ADVANCES IN THE STUDY OF MAMMALIAN BEHAVIOR

EDITED BY

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SPECIAL PUBLICATION NO. 7
THE AMERICAN SOCIETY OF MAMMALOGISTS
PUBLISHED 11 MARCH 1983

KIN IDENTIFICATION, MATRIARCHIES, AND THE EVOLUTION OF SOCIALITY IN GROUND-DWELLING SCIURIDS

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Abstract

THE social organization of North American ground-dwelling sciurids is reviewed. The five grades of social structure identified—asocial, single-family female kin clusters, female kin clusters with male territoriality, polygynous harems with male dominance, and egalitarian polygynous harems—form a continuum of sociality, based on the mother-headed family as the fundamental social subunit. Three simultaneous trends characterize the sequence of sociality: retention of daughters near or in the mother's range (single-family clusters), relaxation of distinctions between adjacent litters (cohesive multiple-family clusters), and superimposition of male territories, maintained beyond the breeding season, over female ranges (polygynous harems).

Social structure is based upon genetic relatedness between females. Familiarity with close kin, established via socialization in amicable social contexts during the first 4 to 6 weeks of life, is proposed as the proximate mechanism determining differential behavioral responses to conspecifics that vary in their degree of genetic relatedness.

Social structure correlates with the proportion of their preadult life that immatures are simultaneously in the active, above-ground population with adults. Prolonged active seasons for adults and/or increased number of seasons required for juveniles to attain maturity permit greater coincidence in the seasonal activity of adults and immatures. The selective factors that have determined the timing of the circannual cycle are proposed to have indirectly promoted the evolution of sociality.

Introduction

Biologists are increasingly aware that by combining comparative studies of the social behavior of closely related species with the fundamental concept of natural selection acting at levels no higher than the individual, the evolution of social behavior is amenable to interpretation and to the formulation of predictive hypotheses. Discussions of the evolution of social behavior and of mating systems (for example, see Alexander, 1974; Orians, 1969; West Eberhardt, 1975; Wittenberger, 1980) have led to classificatory systems or models useful for providing functional descriptions of social systems in terms of adaptive behavioral strategies to environmental constraints (Crook et al., 1976; Emlen and Oring, 1977). When a range of social systems occurs within a taxonomic group, adaptive radiation in relation to ecology is probable (Barash, 1974; Clutton-Brock, 1974; Crook et al., 1976; Eisenberg et al., 1972). The social systems of related species can be analyzed for common, underlying social subunits and for overlying, more recently evolved social trends.

Among mammals, the ground-dwelling sciurids (Sciuridae) have attracted scientific interest because they include several highly social species that are readily observable in field situations and because most North American species are obligate seasonal hibernators. An ever-increasing body of information is available on the social organization and on the hibernation physiology of several North American species. The aims of this article are: 1) to review the current literature on social organization of North American sciurid species; 2) to classify sciurid social systems; 3) to identify common themes and evolutionary trends in social organization; 4) to discuss the role of kin identification in maintenance of the social system; and 5) to relate sociality to environmental constraints and circannual rhythmicity.

Classification

The North American Sciuridae are classified as arboreal (tree squirrels and flying squirrels) or terrestrial (chipmunks and ground squirrels). The semi-fossorial ground squirrels are further subdivided into the giant ground squirrels (subtribe Marmotina) and the ground squirrels, prairie dogs, and antelope squirrels (subtribe Spermophilina) (Moore, 1961). The antelope squirrels, which have

an earlier origin than the other living species of Nearctic ground squirrels (Hight et al., 1974) and which are not obligate hibernators, are not treated in this review because of the paucity of data on their social behavior and organization. The remaining members of the Spermophilina belong to two genera, *Spermophilus* (ground squirrels) and *Cynomys* (prairie dogs); the latter are a specialized, recently evolved group whose closest affinities are to ground squirrels of the subgenus *Spermophilus* (Hight et al., 1974; Nadler et al., 1971; Seaman, 1976).

Circannual Cycles

Obligate seasonal hibernation is characteristic of the majority of species of North American ground-dwelling sciurids that occur north of 30°N. In such species each year is divided into an active season, during which some or all of the individuals enter the above-ground population daily, and an inactive (hibernation) season, in which all members of the population remain below ground continuously for several months. Mating occurs shortly after adult females emerge from hibernation, and juveniles typically enter the above-ground population 56 to 60 days after adult females first appear from hibernation (Knopf and Balph, 1977; Michener, 1977*a*, 1977*b*, 1980*a*; Morton, 1975; Murie and Harris, 1982). The emergence of juveniles from the natal burrows results in a dramatic increase in the density of the surface active population. However, the density typically begins to decline shortly thereafter with the immergence of adults. The sequence of late summer and autumn immergence into hibernation for most species is adult males, adult females that failed to wean offspring, adult females that successfully reproduced, juvenile females and, finally, juvenile males (Clark, 1977; Grizzell, 1955; Iverson and Turner, 1972; Loehr and Risser, 1977; McCarley, 1966; D. Michener, 1974; Michener, 1977*a*, 1978, 1979*a*; Morton and Parmer, 1975; Murie, 1973; Skryja and Clark, 1970). If there is a non-breeding yearling age class, these animals usually disappear after the adults but before the juveniles. Exceptions to the above sequence are Uinta ground squirrels (*Spermophilus armatus*), in which adult males immerge shortly after adult females but before yearlings and juveniles (Knopf and Balph, 1977), and Arctic ground squirrels (*Spermophilus parryii*), in which adult males remain active later than adult females, sometimes not disappearing until late autumn at the same time as juvenile males (Green, 1977; McLean

and Towns, 1981). Of the ground-dwelling sciurids whose ranges extend north of 40°N, only the black-tailed prairie dog (*Cynomys ludovicianus*) is not an obligate hibernator. King (1955) and Koford (1958) noted that prairie dogs were active on all but the most inclement days during winter, with any individual rarely continuously underground for more than a couple of days.

Among the species of ground-dwelling sciurids, there are variations in the amount of time that different cohorts are simultaneously active (Table 1) and, therefore, able to interact socially. Once juvenile black-tailed prairie dogs have emerged from the natal burrow, their above-ground activity coincides with that of all other cohorts for the remainder of their lives. In contrast, for some of the hibernating species there is a period of only a few weeks when all age and sex classes are simultaneously active. Because of the early immergence of adult males in most species, the cohorts with the least amount of coincidence in their activity patterns are adult males and juveniles. Richardson's ground squirrels (*Spermophilus richardsonii*) have a short period of overlap in the activity of adult males and juveniles, with juveniles typically spending the last 10 weeks of their first summer of life out of contact with males. The atypical immergence pattern of adult male Arctic ground squirrels results in their presence throughout the entire period that juveniles are active. For those species in which reproductive maturity is delayed until years 2 or 3, coincidence in the seasonal activity of adults and immatures is high (Table 1).

Grades of Social Structure

Isolated individual ground squirrels are rare; typically aggregates of conspecifics are found wherever suitable resources (primarily food and burrows) occur. Although rarely geographically solitary, some species are characterized by social solitariness. Sociality will have evolved from ancestral, asocial aggregations if social integration and cohesiveness increased the survival and reproductive success of individuals in the group.

The social organization of North American ground-dwelling sciurids forms a continuum ranging from asocial species, such as the woodchuck (*Marmota monax*) and Franklin's ground squirrel (*Spermophilus franklinii*), to highly social species, such as the Olympic marmot (*Marmota olympus*) and black-tailed prairie dog. Between these extremes are species with intermediate degrees of

TABLE 1

SELECTED LIFE HISTORY TRAITS OF 18 SPECIES OF GROUND-DWELLING SCIURIDS RANKED BY INCREASING SOCIAL GRADE

Species	Social grade	FAFR	Size	Seasonal hetero-thermy	Subadult active season (days)	Adult-subadult seasonal coinci-dence as percent	References
→*Spermophilus franklinii*	1	Y	M	O	65–90	40–60	Iverson and Turner (1972); Murie (1973); Sowls (1948)
Spermophilus lateralis	1	Y	S	O	110–130	50–60	Cameron (1969); Ferron (1977); Kivett et al. (1976); Skryja and Clark (1970); Tevis (1955); Wirtz (1967)
→*Marmota monax*	1	Y (2)	VL	O (P)**	140–160	80–90**	Grizzell (1955); Snyder et al. (1961)
Spermophilus townsendii	1 or 2	Y	S	O	60–75	65	Alcorn (1940); Rickart (in press)
→*Spermophilus tridecemlineatus*	1 or 2	Y	S	O	85–100	40–65	McCarley (1966); Rongstad (1965)
Spermophilus elegans	2	Y	M	O	80	45	Clark (1970)
→*Spermophilus richardsonii*	2	Y	M	O	100–130	30–60	Dorrance (1974); D. Michener (1974); Michener (1977*a*, 1978, 1979*a*, 1979*c*)
→*Spermophilus beldingi*	2	Y	M	O	65–70	60	Loehr and Risser (1977); Morton and Parmer (1975); Morton et al. (1974)
Spermophilus armatus	2	Y	M	O	65	45–70	Knopf and Balph (1977)
→*Spermophilus tereticaudus*	2	Y	S	O	130	80–100	Dunford (1977*b*); Neal (1965)
→*Cynomys leucurus*	2	Y	L	O	120–140	35–55	Clark (1977); Tileston and Lechleitner (1966)
Spermophilus beecheyii	2 or 3	Y	L	P (O)#	300	50–100	Bickford (1979); Fitch (1948); Owings et al. (1977); Storer et al. (1944); Tomich (1962)

TABLE 1
CONTINUED

Species	Social grade	FAFR	Size	Seasonal heterothermy	Subadult active season (days)	Adult-subadult seasonal coincidence as percent	References
→*Spermophilus parryii*	3	Y	L	O	75–100	70–95	Carl (1971); Green (1977); McLean (1981); McLean and Towns (1981)
→*Spermophilus columbianus*	3	2	L	O	140–150	70–95	Michener (1977*a*); Murie and Harris (1982)
Cynomys gunnisoni	4	(Y) 2	L	O	140–150	80–95	Fitzgerald and Lechleitner (1974); Rayor (1980)
→*Marmota flaviventris*	(1)† 4	(2) 3∞	VL	O	350∞	95–100	Armitage et al. (1976); Kilgore and Armitage (1978)
→*Marmota olympus*	5	3	VL	O	240	90–100	Barash (1973*a*)
→*Cynomys ludovicianus*	5	(Y) 2	L	T	650	100	King (1955); Koford (1958)

* See text for descriptions of the five social grades. → indicates species discussed in detail in the text. FAFR is the typical female age at first reproduction (symbol in parentheses indicates age at which some females first reproduce): Y, yearling; 2, 2-year-old; 3, 3-year-old. Size classifies species by head plus body length: S, <200 mm; M, 200–250 mm; L, >250–350 mm; VL, >350 mm. Seasonal heterothermy: O, obligate hibernator; P, permissive hibernator; T, occasional torpor. Subadult active season is the typical total number of days immatures are active from first emergence from natal burrow to immergence in final subadult season, and hence is cumulative over several seasons for species in which reproductive maturity is not achieved until 2 or 3 years of age. Adult-subadult seasonal coincidence indicates the proportion of the number of days immatures spend above ground that adults are also present in the surface-active population. Figures represent modal values rather than extreme values.

