among those species not forming discrete harems, female *S. armatus* (Slade and Balph 1974), *S. richardsonii* (Michener and Michener 1973), *S. beecheyi* (Fitch 1948), and *S. tereticaudus* (Dunford 1977a) settle within or adjacent to their mother's territory. *S. richardsonii* and *S. tereticaudus* kin recognize each other into adulthood and appear to form incipient social groups or kin clusters (Dunford 1977a). If a male defended a group of females, the organization characteristic of *S. parryii* would occur (Carl 1971). In all of these species females live as individuals. Cohesive behaviour among adults is rare, even among related females (*S. richardsonii*, Quanstrom 1971; Yeaton 1972; Michener 1973b; *S. tereticaudus*, Dunford 1977a), or absent (*S. armatus*, Balph and Stokes 1963; *S. parryii*, Watton and Keenleyside 1974; *S. tridecemlineatus*, McCarley 1966; Wistrand 1974; *S. beecheyi*, Fitch 1948; Owings et al. 1977; *S. lateralis*, Wirtz 1967; *M. monax*, Bronson 1964). Among the social species, cohesive behaviors among harem members characterize their behavior (*S. columbianus*, Betts 1976; Steiner 1970; *M. flaviventris*, Armitage 1962; *M. olympus*, Barash 1973; *C. ludovicianus*, King 1955). Cohesive behaviors predominate among kin, who are often burrowmates, but agonistic behavior characterizes social behavior of non-kin (Johns and Armitage 1979). These social species are also characterized by social play, by cohesive behaviors between juveniles and adults which continue at least into the yearling year, and the formation of yearling social subgroups within the larger social unit (Armitage 1962, 1974, 1975; Barash 1973; King 1955; Steiner 1970, 1971). Thus the evolution of sociality in these

species required the continuation of cohesive behaviors beyond the early mother-infant period into adulthood and the extension of these behaviors to at least some adults. Because these adults are likely to be either sibs or offspring, the evolution of sociality likely involved kin selection (West Eberhard 1975). In other words, new behaviors or social relationships were unnecessary; sociality occurred when behaviors characteristic of mother-young (Michener 1973b, 1974) were prolonged.

Exploitation of resources and anti-predator defense are generally considered the major factors causing grouping. Clearly predation has modified the behavior of these animals. Alarm calls are the best example of anti-predator behavior. Alarm-calling is widespread among ground squirrels and occurs at all levels of sociality. These calls alert kin in individualistic species (Dunford 1977b; Sherman 1977) and doubtless alert kin in the harem-forming species where harem members are likely to be kin. The evidence that kin selection may account for the evolution of alarm-calling supports the model that sociality in ground squirrels also evolved by kin selection.

Predation on ground squirrels may be intense. Hawks and snakes are the predominant predators on *S. townsendii* (Alcorn 1940), *S. beecheyi* (Edge 1931; Evans and Holdenreid 1943; Fitch 1948), *S. richardsonii* (Michener and Michener 1977) and *S. beldingi* (Morton 1975); foxes, coyotes, and badgers are the major predators of *S. parryii* (Carl 1971), *S. armatus* (Slade and Balph 1974), *M. monax* (deVos and Gillespie 1960), *C. ludovicianus* (Koford 1958), *C. gunnisoni* (Longhurst 1944); weasels probably prey on the young of many of these species including the social *S. columbianus* (Manville 1959). Coyotes and marten prey on *M. flaviventris* (Powell 1972). I have watched weasels prey on *S. lateralis*; entire litters of several females living on the same hillside may be exterminated (Svendsen, pers. com.). My students and I collected yearling *M. flaviventris* skulls from a golden eagle nest and have seen golden eagles feeding on dispersing yearlings. Predation may remove half the annual crop of young *S. beecheyi* (Fitch 1948) and may be very heavy on *S. tridecemlineatus* (McCarley 1966). Where losses of animals have been documented, they are heavier in young than in adults (Armitage and Downhower 1974; Fitch 1948; King 1955; Michener and Michener 1977; Murie 1973; Rongstad 1965). Generally, the causes of losses are undetermined. Substantial losses occur over winter in *S. lateralis* (McKeever 1964), *S. elegans* (Clark 1970), *S. franklinii* (Iverson and Turner 1972), *S. richardsonii* (Michener and Michener 1973), *S. armatus* (Slade and Balph 1974), *S. parryii* (Carl 1971), *M. flaviventris* (Nee 1969; Armitage and Downhower 1974; Svendsen 1974), and *M. olympus* (Barash 1973). Some of these losses occur because predators, such as badgers and bears, dig out the hibernators; other losses are physiological. Losses to predators and to overwintering are independent of level of social organization. In fact, some of the heaviest losses to predation occur in the spermophiles that live individually within aggregations. If predation were the selective force causing sociality, one could expect these species to be more social than they are.

Dispersal accounts for some losses in *M. flaviventris* (Armitage and Downhower 1974), *M. olympus* (Barash 1973) and *M. monax* (Grizzell 1955; de Vos and Gillespie 1960). Normally, all young of *M. monax* disperse but only some subadults of *M. flaviventris* and *M. olympus* disperse. Dispersal also characterizes losses in other species: *S. armatus* (Slade and Balph 1974), *S. richardsonii* (Yeaton 1972), *S. tereticaudus* (Dunford 1977a), *S. beecheyi* (Evans and Holdenreid 1943; Fitch 1948), *C. ludovicianus* (King 1955; Smith 1958), and *C. leucurus* (Tileston and Lechleitner 1966). In the individualistic species, unless the mother

dies, all juveniles surviving beyond weaning must disperse from the natal burrow. By contrast, juveniles often share burrows with their mother through hibernation and all members of a colony may hibernate in groups in one (*M. olympus*, Barash 1973) or a few burrows (*M. flaviventris*, Johns and Armitage 1979).

Dispersal should be timed to maximize the individual fitness of the disperser or the inclusive fitness (Hamilton 1964) of the disperser and its parent. Early dispersal by juvenile *M. flaviventris* results in a much lower survival to the second summer (Downhower and Armitage 1971; Andersen et al. 1976). Thus early dispersal represents genetic loss and reduced individual and inclusive fitness. It little matters what the sources of mortality are; e.g., predation or inability to find hibernacula, once the animals disperse for in this system early dispersal is equivalent to mortality. Thus, the evolution of sociality through delayed dispersal should be considered a mechanism for continuing reproductive investment in order to maximize individual or inclusive fitness.

This model of the evolution of ground squirrel sociality requires that the animals form some type of group prior to the formation of harems. Group formation in these species is associated with resources, especially food. The density of the individualistic *S. lateralis* was associated with the density of herbaceous vegetation (McKeever 1964). The individualistic *M. monax* were concentrated in and around a clover field (Anthony 1962); home ranges were smaller and overlapped in good habitat and were larger and non-overlapping in marginal habitat (deVos and Gillespie 1960). *S. beecheyi* were closely grouped at a rich food resource (Edge 1934). The other species of *Spermophilus* and *Marmota* occur in a variety of grass-forb meadows (Table 1). These meadows usually represent an abundant, clumped resource (e.g., Carl 1971; Slade and Balph 1974; Svendsen 1974). Where the area of the resource is large enough, multi-harem colonies occur (Johns and Armitage 1979). Multi-harem colonies characterize the social structure of *C. ludovicianus* (King 1955; Tileston and Lechleitner 1966). *C. leucurus* and *C. gunnisoni* occur as concentrations of animals in a favorable habitat and populations of *C. ludovicianus* are concentrated on favorable areas and do not expand when blocked by unfavorable habitat (Koford 1958).

The social organization of prairie dogs is inadequately described. *C. leucurus* and *C. gunnisoni* are considered social but their harem structure is reported to be less definite than that of *C. ludovicianus* (Longhurst 1944; Tileston and Lechleitner 1966; Fitzgerald and Lechleitner 1974; Hoogland 1979). We attempted to predict the sociality of these species based on their life-history traits. Stepwise discriminant analysis classified the 24 populations correctly according to the sociality index (Table 1). When canonical variable 2 was plotted against canonical variable 1, there was no overlap among groups. Groups 1 and 2 lay close together; all other groups were quite distinct. When *C. leucurus* and *C. gunnisoni* were run as unknown, all known populations were correctly classified; *C. jeucurus* was classified as solitary and *C. gunnisoni* was placed in group 5. The sole member of group 3, *S. parryii*, lay close to group 2. Because group 3 was defined by male behaviour whereas the other groups can be defined independently by female organization, (females are similar to group 2) group 3 was eliminated, *S. parryii* was placed in group 2, and *C. leucurus* and *C. gunnisoni* were run as unknowns. All known populations were correctly classified; *C. leucurus* again was classified as solitary and *C. gunnisoni* was classified in group 5. When *C. leucurus*, *C. gunnisoni*, and *S. parryii* were run as unknowns, all known populations were correctly classified, *S. parryii* was placed in group 2 and the