** Anthony (1962) reported some activity by woodchucks in southern Illinois throughout winter, in which case adult-subadult coincidence is 100%.

‖ Storer et al. (1944) reported that all California ground squirrels at 3000 m elevation are underground from December to March. At lower elevations most adults hibernate for varying time periods whereas most juveniles remain active throughout the winter months (Fitch, 1948; Tomich, 1962).

† 25–50% of adult marmots occupy satellite sites and are not members of harems (Armitage and Downhower, 1974; Svendsen, 1974).

∞ Although some 2-year-old yellow-bellied marmots do reproduce, Armitage and Downhower (1974) reported that fewer than half do so, with most first producing young as 3-year-olds; subadulthood has therefore been considered to typically extend over 3 summers. Even for those marmots which first reproduce as 2-year-olds, about 95% of subadulthood is coincident with adult activity.

sociability and group cohesiveness. The aims of this section are to describe the characteristic social and spatial organization of several well-studied species of ground-dwelling sciurids and to classify them into one of five grades of sociality. Classification necessarily breaks a continuum into discrete units, but this does not imply that the social grades are absolutely distinct from each other.

The proposed grades of sociality are:

1. *Asocial.*—Males and females do not share territories. Juveniles disperse shortly after weaning with each establishing a home range distinct from those of the mother and littermates. Social interactions, even between kin, are mainly agonistic.
2. *Single-family female kin clusters.*—After the breeding season males and females occupy individually distinct ranges. Sons disperse from the natal area, whereas daughters often remain in or near the mother's range throughout life with subsequent sharing of the ancestral range between mother and adult daughters and among littermate sisters. Juveniles from different litters do not intermingle; a mother and her offspring form a sociable, moderately cohesive group that is unsociable with and aggressive toward adjacent groups.
3. *Female kin clusters with male territoriality.*—Adult males maintain their territories beyond the breeding season, defending an area that overlaps the smaller ranges of several adult females (composing one or more kin clusters) and their offspring. Juveniles from adjacent litters may associate together after weaning, and mothers show no strong discrimination between their own offspring and those of adjacent females. Dispersal is sex-biased with more sons than daughters leaving the natal area and with males moving further than females.
4. *Polygynous harems with male dominance.*—The harem male maintains a territory throughout the active season within which several females and their offspring live. The male dominates all other harem members. Juveniles from different litters within a harem frequently intermingle after weaning. Sons leave the harem but daughters may be recruited.
5. *Egalitarian polygynous harems.*—A male and several females form a cohesive group that maintains and defends a common range. Males do not dominate females and they engage in amicable contacts with juveniles. Litter distinctions are not main-

tained following emergence from the natal burrow, and adults do not discriminate between young from different litters. Sons leave the harem whereas daughters are recruited.

The accuracy of assigning particular species to a given grade is limited by the information available in the literature. The following descriptions include only those species for which assignment can be made with reasonable confidence. Table 1 provides a more extensive list of species with their probable social grade. Although grade assignment is based on the typical or most commonly described social pattern exhibited by the species, such assignment does not imply inflexibility in the social system of that species.

Asocial

Because of the unrewarding nature of studying their social behavior and organization, little quantitative information is available on those ground-dwelling sciurids that show minimal social integration. Information is most extensive for the woodchuck, *Marmota monax* (Anthony, 1962; Bailey, 1965; Bronson, 1963, 1964; Grizzell, 1955; Hayes, 1977; Merriam, 1971; Snyder, 1976). After the breeding season, each adult woodchuck defends a den and foraging area. Juveniles disperse from the natal den shortly after first emergence above ground. Although littermates may share a burrow initially, aggression between siblings ultimately results in each animal establishing its own range. Snyder (1976) suggested that dispersal, particularly of juveniles, is sex-biased, with males moving further than females.

Limited field data indicate that Franklin's ground squirrels (*S. franklinii*) are the least social of the six species of *Spermophilus* found in Canada (Kivett et al., 1976; Sowls, 1948). Captive Franklin's ground squirrels rarely scent-mark, and they interact infrequently, maintaining interindividual spacing primarily by mutual avoidance.

Wistrand (1974) described thirteen-lined ground squirrels (*S. tridecemlineatus*) as being social only at courtship and during rearing of litters; at other times individuals tend to avoid each other. Evans (1951) noted apparent family groupings consisting of a mother and several juveniles, but McCarley (1966) reported that family units began to break up within 2 weeks of juvenile emergence. Four weeks after emergence, juveniles were living in separate burrow

systems. Juvenile females usually remain closer to the natal area than juvenile males, and adult females tend to be sedentary (McCarley, 1966; Rongstad, 1965), so groupings of closely related females may occur, though this has not been documented. Because Rongstad, McCarley, and Wistrand studied thirteen-lined ground squirrels on golf courses, cemeteries, and mown park lawns, their observations on social behavior may not be typical for the species. Based on the brief study by Evans (1951) on an abandoned field, *S. tridecemlineatus* might more appropriately be placed in the next grade of social organization.

Single-Family Female Kin Clusters

Belding's ground squirrels (*S. beldingi*; Sherman, 1977, 1980, 1981*a*; Sherman and Morton, 1979), round-tailed ground squirrels (*S. tereticaudus*; Dunford, 1977*a*, 1977*b*), Richardson's ground squirrels (*S. richardsonii*; D. Michener, 1972; Michener, 1973*a*, 1973*b*, 1979*b*, 1980*b*), and white-tailed prairie dogs (*Cynomys leucurus*; Clark, 1977; Hoogland, 1979*a*, 1979*b*, 1981*a*; Tileston and Lechleitner, 1966) have similar social systems based on matrilineal kin groups. Females tend to be sedentary, remaining in or near the natal area throughout life, and ancestral homesites are ultimately occupied by daughters and granddaughters. Males typically disperse individually as juveniles or as yearlings. Consequently, males do not tend to be resident near to kin of either sex, whereas females tend to live in proximity to near and distant female relatives. Adult males typically move extensively during or after the breeding season (Michener, 1979*c*; Sherman, 1977), so fathers are rarely in proximity to offspring. Males do not defend a postbreeding territory nor do they defend resources that could be used by mate(s) and progeny. Each female rears young in isolation and defends the nest burrow from all conspecifics, including her mate and female relatives.

Round-tailed ground squirrels (Dunford, 1977*a*), Richardson's ground squirrels (Michener, 1979*b*), and white-tailed prairie dogs (Clark, 1977) show corresponding patterns of spatial and social relationships throughout the active season. All exhibit site-dependent dominance and site-attachment. The home range is not overtly defended but individuals tend to concentrate activity in one area (core area) which is unlikely to be simultaneously occupied by another animal. Clark (1977) described this as "core monopoliza-

tion," and Michener (1979*b*) suggested that Brown's term "dominion" (Brown, 1975:62) would apply to such a spatial-behavioral system. Following the emergence of adult females in spring, four major phases can be identified in the spatial and social patterns among conspecifics throughout the active season. First, during the copulatory phase, interaction rates (especially between individuals of opposite sex) are high. Adult males are conspicuous and active, often sustaining numerous wounds. Males tend to dominate females, and they frequently intrude into female core areas. The second phase, pregnancy-lactation, is characterized by even dispersion of home ranges and core areas with a minimal amount of overlap. Males are relatively inconspicuous and asocial, and are dominated by females, except when within their own core area. Pregnant and lactating females are aggressive toward conspecifics, confine their activity to a relatively small area around the natal burrow, and intrude into the areas of only immediately adjacent neighbors. During the third phase, juvenile emergence, females spend more time above-ground and they range over a larger area. Overlap of home ranges is maximal but core areas continue to remain essentially distinct. Following emergence, juveniles gradually increase their ranges of activity around the natal burrow and, after about 2 weeks, start interacting with juveniles from neighboring litters. Social interactions among littermates and between mother and offspring are predominantly amicable, whereas those between non-kin are predominantly agonistic. Mothers and offspring form family units that are distinct from and aggressive toward other family units. The final phase, prehibernation, is characterized by a decrease both in the amount of time spent above ground and in the range of activity of adults. Juveniles cease sharing burrows with siblings or mother; each juvenile establishes its own core area that is essentially distinct from, although in proximity to, those of its family members. In effect, each mother and any of her offspring (primarily daughters) that do not disperse, subdivide and share the range she had previously occupied. Interaction rates are low, but kin continue to interact amicably and non-kin agonistically. Juveniles are behaviorally indistinguishable from adults both in terms of the use of space and the nature of interactions with conspecifics. By late summer, juveniles have attained 90% of adult size and are virtually indistinguishable morphologically from adults. There is no conclusive evidence that animals hibernate communally; judging from the establishment

of separate core areas and the cessation of burrow sharing by family members, hibernation in isolation seems probable.

Female Kin Clusters with Male Territoriality

Arctic ground squirrels (*S. parryii*; Carl, 1971; Green, 1977; McLean, 1981, 1982, in press; Watton and Keenleyside, 1974) and Columbian ground squirrels (*S. columbianus*; Betts, 1976; Festa-Bianchet and Boag, 1982; Michener, pers. observ.; Murie and Harris, 1978; Steiner, 1970) have a social system that is based on matrilineal kin groups. However, compared with the previous category, adult males play a more prominent role in the social organization, and thier territorialism is more pronounced, with territorial defense continuing at least until juveniles emerge. The male's territory overlaps the ranges of several females and offspring.

Although Arctic and Columbian ground squirrels show similarities in social systems, there are major differences between the species in life history traits. Litter size is smaller in *S. columbianus*, with females typically weaning 2.5 young (Murie et al., in press), whereas *S. parryii* typically wean 6.1 young (McLean, 1980). Columbian ground squirrels are 10 to 12 weeks old when they first enter hibernation and they rarely breed as yearlings (Festa-Bianchet, 1981; Michener, 1977*a*; Murie et al., 1980), whereas Arctic ground squirrels are 18 to 22 weeks old at first immergence and are reproductively competent the following spring, with all yearling females and most yearling males breeding (McLean and Towns, 1981). A second summer of growth is required to attain adult size in *S. columbianus* (Boag and Murie, 1981*a*). Coincidence of the active seasons of adults and subadults is high in both species (Table 1) despite the difference in age at maturity. Although Columbian ground squirrels can reproduce as 2-year-olds, males probably do not first reproduce until 3 to 4 years old when they are capable of maintaining territories (Murie and Harris, 1978).