two *Cynomys* were classified as before. When canonical variable 2 was plotted against canonical variable 1 in the two runs with group 3 eliminated, the two *Cynomys* did not closely associate with any group but lay between groups 1 and 5 whereas *S. parryii* lay well within the cluster of group 2. Therefore, several variations of group 3 composition were tried. When *S. parryii* was run as the unknown and *C. leucurus* and *C. gunnisoni* placed in group 3, all known populations were correctly classified and *S. parryii* was placed in group 2. However, if *C. gunnisoni* were run as the unknown, groups 1 and 3 overlapped, *S. franklinii* was misclassified into group 3, and *C. gunnisoni* was placed in group 5. When both *C. gunnisoni* and *S. parryii* were run as unknown, all known populations were correctly classified, *S. parryii* was classified in group 2 and *C. gunnisoni* joined *C. leucurus* in group 3. Clearly, the manner in which group 3 is defined affects the classification of the unknowns. Throughout these stepwise discriminant analyses, the most important life history traits entering the model were total length of active season, length of adult active season, age of first reproduction, age adult weight achieved, litter size, hibernation weight, and length of gestation. These traits correspond closely with the two principal components seasonality and age of maturity.

This analysis supports the general statement that *C. leucurus* and *C. gunnisoni* do not form typical harems and may have similar social structure. The data available do not permit an accurate prediction of their degree of sociality. Many of their traits correspond closely with those of *C. ludovicianus*; possibly other selective factors not included in the model have molded prairie dog sociality. One possible factor is that males defend females as a resource, but females remain essentially individualistic. Home range overlap among females and a lack of sharp territorial boundaries among males could produce a social system likened to a "loose harem" Possibly the males defend a resource, burrow sites or food, where females accumulate. This system would be resource defense polygyny (Emlen and Oring 1979).

Nutrition may be a second factor in the evolution of prairie dog sociality. Vegetation in prairie dog colonies often is sparse (Koford 1958; Smith 1958; Tileston and Lechleitner 1966). *C. ludovicianus* often occurs on rangeland overgrazed by cattle and historically was associated with bison whose grazing drastically modified and reduced the amount of vegetation (Koford 1958). Bison feeding in the South Dakota area modified the vegetation and probably reduced the nutrient level available to the prairie dogs (King 1955). King's black-tailed prairie dogs weighed 100–150 gms less in July and August than the young prairie dogs in Colorado where nutrition was reported to be good (Tileston and Lechleitner 1966). The Colorado prairie dogs bred as yearlings; the South Dakota animals bred at age two. Thus, there is abundant indirect evidence that the social biology of *C. ludovicianus* evolved in a nutritionally poor environment which delayed maturity which in turn is associated with delayed dispersal and sociality.

A third factor which may have contributed to the evolution of prairie dog sociality is the prolonged association of young with adults through the winter. *C. ludovicianus* apparently does not hibernate, although captive animals kept at 10° C and deprived of succulent food entered dormancy (Anthony 1953). There is a marked decrease in activity during the winter, but adults and young may be seen above ground (King 1955; Koford 1958) and young continue growth and reach adult size when about 15 months old (King 1955). Young of the similar sized *S. beecheyi* grow until December by which time they are mature (Tomich 1962). Although the young are active when the juveniles of most species are hibernating, the adult *S. beecheyi* probably

are hibernating (Fitch 1948). Thus the young of *S. beecheyi* extend their growing season and mature at one year of age, but this extended period of growth is not associated with adult activity and *S. beecheyi* is individualistic.

To summarize, sociality in ground squirrels is associated with delayed maturity. Maturity is delayed because of the interaction of large size with a relatively short active season or possibly because of poor nutrition. Sociality probably evolved as a male with a harem by retaining female kin within a male's territory. Although male and female social strategies are related, they are not identical. Much additional research is needed to clarify the roles of male mating strategies and female reproductive investment in the evolution of ground squirrel sociality.

8. Ground Squirrels and *r*- and *K*-Selection Models

Models of *r*- and *K*-selection are prominent in the analysis of life-history tactics (see Stearns 1976 and Pianka 1978:122, for reviews of *r* and *K*). However, these models as currently used are inappropriate for understanding the pressures selecting life-history tactics in ground squirrels. Because endothermic homeotherms allocate such a small proportion of their energy, usually about 2%, to reproduction, they, including ground squirrels, should be considered *K*-selected. Absolute size of offspring is a function of body size (Fig. 1), but larger, and presumably more *K*-selected squirrels, produce relatively smaller young. Furthermore, the intrinsic rate of natural increase of homeotherms and poikilotherms is closely linked with body size (Blueweiss et al. 1978; Southwood 1976).