Male *S. parryii* and *S. columbianus* establish territories following emergence in spring. Males are aggressive and wounding results from boundary disputes. Males unsuccessful in establishing territories become "floaters" in the population and are subordinate to territorial males although tolerated by them. Others disperse and become "refugees" in suboptimal and peripheral habitat. Females establish ranges, which are smaller than and typically overlap with

the territory of at least one male (Murie, 1980). A minimum of fighting and wounding is involved in interfemale disputes, probably because females are familiar kin or neighbors from the previous year. The ranges of males and females are established independently; females occupy a burrow system in spring and, incidentally, select the male within whose territory the system is located. Males do not "herd" females (Wittenberger, 1980) or attempt to prevent them from leaving the defended area. Murie and Harris (1978) hypothesized that the main function of male territoriality in *S. columbianus* is to provide access to estrous females. McLean (in press) suggested that, because the territories of male *S. parryii* are more exclusive after than during the breeding season, the main function of territorial defense by males of that species is to protect offspring born within each territory.

As with the previous grade of social structure, sciurids in this category rear litters in isolation; females defend the area around the natal burrow from the territorial male as well as other females and intruders. However, intermingling of juveniles from different litters may occur shortly after emergence from the natal burrow. In Arctic ground squirrels, up to three females who are close kin (mother-daughter, littermate sisters) may bring litters to a common burrow system following juvenile emergence (McLean, 1982). Juveniles, therefore, frequently interact with conspecifics other than their family members within a few days of initial emergence.

In Arctic ground squirrels, there is sex-biased dispersal of juveniles, commencing about 4 weeks after weaning (when young are about 8 weeks old), with more males disappearing than females. In Columbian ground squirrels, juveniles tend to remain in or near the natal area through the first summer, but then leave the mother's area as yearlings (Boag and Murie, 1981*b*). Yearlings from different litters aggregate and frequently play in early spring. Such play becomes more aggressive as the season progresses, and the yearling groups break up in mid-summer when most yearling males disperse. Yearling groups may be composed of squirrels of both sexes (Michener, pers. observ.) or primarily of males (Murie and Harris, pers. comm.). Sex-biased dispersal of juveniles (*S. parryii*) and yearlings (*S. columbianus*) and the sedentariness of females permit formation of female kin clusters. Related adult females (mother-daughters, siblings) engage in amicable social interactions more frequently than do more distantly related squirrels, and they

are more likely to share space, food, and burrow systems (with the exception of the natal burrow during lactation). Combining of litters after weaning of adjacent close kin and prolonged territorial defense by adult males may represent behavioral adaptations to protect pups from predators and aggressive males (McLean, 1982, in press; Steiner, 1972). Kivett et al. (1976) suggested that the territorial adult male is a unifying force in the social system of Columbian and Arctic ground squirrels. Territorial males initiate the majority of social interactions within the social groups, they are aggressive towards neighboring conspecifics, and they scent-mark the territory more frequently and more consistently than do females.

Polygynous Harems with Male Dominance

The basic social group in yellow-bellied marmots (*Marmota flaviventris*) is a harem composed of one adult male, one to several adult females, and variable numbers of yearlings and juveniles (Armitage, 1973, 1974, 1975, 1977; Armitage and Downhower, 1974; Barash, 1973*b*; Downhower and Armitage, 1971; Johns and Armitage, 1979; Nowicki and Armitage, 1980; Schwartz and Armitage, 1980; Svendsen, 1974). These marmots have been studied at medium to high elevations, where they inhabit subalpine and alpine meadows in discontinuous habitat. Typically any one suitable location sustains only one harem.

In *M. flaviventris* the harem male is territorial throughout the active season, is behaviorally conspicuous, is socially dominant to other harem members, and is aggressive toward all other males, who tend to avoid him. The foraging ranges of harem members overlap extensively, with the adult male moving over a larger area than any individual female. The adult male and females within a harem interact infrequently except when an unfamiliar male takes over a harem. According to Armitage (1974) the advantages of territoriality to males are: creation of a socially stable environment optimal for reproductive success; enhancement of outbreeding through the presence of only one male and through the dispersal of sons born within the harem; and maximization of male fitness through access to several estrous females.

Yearlings do not reproduce and, although 2-year-olds may reproduce, most females produce their first litter as 3-year-olds. Females typically rear their young in isolation from other litters and from

offspring of the previous year. Young remain in close contact with parents beyond the age of weaning, sharing summer burrows, foraging areas, and hibernacula with them. Harem females are dominant to yearlings but interactions between parents and yearlings are typically more amicable than those between adults and unrelated yearlings. Yearling males disperse, usually after the snow has melted and before juveniles emerge. As adults, males are rarely resident in the harem of birth. In contrast, half or more of the adult females within a harem were born there. Typically those females that, as yearlings, establish home ranges that extensively overlap the home range of the mother are recruited into the natal harem. Male tenure in harems is dynamic with male turnover every 2 or 3 years, whereas female tenure is more static with some females residing in the same locality for 11 years. The differential length of tenure of male and female marmots and the likelihood of daughters being recruited into the natal harem, means that harems are typically matriarchies.

Although the basic social unit is the polygynous harem, yellow-bellied marmots living alone or in pairs in suboptimal habitat are common; Svendsen (1974) classed 24% of 67 adults in his population as satellite occupants, and Armitage and Downhower (1974) first captured 52 of 98 adults and 11 of 21 yearlings at satellite sites. Such animals are resident for shorter periods than harem animals, they suffer higher mortality, and their lifetime reproductive success is lower. Individuals may vary between satellite and harem sites between years.

Egalitarian Polygynous Harems

Olympic marmots (*Marmota olympus*; Barash, 1973*a*) and black-tailed prairie dogs (*Cynomys ludovicianus*; Hoogland, 1979*a*, 1979*b*, 1981*a*, 1981*b*; King, 1955; Smith et al., 1973; Tileston and Lechleitner, 1966) live in closed social groups that are characterized by weak or non-existent dominance relationships, by amicable social interactions, by frequent "greetings" (oral and nasal contacts), by unrestricted use of space and burrows (except a female's natal burrow), and by communal use of sleeping burrows and winter burrows.

Although the two species have similar social systems, differences in life-history patterns and social demography coincide with differ-

ences in the habitat each occupies. Olympic marmots, which inhabit alpine meadows with short vegetational growing seasons, are obligate hibernators and biennial breeders. Young attain adult size and sexual maturity at 3 years of age, so the subadult cohort is composed of both yearlings and 2-year-olds. Yearlings reside with the mother; those marmots which disperse do not leave until they are 2 years old. Because of the discontinuous nature of the habitat, many harems are isolated and solitary. In contrast, black-tailed prairie dogs inhabit open, short-grass prairie where harems are tightly packed into the continuous habitat. The growing season is longer and prairie dogs are not obligate hibernators. Prairie dogs typically disperse as yearlings, first reproduce as 2-year-olds, and breed annually.

Olympic marmot harems (called colonies by Barash, 1973*a*) are typically composed of one adult male, two adult females (one of which bred the previous year, the other in the current year), the yearling offspring of one female, the juvenile offspring of the other, and several 2-year-olds. Black-tailed prairie dog harems (called coteries by King, 1955) are typically composed of one adult male, one to four adult females, and variable numbers of yearlings and juveniles. Isolated sites occupied by solitary animals have not been reported for either species. A second, subordinate adult male may be associated with a harem. Among Olympic marmots, such an additional male occupies peripheral burrows in early summer but, with a decline in aggressive chasing by the harem male, he is increasingly incorporated into group activities and he hibernates with other harem members. The subordinate male in a black-tailed prairie dog coterie is able to remain within the harem unmolested by the harem male unless he attempts to mate with females, which then results either in his eviction or in the splitting of the coterie into two groups.

Because a black-tailed prairie dog coterie is surrounded by other coteries with which it has contiguous boundaries, intracoterie versus intercoterie social relationships can be compared. Whereas intercoterie interactions are hostile, intracoterie interactions are amicable, except when they involve pregnant and lactating females (Michener and Murie, in press). Coterie members communally and cooperatively engage in burrow and mound construction, in modification of vegetative cover, in nest building, in territorial defense, and in predator defense. Coterie members also sleep communally, with the exception of pregnant and lactating females who maintain

individual nest burrows that are defended against all coterie members. Following weaning of pups, females cease maintaining nesting territories and again all members have equal access to all burrows within the coterie. Although juveniles interact only with the mother and littermates during the first 6 weeks of life, mingling of litters within a coterie commences immediately after juveniles first leave the natal burrow. As a result, a juvenile may sleep with group members other than its immediate family within days of first coming above ground. Mothers show no discrimination between pups from various litters within the coterie, and all coterie members, including males, are amicable toward newly emerged pups. Consequently juveniles enter a social environment that is characterized by frequent amicable interactions with all coterie members. Juveniles are not, however, tolerated by the adults in adjacent coteries. As with older animals, intercoterie interactions involving juveniles are characterized by aggression and by defense of the mutual coterie boundary.

The prairie dog coterie is an egalitarian society. There are no dominance relationships among adult females, among juveniles, or between the harem male and females. If two adult males are resident within the same coterie one will be dominant, but such males share burrows and allogroom. All coterie members, regardless of age and sex, actively defend the coterie boundary, range over the entire coterie area, and have equal access to all but natal burrows.

Black-tailed prairie dog coteries, although described in terms of a male and associated females, are matriarchies. Because daughters usually stay within the coterie of birth, whereas sons disperse (usually as yearlings), the adult females are typically native to a coterie, whereas the adult male is an immigrant. When a coterie splits into two, the females that are nominally associated with each male continue to interact with each other amicably—as they had prior to fission. Occasionally a male incorporates an adjacent coterie with his original one, in which case the two sets of females will continue to interact agonistically—as they had prior to fusion. The constant factor in the social composition of a coterie is membership via the female line. King (1955) classed the coterie territory as a heritable resource passed "on from generation to generation and from individual to individual." Inheritance is matrilineal. Sons do not inherit the father's coterie; daughters do inherit the mother's coterie.

Although I have identified five grades of social structure among

the ground-dwelling sciurids and have allocated certain species to particular grades, I must emphasize that these grades form a continuum with intergradations between each, that species placed in the same category have similar but not identical social systems, and that, because social organization can vary with habitat, different populations of the same species could be allotted to different grades. For yellow-bellied marmots, individuals within the same population can be either asocial (in satellite sites) or integrated into a harem. Furthermore, distinctions between the social systems of some species (for example, Columbian ground squirrels and yellow-bellied marmots) may be due more to habitat differences than to social differences. Because of their larger size and more discontinuous habitat, yellow-bellied marmots occur in smaller groups than do Columbian ground squirrels. Typically there is only one marmot harem per site, whereas aggregations of Columbian ground squirrels may include several hundred animals. In a more continuous habitat, the marmots may have less well-defined harems, and males may not have exclusive access to estrous females.

Trends in Sociality

Three simultaneous trends characterize the range of ground-dwelling sciurid social organization from asocial individuals to cooperative polygynous harems: 1) retention of daughters within the mother's range and subsequent sharing of this range when the daughters are themselves reproductively mature (single-family kin clusters); 2) a relaxation of distinctions between litters of adjacent females such that inter-litter interactions are amicable (cohesive multiple-family kin clusters); 3) male territoriality extending beyond the breeding season, with territories encompassing the areas used by several females (polygynous harems). Hypothetical evolutionary pathways for the utilization of space based on daughter retention and female cohesiveness, and on male territoriality are depicted in Figs. 1 and 2, respectively.

The mother-infant bond, specifically the mother-daughter bond, is the most fundamental unit of ground-dwelling sciurid social organization, and it forms the basis from which other social units have derived. Single-family female kin clusters develop from the mother-daughter bond via extended social tolerance such that a female remains in spatial proximity to both her adult female offspring and her adult littermate sisters. Ultimately such tolerance permits

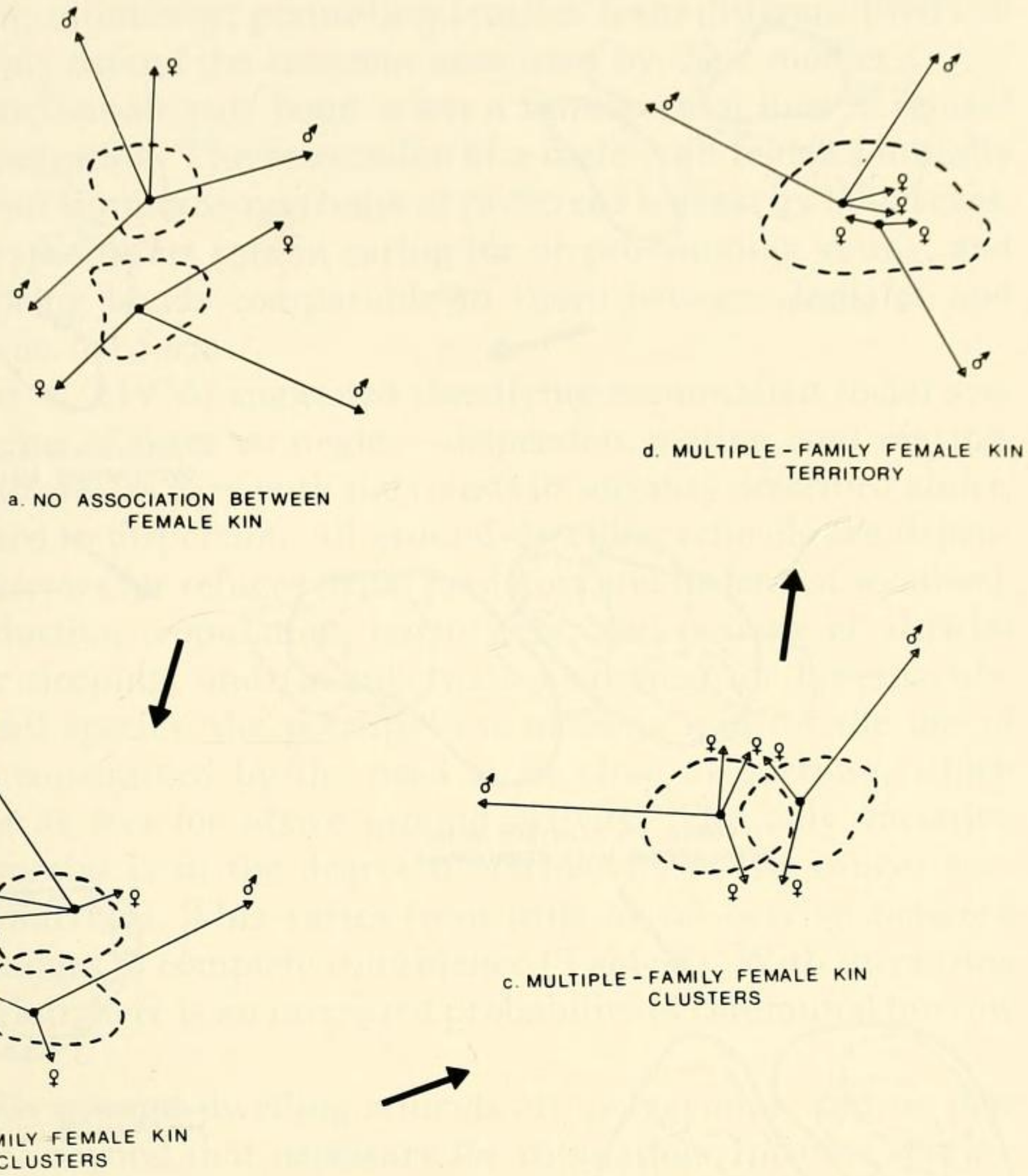


FIG. 1. Hypothetical evolutionary pathway showing increased social complexity based on retention of daughters near or in the mother's range and on relaxation of litter distinctions. Dashed lines indicate ranges of adult females. Solid circles indicate location of the natal burrow. Radiating lines indicate movement of offspring from the natal burrow. a, probable ancestral condition in which both sexes disperse from the natal area and no associations form between kin; b, sons disperse from the natal area but daughters establish ranges close to the mother's area, leading to clusters of females from the same family; c, sons disperse from the natal area, daughters establish ranges close to the mother's area, and daughters from litters of adjacent (closely related) females associate together; d, sons disperse from the natal area but daughters remain entirely within and codefend the mother's area along with daughters from other litters and their mothers.

daughters to remain entirely within the mother's range, and to cooperatively defend it with her. Multiple-family kin clusters result when litter distinctions relax, permitting daughters of adjacent females (who are themselves likely to be close kin) to associate as

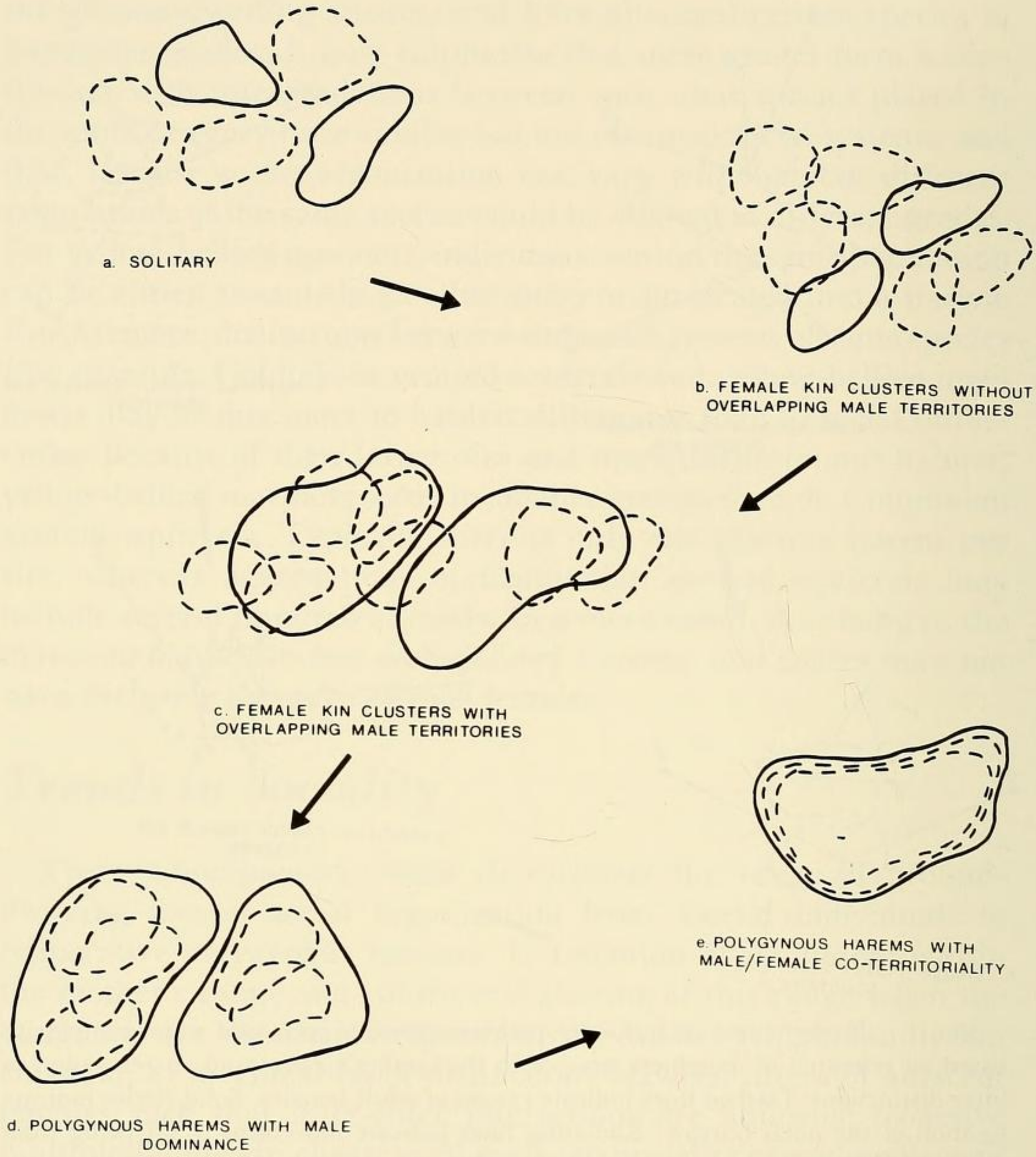


FIG. 2. Hypothetical evolutionary pathway showing increased social complexity based on superimposition of the post-breeding territories of adult males over female ranges. Solid lines indicate ranges of males. Dashed lines indicate ranges of females. a, probable ancestral condition in which both sexes maintain individually distinct ranges; b, related females occupy overlapping ranges that are distinct from the ranges of males; c, related females occupy overlapping ranges that may be overlapped by the territory(ies) of post-breeding male(s); d, related females occupy overlapping ranges that lie within the territory of the harem male; e, related females occupy and codefend a common range with the male.

adults, and, ultimately, permitting females from different litters to cooperatively defend the common area used by their mothers.

The male-female pair bond is not a fundamental unit in sciurid social organization. The association of a male with females initially derived from simultaneous choice of preferred habitat by both sexes. Males play no direct role in caring for or provisioning young, and male-offspring bonds comparable to those between females and daughters do not form.