Parental care is less in *r*-selected species. All mammals nurse; therefore, there is at least a minimal level of parental care. Gestation, but not lactation, is also linked with body size. Lactation is less the shorter the active season (Table 2). For example, *M. marmota* juveniles are weaned in 25 days whereas juveniles of the similar-sized *M. monax* are weaned in 44 days (Table 1). On this basis, *M. monax* would seem to be the more *K*-selected. However, juveniles grow more rapidly after weaning than while nursing. Therefore, early weaning leads to increased growth of young in a short active season. In general, the growth constant is inversely related to the length of the homeothermal period (Kiell and Millar 1978). Again, *M. flaviventris* would be more *r*-selected than *M. monax*. But *M. flaviventris* evidences more parental care through sociality and would be considered more *K*-selected than *M. monax*. Further comparisons of this sort are possible, but these should suffice to demonstrate that the *r*-*K*-selection model is not useful and leads only to tedious comparisons of particular traits between two species.

Western (1979) suggested that life history parameters which arise as a consequence of size (e.g., gestation time, growth rates, lifespan, litter weight), the first order strategies, should be distinguished from those that vary between populations and according to environmental circumstances, the second order strategies. The size-related natural history trait is a continuum; species or populations lying above the regression line describing the relationship between a particular trait and size would be relatively *r*-selected for that trait. Species or populations lying below the regression line would be relatively *K*-selected. For example, *S. richardsonii* would be relatively *r*-selected for reproductive effort and *C. gunnisoni* would be relatively *K*-selected (Fig. 5, 6). Unfortunately there is a tendency to characterize different populations of a species or closely related species as being more *r*- or *K*-selected than the other population or species (e.g., Nichols et al. 1976; Tamarin 1978; Kirkland and Kirkland 1979) without determining the proximal factors causing the observed differences. It is of greater biological significance to determine the proximal

factors affecting life-history traits than to try to fit a species or population into an *r*-*K*-selection model.

9. Conclusions and Predictions

I conclude that the major determinant of reproductive effort in hibernating ground squirrels is body-size energetics. These species maximize reproductive effort, but a primary proximal factor affecting the expression of reproductive effort is nutrition. Sociality continues reproductive investment beyond weaning in those large-sized animals living where the active season is too short to enable offspring to become reproductively mature in their first year of life. Reproductive investment is expressed through delayed dispersal which, in turn, necessitated the evolution of sociality and the acquisition of cohesive behaviors. The fundamental social unit is a group of females, probably kin, who are likely members of a harem, but a harem may contain two or more female lineages.

This analysis of the life-history traits of one group of mammals strongly supports the conclusions of Blueweiss et al. (1978) and Western (1979) that body-size scales many life-history traits and should be a central theme in ecology. Because changes in energetic relationships that accompany changes in size impose certain constraints on several life-history traits that, in turn, effect social behavior (Western 1979), more attention should be focused on selective factors leading to changes in body size.

The model developed here predicts that all chipmunks (*Tamias* and *Eutamias* with body weight <100 gm) have a high specific reproductive effort and are asocial. No *Spermophilus* with a mean minimum adult weight <600 gms and a total active season of 5 months will be social. All larger species, including *Cynomys* and *Marmota*, will be social unless the active season is about 6 months. Smaller species may be social if the active season is <4 months. Cohesive behaviors among adults will be rare or absent in all species except those with sociality. The nearest neighbors of adult females will be more closely related than more distant residents. Dispersal patterns will differ between the sexes with males dispersing greater distances. The nearest neighbors of males will not be closely related to the male. The proximal causes of dispersal will differ between those species expressing sociality and the others. In the social species, agonistic behavior will be directed toward non or distantly related kin and amicable behavior will be directed toward closely related kin. Therefore, mothers will tend to recruit daughters but attempt to expel other females. Sibs will tend to form social units within harems or settle near one another in the individualistic species and will behave agonistically toward other females. Those sibs forming social units within harems will behave cohesively toward their mother and toward daughters produced by any members of the sib group. These predictions are simplified because over time lineages should split into two or more lines of descent and members of these lines should behave agonistically toward one another. In other words, only the closest kin should form cohesive social groups. All of the predictions described above may be tested by long term studies of marked individuals of known relationship in the field.

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