Crook et al. (1976) suggested classifying mammalian social systems in terms of three strategies—dispersion, mating, and rearing. All three strategies vary with the trends in sociality described above. With regard to dispersion, all ground-dwelling sciurids are dependent on burrows for refuges (from predators and inclement weather), for reproduction (copulation, parturition, and rearing of altricial pups), for sleeping, and (in hibernating species) for hibernacula. Thus, in all species, the potential for mobility and for the use of space are constrained by the need to be close to burrows, which then serve as foci for above ground activity. The only variation between species is in the degree of exclusivity of the ranges surrounding burrows. This varies from little or no overlap between adjacent ranges to complete coincidence (Table 2). With increasing range overlap there is an increased probability of communal burrow use.

Typically ground-dwelling sciurids are polygynous, and no pair bond forms beyond that necessary for copulation. In some species, such as Richardson's ground squirrel, where the adult sex ratio is biased in favor of females (Michener, 1979*a*, 1980*b*; Michener and Michener, 1971), polygyny is an inevitable outcome of population demography. In others, in which the adult sex ratio approximates 1:1, polygyny results from differential male access to estrous females. Differential access could also occur in species with a biased adult sex ratio, but has not been documented. Reproductive success among male Belding's ground squirrels is asymmetric with about a quarter of the males accounting for two-thirds of copulations (Sherman, 1980; Sherman and Morton, 1979). Age is an important factor; most of the successful copulations involve males that are 3 to 4 years old. Similar asymmetric reproductive success, at least partly related to age, probably occurs in *S. columbianus* (Murie and Harris, 1978), *S. parryii* (Carl, 1971), and *M. flaviventris* (Armitage, 1974), all

TABLE 2
CLASSIFICATION OF SCIURID SOCIAL ORGANIZATION (AFTER CROOK ET AL., 1976)

Social organization	Strategies						
	Dispersion		Mating	Rearing			
Basic patterns	Refuge utilization		No pair bonding	Litters isolated in individual natal burrows, male not directly involved in rearing			
Variable patterns	Degree of range exclusivity		Type of polygyny	Duration of M-I bond† with		Male association with rearing group	
				Daughters	Sons (age at dispersal*)	Present	Duration
	♀–♀	♀–♂					
Asocial	High	High	Promiscuous	Short <1 summer	J	no	—
Single-family female kin cluster	Medium	High	Promiscuous	Prolonged weak assocn	J	no	—
Female kin cluster with male territoriality	Medium	Low	Limited access (resource defense)	Prolonged	J or Y	yes	To male immergence (1 or 2 summers)
Harem with male dominance	Low	None	Harem (resource defense)	Prolonged	Y	yes	To male immergence (2 summers)
Egalitarian harem	None	None	Harem (?harem defense)	Continuous	Y or 2	yes	Continuous or to male immergence (3 summers)

* J, juvenile; Y, yearling; 2, 2-year-old.
† M, mother; I, infant.

species in which the adult sex ratio approximates 1:1. Asymmetry is primarily related to the inability of some males, particularly younger animals, to establish territories in spring. In these three species, the mating strategy approaches Emlen and Oring's (1977) classification "resource defense polygyny," where the successful males monopolize a resource (burrow system) used by females. Because black-tailed prairie dogs live in continuous habitat that is partitioned among groups of female kin, the male mating strategy approximates that of "harem defense polygyny." In both types of polygynous systems the males neither control nor herd the females, but males "acquire" females by simultaneously using the areas occupied by females.

The three variables that Crook et al. (1976) considered in their classification of rearing strategies were: 1) whether or not the male was present in the rearing group; 2) the duration of the male's presence; 3) the duration of the mother-infant bond. These factors vary across the continuum of social organization exhibited by ground-dwelling sciurids (Table 2). The male is associated with female(s) and young only in those species in which the males maintain territories beyond the breeding season. In these systems, the duration of the male's association with subadults is influenced by the circannual cycle (Table 1). The duration of the mother-infant bond varies with sex of offspring and, for daughters, covaries with the extent of range exclusivity. In all species sons disperse, thereby terminating the social bond with the mother. This termination may occur as early as 3 to 6 weeks after weaning (for example, Richardson's, Belding's, and round-tailed ground squirrels), or not until the second (for example, *M. flaviventris*, *S. columbianus*, and *C. ludovicianus*), or third summer (for example, *M. olympus*) of life. With the possible exception of the asocial species, the mother-daughter bond is not usually abruptly terminated. Daughters typically establish home ranges that overlap with the mother's range and so the opportunities for social interactions persist into adulthood. Among *S. richardsonii*, mothers and daughters continue to interact amicably more often than agonistically but, because they spend the majority of the time in non-overlapping core areas, such interactions are not frequent. Female black-tailed prairie dogs occupy ranges that coincide with their mother's range throughout their life-time, permitting continued cohesive behavior.

The trends in the evolution of sociality among ground-dwelling

sciurids pose three fundamental questions: 1) what are the selective advantages of female sedentariness and male dispersal; 2) what are the selective advantages of female clumping and range sharing; and 3) what are the selective advantages to both males and females of male territoriality.

Costs of dispersal are probably high. A male that leaves the natal area must forage, avoid predators, locate sleeping burrows and hibernacula, etc., in unfamiliar terrain, with no guarantee that he will ultimately locate a suitable environment, ecologically and socially, in which to settle. Both the proximate and ultimate causes of dispersal remain elusive for ground-dwelling sciurids (Dobson, 1979; Downhower and Armitage, 1980; Dunford, 1977*b*; Green, 1977; Michener, 1979*c*; Michener and Michener, 1973, 1977; Pfeifer, 1980; Schmutz et al., 1979; Yeaton, 1972) and for other mammals (see Bekoff, 1977, for review). One obvious result of sex-biased differential dispersal is the avoidance of inbreeding (Hoogland, 1982), which could be achieved either by male or by female dispersal. Male sedentariness, however, is the exception among mammals (see Greenwood, 1980, and Packer, 1979, for reviews), implying that advantages typically accrue to females that remain in the natal group or area to reproduce. For ground-dwelling sciurids, burrows are an essential resource for both survival and reproduction. By remaining in or near the natal area, females have an opportunity either to use burrows already proven adequate by the survival and reproductive success of the mother, or to locate nearby burrows readily before hibernation commences. Dispersing males, in unfamiliar terrain, must locate unused burrows or excavate new burrows that are of suitable quality (depth and drainage) to survive overwinter. Males could avoid the costs of dispersal and of inbreeding by being able to identify close female kin and not copulating with them. Selection has not favored this alternative in ground-dwelling sciurids, in part because the rearing of litters in isolation permits positive identification of only the mother and littermate sisters, and in part because the majority of females in and around the natal area are relatives of varying degrees of kinship, providing a sedentary male with few opportunities to locate unrelated females even if he were able to identify them.

Aside from avoidance of inbreeding, other potential benefits accruing to males that disperse include increased access to females and avoidance of aggression from members of the natal group. The

eviction of subadult males (including sons) by a territorial male reduces intrasexual competition for females within the territory (Armitage, 1974; McLean, in press; Slobodchikoff, pers. comm.). Emigration by subadult males in response to conspecific aggression will have evolved only if the costs of resisting eviction outweigh the costs of leaving the natal area. To date, the factors promoting the evolution of sex-biased differential dispersal have not been adequately explained for any species of ground-dwelling sciurid. Potential advantages of differential dispersal by males include promotion of outbreeding (advantageous to both sexes), reproduction by females in a familiar area (primarily advantageous to females), location by males of more mates (primarily advantageous to dispersing males), reduction of intrasexual competition for mates (primarily advantageous to territorial males), and avoidance of intraspecific aggression (primarily advantageous to dispersing males).

Various automatic costs result from coloniality (Alexander, 1974) and group living will be maintained via selection only if individuals benefit more from membership than they suffer. The probable major advantage of female clumping and range overlap is improved predator detection; deterrence of predators (Stromberg, 1974) and statistical avoidance of becoming the predator's victim (see Bertram, 1978, for review) are additional advantages. Females spend less time alert when they are in larger groups and when they are centrally located (Hoogland, 1979*a*, 1981*a*; Svendsen, 1974). The prevalence of alarm calling and the tendency for callers to be females, especially reproductives with living family (Dunford, 1977*c*; Leger and Owings, 1978; Sherman, 1977; Schwagmeyer, 1980) further suggest that the prime advantages of daughter retention and female clumping are improved survival and reproductive success via early warning of impending danger. Armitage (1981) emphasized that retention of daughters can be viewed as a mechanism permitting continued reproductive investment by parents (particularly mothers), thereby increasing their reproductive success and that of the daughters.

Hoogland (1979*a*, 1981*a*) and King (1955) concluded that, for black-tailed prairie dogs, the most important benefit of coloniality is predator defense. The unrestricted access that coterie members have to all burrows (except natal burrows in spring) ensures proximity to a refuge; the clipping of vegetation and the general modification of ground cover through burrowing and feeding ensures

greater visibility and rapid detection of approaching predators; alarm calling by conspecifics warns colony members of impending danger. However, females do not communally nurse pups, instead they actively defend a natal territory against coterie members, even though the offspring will mingle with juveniles of other litters in the coterie immediately following weaning. The costs of extending communal and cooperative behavior to rearing of pups have not been identified (Michener and Murie, in press). In general, communal nursing is rare among group-living mammals (Bertram, 1978) (but see Rood, this volume, for joint nursing in the dwarf mongoose, *Helogale parvula*).

Armitage (1981) noted that social grade correlates positively with delayed maturity, and that prolonged amicable associations between parents and offspring permit offspring to remain in the natal area until the age of dispersal (sons) or recruitment (daughters). Although it is appropriate that the male associated with a female group behaves so as to permit (his) offspring to remain with mothers, Armitage (1981) did not address the question of why harem systems evolved from female clusters originally. The selective advantages of the superimposition of male territories over female ranges are probably associated with greater assurance of access to estrous females and greater protection of offspring born within the territory (see Barash, 1975, for discussion of paternal behavior in the hoary marmot). For species in which males defend territories after the breeding season, the territorial male is probably the sire because of his preferential, if not exclusive, access to the females within his territory (Murie and Harris, 1978; McLean, in press). From the female's point of view it is unimportant which male controls the territory provided that the male tolerates her offspring and is successful at repelling conspecifics and reducing risks of predation. Consequently, there is a potential asymmetry in the value of male territorial behavior to males and females. Males are not assured of paternity because they do not control the movements of females in and out of the territory (Carl, 1971; Murie and Harris, 1978); the system will have evolved only if, on average, the male is actually protecting his own genetic investment rather than that of some other male, and if males defending territories have greater reproductive success than those without territories. Little information is available on alarm calling in the more social species; territorial males, because of association with (their) offspring, are expected to be more frequent callers than are males in the non-territorial systems. McLean (in press) noted that

during the period when pups were in the burrow, male Arctic ground squirrels vocalized more than females, but once pups emerged both sexes called equally frequently. Hoogland (1981*b*) reported that adult and yearling male black-tailed prairie dogs with relatives in the home coterie alarm-called more often in the presence of a stuffed badger than did males without relatives.

One cost of group living may be increased exposure to intraspecific predation. Killing of conspecifics in free-living populations has been observed or imputed for various ground-dwelling sciurids (Townsend's ground squirrel [Alcorn, 1940]; Belding's ground squirrel [Sherman, 1981*b*]; Columbian ground squirrel [Holmes, 1977; McLean, 1978; Steiner, 1972]; Arctic ground squirrel [McLean, 1981, in press; Steiner, 1972]; yellow-bellied marmot [Armitage et al., 1979]). Where subsequent consumption of the victim occurs, one suggested benefit of killing and cannibalism is acquisition of food, particularly protein (Armitage et al., 1979; Holmes, 1977; Sherman, 1981*b*). Another benefit, reducing competition for space, has been proposed for the two species, Arctic and Belding's ground squirrels, in which infanticide (killing of unweaned young that have not yet left the natal burrow) has been documented (McLean, 1981, in press; Michener, in press; Sherman, 1981*b*). Because of the vulnerability of young animals to intraspecific predation, selection should favor behaviors promoting defense of progeny by the parent(s). One consequence of exclusion of (unrelated) conspecifics from the area surrounding a natal burrow is protection of infants. Active defense, via physical attack directed at the intruding male, of recently weaned juveniles by the mother or her female relatives occurs in Arctic ground squirrels. I have previously noted (Michener, 1973*b*) that immature animals are more vulnerable to attacks by adult males, sometimes leading to death, in species in which adult males are territorial than in species in which males have no prominent social position after the breeding season. This correlation between male aggression toward juveniles (and yearlings in species with delayed maturity) and sociality may extend to male-infant interactions; in *S. parryii* infanticide is typically perpetrated by adult males establishing new territories and includes attacks on recently weaned young (McLean, in press), whereas in *S. beldingi* infanticide is most frequently committed by adult females (that have lost their own young to interspecific predators) and ceases once infants reach weaning age (Sherman, 1981*b*). Although female Arc-

tic ground squirrels defend their progeny, they are not as successful as the territorial male at evicting intruding males or preventing attacks from culminating in infant or juvenile mortality. As McLean (in press) suggested, male territorial behavior persisting through the period when infants are underground may represent paternal protection, necessary in a species in which adult male intruders can overcome the mother's defense and kill some or all of her offspring. Unresolved, in the evolutionary perspective, is whether male territoriality evolved in order to thwart infanticide or whether male-committed infanticide evolved in order to reduce competition for space (i.e., whether infanticide is a cause or a consequence of the social system).

Kin Identification

The social systems of ground-dwelling sciurids are derived from mother-daughter and littermate associations, and consequently tend to be matrilocal, matrifocal, and matrilineal. Kinship forms the basis of the social system, raising the question of how (and if) kin are identified.

Because litters are reared individually and in isolation from other litters in all species of ground-dwelling sciurids, the primary socialization of juveniles is always with the mother and littermates. Juveniles do not normally first encounter other conspecifics until some time after emerging from the natal burrow. Among species such as Richardson's ground squirrels, these encounters are both rare and agonistic during the first 2 to 3 weeks of above-ground activity, and do not result in amicable bonds forming with members of other families. Occasional exceptions occur in *S. richardsonii* when the mothers are littermate sisters living in close proximity; litters may amalgamate around the time of weaning to form a single supra-litter (G. Michener, 1972). Among black-tailed prairie dogs, encounters with conspecifics occur as early as the first day of above-ground activity, are amicable, and often result in juveniles sleeping with coterie members other than the mother and littermates. Because female black-tailed prairie dogs do not discriminate between juveniles from different litters within the coterie, Hoogland (1979*b*) concluded that they cannot distinguish their own young from those of other females in the coterie. However, there is a distinction between whether a mother *can* identify her offspring and whether

she *does* identify them. Prairie-dog mothers may recognize their own juveniles but not behave preferentially toward them.

The quality of interactions occurring between conspecifics in black-tailed prairie dogs requires identification of conspecifics into one of two classes—coterie members versus non-coterie members. Typically this distinction coincides with (apparent) discrimination between close genetic relatives and distant genetic relatives. Although there are varying degrees of genetic relatedness between members of the same coterie (full-sibling, half-sibling, grandmother, granddaughter, first cousin), differential behavior based on differences in genetic relatedness has not been documented. Among Belding's and Richardson's ground squirrels, animals discriminate two classes of conspecifics that coincide with genetic relatedness; mother-offspring and littermate combinations (family) are differentiated from all other possible degrees of relatedness (non-family). For all species, family (or harem) membership, genetic relatedness, and familiarity via early socialization covary; observed patterns of social discrimination could be based on any of these factors.

In no sciurid has individual recognition been established. In all cases where discrimination between two classes of conspecifics has been demonstrated experimentally (Harris and Murie, 1982; Michener, 1973*a*, 1974; Michener and Sheppard, 1972; Sheppard and Yoshida, 1971), the most parsimonious explanation is discrimination of familiar versus unfamiliar animals. In natural contexts the class of familiar conspecifics is typically established through primary socialization in the natal burrow and socialization occurring during the first few days of above-ground activity. Should associations between non-family members occur during this period, recognition "errors" result; that is, an individual behaves toward a non-relative in the same manner it normally does toward its closest genetic relatives. Such "errors" have been documented in Richardson's and Belding's ground squirrels (G. Michener, 1972; Sherman, 1980). Newly emerged *S. beldingi* pups occasionally inadvertently attach themselves to a neighboring litter and subsequently treat former littermates (siblings) and mother as unfamiliar (unrelated) animals. If a *S. richardsonii* pup, up to at least 16 days old, is fostered to a lactating female in the field or laboratory, subsequent social interactions between the weaned juvenile and its foster mother are amicable, whereas those with the biological mother are agonistic. Lactating Richardson's ground squirrels do not discriminate

between pups, retrieving both their own and others, but discrimination does occur by the time young are 5 weeks old (G. Michener, 1972, 1974). Pups as young as 20 to 24 days old and with unopened eyes respond differentially to the mother and to an unfamiliar lactating female (G. Michener, 1974) but, in the field, newly emerged pups sometimes fail to identify an intruding adult when that adult is in an area normally used by the mother. Within 2 to 3 weeks of emergence, juveniles correctly distinguish between the mother and all other adults regardless of the location of the interaction (Michener, 1973*a*, 1981). These various observations suggest that, in natural contexts, squirrels identify close relatives on the basis of familiarity established via amicable interactions with these relatives during the first 4 to 6 weeks of life.

Incorporation of those conspecifics that are frequently encountered in amicable contexts during the first few days of above-ground activity into the same class as mother and littermates, would account for the inclusion of coterie members in black-tailed prairie dogs and of older non-littermate sisters in Belding's ground squirrels into the class of preferred conspecifics. The social context within which such extrafamilial conspecifics are encountered influences the ultimate significance of the encounter. For instance, juvenile *S. beldingi* only behave toward older sisters as they do toward littermates if they encounter them in the presence of the common mother (Sherman, 1980). The extent to which adult prairie dogs are necessary to facilitate litter mixing and amicableness within a coterie is not known.

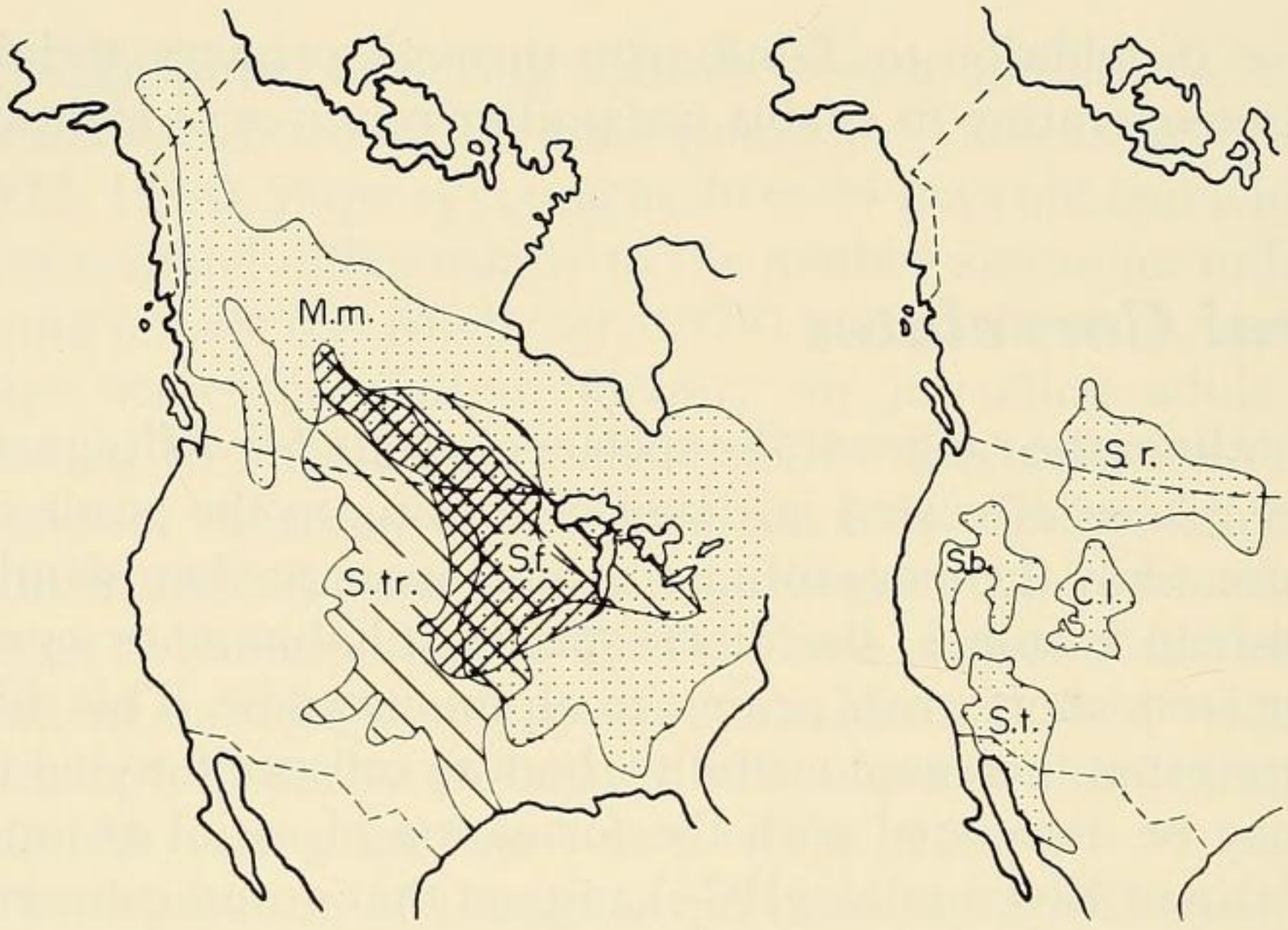
The coincidence between genetic relatedness and familiarity is reduced if there is multiple siring of litters in polygynous species because half-siblings could either be littermates (same mother, different fathers) or non-littermates (same father, different mothers). Female Belding's ground squirrels copulate with more than one male, and resulting litters are typically multiply-sired (Sherman, 1977; Sherman and Morton, 1979; Hanken and Sherman, 1981). Although less common, female black-tailed prairie dogs sometimes copulate with more than one male (Hoogland, 1981*b*), where the second male is from an adjacent coterie. Assuming that differential favoritism is based solely on familiarity, littermate half-siblings are expected to interact as do littermate full siblings whereas non-littermate half siblings are expected to interact as do totally unfamiliar conspecifics. If this prediction is not fulfilled, a mechanism

other than, or in addition to, familiarity through primary socialization must be operating to enable unfamiliar relatives to identify each other.

Ecological Correlates

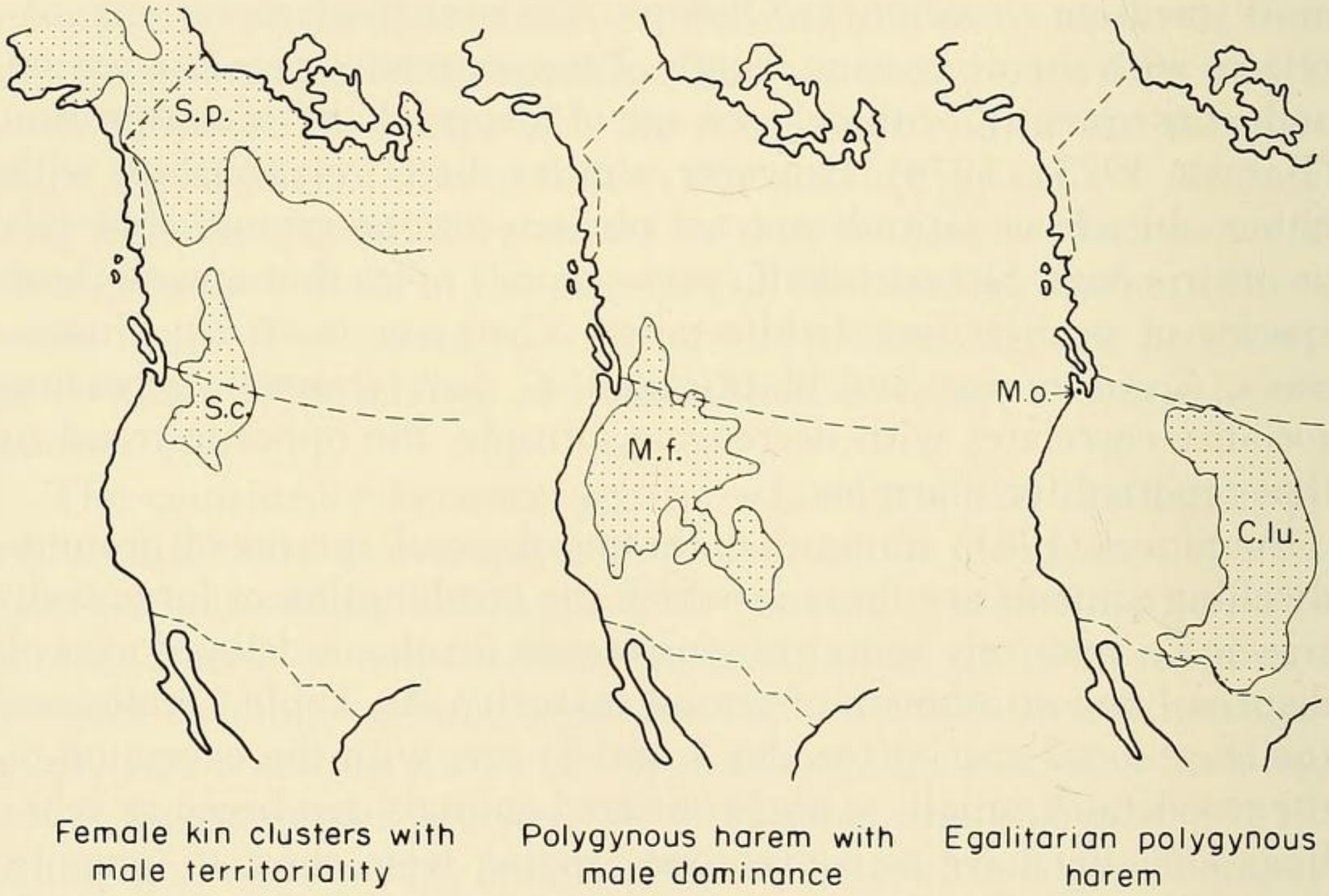
Figure 3 outlines the ranges of the species of ground-dwelling sciurids that have been discussed in detail, according to the grade of social structure. Only the more solitary species occur predominantly in woodland-field ecotones; the other species inhabit more open areas varying from short-grass prairie to alpine meadow. This difference suggests that increased visibility, both to conspecifics and to predators, may be associated with the formation of social groups. Barash (1974) and Kivett et al. (1976) suggest that group cohesion is associated with increased harshness of the environment. This trend is exhibited among species of *Marmota,* where the increasing sociality from woodchucks (low elevation) to yellow-bellied marmots (medium elevation) to Olympic marmots (high elevation) correlates with the decreasing length of the vegetative growing season and, consequently, with delayed age of dispersal and of maturation (Barash, 1973*a,* 1974). However, similar direct relationships with either altitude or latitude are not obvious among ground squirrels or prairie dogs. Slobodchikoff (pers. comm.) notes that among three species of prairie dogs (white-tailed, *Cynomys leucurus*; Gunnison's, *C. gunnisoni*; and black-tailed, *C. ludovicianus*) increasing sociality correlates with decreasing altitude, the opposite trend to that reported for marmots.

Armitage (1981) stated that the more social species of ground-dwelling sciurids are those in which the combination of large body size and a relatively short growing season results in delayed ages of dispersal and attainment of sexual maturity. As Table 1 indicates, the least social species (grades 1 and 2) are, with the exception of the woodchuck, small- to medium-sized animals that breed as yearlings and that have active seasons ranging from short to long. In the higher social grades, in which adult males play a prominent role (grades 3, 4, and 5), are species that first reproduce as yearlings, 2-year-olds, and 3-year-olds. Although these social species are all large sciurids, their active seasons range from short, to long, to continuous. What characterizes the social species is the prolonged association between adults and subadults. High adult : subadult sea-



Asocial

Single-family female kin clusters



Female kin clusters with male territoriality

Polygynous harem with male dominance

Egalitarian polygynous harem

FIG. 3. Range maps of selected species of ground-dwelling sciurids grouped according to the grade of social structure exhibited by the species (maps modified from Hall and Kelson, 1959). Asocial: M.m., *Marmota monax,* S.f., *Spermophilus franklinii*; S.tr., *S. tridecemlineatus.* Single-family female kin clusters: S.r., *S. richardsonii*; S.b., *S. beldingi*; S.t., *S. tereticaudus*; C.l., *Cynomys leucurus.* Female kin clusters with male territoriality: S.p., *S. parryii*; S.c., *S. columbianus.* Polygynous harem with male dominance: M.f., *M. flaviventris.* Egalitarian polygynous harem: M.o., *M. olympus*; C.lu., *C. ludovicianus.*

sonal coincidence is achieved either by delayed adult immergence which prolongs the active season (for example, Arctic ground squirrel), by delayed age of sexual maturity which prolongs subadulthood over several years (for example, Olympic marmot), or by year-round activity (for example, black-tailed prairie dog). Among the 18 species listed in Table 1, the typical age at which females first reproduce (FAFR) is a good predictor of social grade, accounting for 70% of the variation in social grade ($n = 18$, $r = 0.838$). However, among the seven species listed with social grades higher than 2, adult : subadult seasonal coincidence (taken as the mid-point value of the range given) is a better predictor of social grade ($r = .915$, $P < .01$, variance explained = 84%) than is FAFR ($r = .719$, $P > .05$, variance explained = 52%).

Because social species are characterized by large size and by synchrony in the active seasons of various cohorts, whereas relatively asocial species are characterized by early immergence of adults, especially males, it is relevant to know why the circannual cycle is asynchronous among cohorts in the smaller species. In those species with strongly staggered patterns of immergence of the different cohorts, juveniles continue above-ground activity and gain weight for many weeks after the disappearance of adults, implying that adult immergence is not precipitated by inadequate food supplies or inclement weather. Clark (1977) and Yeaton (1972) suggested that early immergence of adults is an adaption to reduce intraspecific competition, particularly competition for food between males and juveniles, but I reject this hypothesis for two reasons. First, early immergence by a male should be favored only if the juveniles that profit from the male's absence are his own progeny; that is, if a male resides close to his progeny. As discussed above, males often do not remain close to their mate(s) and offspring. Second, the disappearance of males is unlikely to significantly increase the food available to juveniles. Among Richardson's ground squirrels, for instance, which have an adult sex ratio of about three females per male and litter size at weaning of four or five pups (Michener, 1979*a*, 1979*c*; Michener and Michener, 1971; I recorded an average litter size at weaning of 9.1, range 7–14, for 13 litters on a pasture in southern Alberta in 1981), there are at least 12 to 15 juveniles in the population for every adult male. The disappearance of the male can have only a negligible effect in providing additional food to these juveniles. Furthermore, adult male *S. richardsonii* are socially subordinate to juveniles when they intrude into the juvenile's core

area (Michener, pers. observ.), so juveniles are unlikely to be limited, either directly or indirectly, from access to food by males. Early male immergence does not benefit juveniles; the short active season of adult males is more likely attributable to survival of the male. Male *S. richardsonii* become obese during June, when daily temperatures approach the maximum for the year, and this increasing size renders them less agile and less able to squeeze down small bolt holes (pers. observ.). Fat males are presumably vulnerable to predation, hyperthermia, and water stress; early immergence represents a compromise between further activity permitting additional weight gain but increasing mortality from predation and environmental stress. Provided that the decreased mortality associated with early immergence more than compensates for the increased mortality associated with the longer period of overwinter dependence on fat stores, the short active season will be favored by natural selection. Morton (1975) suggested that, for Belding's ground squirrels, early entry into hibernation is related to predator avoidance.

Adult male Arctic ground squirrels are atypical in that they do not immerge early. In contrast to female *S. parryii* and to members of the other hibernating species, male Arctic ground squirrels hoard food and they lose relatively little body weight over winter (Green, 1977; McLean and Towns, 1981). By providing energy for thermogenesis in the form of food stores in the hibernaculum, males may be avoiding some of the costs of large and ungainly fat depots, thereby allowing them to prolong the active season.

Some of the apparent inconsistencies in correlating sociality and environment arise from the difficulty of defining "environmental harshness" (see Webb, 1980, 1981). Alpine and subalpine habitats are typically considered severe because of the shortness of the growing season and the possibility of snow through much of the year. However, such habitats are usually moist and experience a relatively narrow range of temperature extremes. Water stress, an environmental hazard unlikely to face high elevation species, is a potential threat to species inhabiting short-grass prairie. Blake (1977) and Davis (1976) suggested that seasonal hypothermia may be an adaptation to stressful conditions imposed by lack of water. Differing abilities to withstand water stress are related to the differences in hibernation patterns between white-tailed and black-tailed prairie dogs (Bakko, 1977; Pfeiffer et al., 1979). White-tailed prairie dogs, unable to tolerate water loss, are obligate hibernators whereas

black-tailed prairie dogs, adapted to withstand dehydration, remain active year-round, permitting continuous social contact.

In summary, increased social tolerance correlates with increased coincidence of the active periods of various cohorts via prolonged active seasons or shortened active seasons associated with delayed dispersal. Consequently, the timing of the circannual cycle and, ultimately, the environmental parameters that have determined that timing, are factors that have promoted the evolution of sociality in ground-dwelling sciurids.

Areas for Future Investigation

Our understanding of ground-dwelling sciurid systems is currently limited by the lack of information on paternity. Not only is paternity difficult to establish but, for most species, it is not known whether females copulate with several males and, if they do, whether they produce multiply-sired litters. For the species whose social organization is based upon single-family matrilineal kin groups, the male residing nearest to a litter cannot be assumed to be the father because males move extensively during and after the breeding season. For those species in which adult males are territorial in spring beyond the breeding season, males may be associated with their mate(s) and progeny (Foltz and Hoogland, 1981). Until paternity testing is performed, the supposition that a territorial male is the father of the juveniles that emerge within his territory is only speculative.

A potential cost of the greater sedentariness of males in species with territoriality is inbreeding. In the yellow-bellied marmot, however, adult males rarely reside for more than 2 to 3 years in a given harem and because females do not commence reproduction until at least 2 years old, often not until 3 years of age, a male is unlikely to mate with a daughter. Black-tailed prairie dogs typically first breed as 2-year-olds, although yearlings have been reported to successfully reproduce in newly established colonies (Franklin, pers. comm.; Halpin, pers. comm.). Because females are sedentary and usually reproduce in the coterie of birth, inbreeding could be avoided by male emigration. Yearling males do disperse and so are unlikely to reproduce with sisters. Hoogland (1981*b*, 1982) suggested that adult males usually reside for a maximum of 2 years in a given coterie and hence are no longer present when daughters achieve

reproductive maturity. Long term studies are necessary with more species to establish whether inbreeding is avoided through dispersal of adult males in the long-lived species with territorial males.

Familiarity and maternal kinship co-vary. Familiarity through primary socialization is likely to be the proximate mechanism by which kin selection can operate. Cross-fostering experiments are the most valuable technique for partitioning out the relative contributions of postnatal familiarity and kinship to observed social patterns. Such experiments are currently being conducted with Arctic and Belding's ground squirrels (Holmes and Sherman, in press, pers. comm.), and Richardson's ground squirrels (Davis, in press, pers. comm.). Preliminary indications are that, for juvenile *S. parryii* and yearling *S. beldingi*, animals reared together rarely interact agonistically, regardless of their genetic relatedness and sex, suggesting that familiarity typically plays a major role in sibling recognition in natural contexts. However, among animals reared apart siblings are less aggressive when subsequently paired than are non-siblings. This effect is greater for female-female pairs than for mixed sex or male-male pairs, and suggests that sisters do not necessarily require lengthy post-natal association to be able to identify each other. Cross-fostered juvenile *S. richardsonii* also exhibit differential responses to unfamiliar siblings versus unfamiliar non-siblings; siblings that were separated on the day of birth approach and touch each other more frequently and remain in greater proximity than do unfamiliar non-siblings. Because littermates share a common uterine and post-natal environment, prior association could account for the apparent ability of siblings to identify each other even when reared apart from within a few hours of birth. Female *S. beldingi* frequently copulate with more than one male, producing multiply-sired litters (Hanken and Sherman, 1981); interactions among yearling female littermate half-siblings are more aggressive than those between littermate full-siblings, suggesting an ability to distinguish between differing degrees of genetic relatedness even when reared together from conception (Holmes and Sherman, in press). Further cross-fostering experiments with more species will assist in assessing the relative significance of early social experience as an underlying mechanism of kin identification, kin preference, and, ultimately, of social structure.

Quantification of rates of social interactions in natural contexts between conspecifics of varying degrees of kinship need to be augmented and improved (see Michener, 1980*c*). Because kin are likely

to be in greater physical proximity than non-kin, measurements of interaction rates need to be corrected for the likelihood that different classes of animals will be physically able to interact. To date, comparisons of interaction rates in the field among conspecifics of varying genetic relatedness are limited (Dunford, 1977*b*; Michener, 1973*a*, 1981; Sherman, 1980; Yeaton, 1972).

Attempts to relate social structure to species ecology require additional information on the timing of the circannual cycle under natural conditions, on the advantages of short active seasons, and on the reasons for age and sex differences in timing of immergence. Intraspecific comparisons of populations located in different habitats, and interspecific comparisons involving data from more of the species of ground-dwelling sciurids would contribute to interpretation of correlations between environment and socioecology. Valuable comparisons could be made of the socioecology and physiological ecology of Richardson's ground squirrels, white-tailed prairie dogs, and black-tailed prairie dogs. Although the latter two species are closely related phylogenetically (Nadler et al., 1971), their social systems diverge. The white-tailed prairie dog social system and circannual cycle correspond with those of the Richardson's ground squirrel despite differences in habitat and despite greater phylogenetic divergence. Richardson's ground squirrels and black-tailed prairie dogs are sympatric over portions of their ranges but they show different adaptations to xeric conditions (obligate hibernation and tolerance of water stress, respectively) and have different social systems.

Summary

The five proposed grades of social structure—asocial, single-family female kin cluster, female kin cluster with male territoriality, polygynous harem with male dominance, egalitarian polygynous harem—form a continuum of sociality based on the mother-headed family as the most fundamental social subunit. Sex-biased differential dispersal results in clustering of female kin in all species. Prolonged social association between mother and daughters and between littermate sisters, increasing overlap of the ranges used by such female kin, and relaxation of social distinctions between the litters of adjacent female kin have led to multiple-family female kin clusters that communally share a common range. The male-female

pair bond is not a fundamental social unit in ground-dwelling sciurid social organization, and the association of males with clusters of female kin probably commenced as an incidental result of males and females independently choosing to live in the same preferred habitat. Increased probability of guaranteed access to estrous females and the improved survival of offspring living under the indirect protection of their father would promote male territoriality and the establishment of uni-male harems. The simultaneous development of female cohesiveness and male territoriality account for the integrated social structure of Olympic marmots and black-tailed prairie dogs.

The prime forces determining the trends in social organization are hypothesized to be increased protection from both intra- and interspecific predation and the avoidance of inbreeding. Sex-biased differential dispersal is the proximate mechanism that leads to formation of female kin clusters. It also promotes outbreeding while permitting females to hibernate and reproduce within a familiar locale already proven successful by the survival and reproductive success of the mother. The clumping of female kin permits improved survival and reproductive success via increased group vigilance, use of alarm calls to warn of danger, sharing of resources, and reduced time spent in establishing and maintaining natal territories. The association of a male (presumably the father) with female kin groups further enhances survival and reproductive success by protection of resources within the territory, by protection from intraspecific aggression, and by increased group vigilance.

Although the social structure of the ground-dwelling sciurids is based upon genetic relatedness between females, the observed patterns of differential behavior to kin and non-kin do not require that animals be able to identify kin as such. Because litters are reared in isolation from all conspecifics, the primary socialization is always with the mother and littermates. For some species these relations compose the group of conspecifics that is distinguished from all other animals. In the more social species, where juveniles engage in amicable contacts with conspecifics other than the immediate family in the days following entry into the above-ground population, the preferred group of conspecifics expands to include these individuals. Typically the additional individuals will be close kin (aunts, non-littermate sisters, cousins). In either situation it is the animals that have been met in amicable social situations during the

first 4 to 6 weeks of life, and hence are familiar, that constitute the favored group. Thus kinship and familiarity covary, and familiarity through early socialization is an adequate proximate mechanism for distinguishing between kin and non-kin classes. The assumption that differential behavior to kin and non-kin is based on familiarity is amenable to testing through cross-fostering experiments and through comparison of the interactions between littermate half-siblings and non-littermate half-siblings.

Degree of sociality does not correlate meaningfully with either latitude or altitude. The two most social sciurid species, Olympic marmots and black-tailed prairie dogs, occur in divergent habitats (alpine meadow and short-grass prairie). Within a given habitat, such as subalpine meadow, social systems range from single-family kin clusters (Belding's ground squirrels), kin clusters with male territoriality (Columbian ground squirrels), to polygynous harems with male dominance (yellow-bellied marmots). Despite these apparent inconsistencies, social structure does appear to have ecological correlates if the timing and patterns of circannual rhythmicity are assumed to be evolutionary adaptations to environmental exigencies. The least socially tolerant species mature as yearlings and have the least amount of coincidence of above-ground activity between adult cohorts and immature cohorts, whereas the most tolerant species have extensive overlap in the active seasons of adults and immatures. Sociality is related to prolonged active seasons for adults and/or to increased number of seasons required for juveniles to attain maturity. Ultimate understanding of the socioecology of ground-dwelling sciurids requires knowledge of the selective factors that have determined the nature of the circannual cycle, and that have thereby determined the degree of coincidence in the seasonal activity of various cohorts.

Acknowledgments

Financial assistance was provided by the Department of Zoology, University of Alberta, by Dr. J. O. Murie via NSERC grant A-5865, and by the Friends of the National Zoo. Secretarial assistance was provided by the Department of Biological Sciences, University of Lethbridge and by EPO Biology, University of Colorado.

The following people generously took time to read and comment on an earlier version of the manuscript and to provide information

on their current research with sciurids: Z. T. Halpin, J. O. Murie, I. G. McLean, W. G. Holmes, and M. A. Harris. I thank my son, Rory, and my husband, Dan, for providing me with the uninterrupted time in which to pursue my interest in sciurid social organization.

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