Life history consequences of social complexity: a comparative study of ground-dwelling sciurids

Daniel T. Blumstein and Kenneth B. Armitage
Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045, USA

We examined life-history consequences of increased social complexity in ground-dwelling sciurid rodents. We derived a continuous metric of social complexity from demographic data. Social complexity increased with the number of age–sex "roles" that interacted in a social group. Data were analyzed by computing phylogenetically independent contrasts and by using phylogenetic autocorrelation to estimate and then remove the maximum amount of variation in life-history variables that could be attributed to phylogenetic similarity. Analyses that incorporated estimates of phylogeny generated consistent results. As social complexity increased, a smaller proportion of adult females bred, there was a greater time to first reproduction, litter size decreased, and there was greater first-year offspring survival. Social complexity influenced neither gestation nor lactation time. Thus, social complexity has costs in terms of a reduction in the annual per-capita number of offspring produced but benefits in terms of enhanced offspring survival. *Key words: Cynomys*, costs and benefits of sociality, life history, *Marmota*, social complexity, *Spermophilus*. [*Behav Ecol 9:8–19 (1998)*]

S ociality involves benefits and costs of forming aggregations and of behaviors in the aggregations. Generally, animals are hypothesized to aggregate to reduce predation risk and/or because of the distribution of critical resources (Alexander, 1974). Social structure and social behaviors may further increase the benefits of aggregation (Alexander, 1974). Thus, behaviors such as alarm calling (Sherman, 1977), allogrooming (Hart and Hart, 1992), dominance relationships (Bernstein, 1981), food calling and sharing (e.g., Benz, 1993; Goodall, 1986; Hauser 1996), helping (e.g., Brown, 1987), individual recognition (Wrangham, 1983), mating systems (Emlen and Oring, 1977), and a variety of other social behaviors can evolve and be elaborated once social groups have formed. Aggregation has its costs: more competition for scarce resources (Wrangham et al., 1993); monopolization of resources by dominant animals (Wrangham, 1981); increased aggression (Walters and Seyfarth, 1986); increased risk of parasite and disease transmission (Brown and Brown, 1986; Mooring and Hart, 1992); attraction of more predators (Kruuk, 1964; Pienkowski and Evans, 1982); increased reproductive competition, which may lead to infanticide (Hoogland, 1995); and prevention, delay, or an influence on reproduction in certain animals (e.g., Abbott, 1987; Packer et al., 1995; Wasser and Barash, 1983). These and other factors may lead to variation in reproductive success among group-living animals.

Each of these specific benefits and costs emerges from sociality. While not specifically stated and defined, more of these costs and benefits are assumed to emerge as social complexity increases. In this paper we explicitly address the question of costs and benefits of increased social complexity. We focus on ground-dwelling sciurid rodents (marmots, *Marmota* spp.; prairie dogs, *Cynomys* spp.; and ground squirrels, *Spermophilus* spp.) and review the literature to summarize a series of life-history variables. Ground-dwelling sciurids are an ideal taxon about which to ask questions regarding the evolutionary impacts of social variation. A large body of literature exists on

social variety in marmots, prairie dogs, and ground squirrels (e.g., Barash, 1989; Bibikow, 1996; Hoogland, 1995; Murie and Michener, 1984). Social organizations range from species in which individuals disperse immediately after weaning and live more or less solitary lives, to species in which individuals exhibit delayed dispersal and in which overlapping generations of individuals share a home range and interact amicably. Moreover, species can be placed objectively along a continuum of social complexity (see below and Blumstein and Armitage, 1997). We ask the following six life-history questions: Does social complexity influence (1) the percentage of adult females who breed, (2) the time to first reproduction, (3) gestation time, (4) average litter size, (5) lactation time, and (6) percent juvenile survival to age 1?

Defining complexity

The term "complexity" is often used but rarely defined explicitly (McShea, 1991, 1996). Complexity can be explicitly defined using information theory (Shannon and Weaver, 1949). A more complex system requires more information (specifically "binary units") to be fully described than does a less complex system. With respect to sociality, a species with 10 different social behaviors is more complex than one with a single social behavior because more discrete behaviors can be used in more ways (Bonner, 1988). As the number of interacting individuals increases, there is an opportunity for more social interactions and for more social behaviors (e.g., solitary animals do not need a repertoire of sophisticated dominance behaviors). We might assume that a species typically living in large social groups is more complex than a species typically living in smaller social groups. Group size has been used as a measure of sociality (e.g., Eisenberg, 1981; Janson and Goldsmith, 1995), yet social group size alone is an inadequate metric of social complexity because social behavior involves relationships between individuals, and the diversity of these relationships is not described by simply using group size. Because social systems are typically defined categorically (e.g., "monogamous" versus "polyandrous" versus "polygynous"), it is not immediately obvious how to objectively compare different social systems with respect to varia-

Life History Consequences
of Social Complexity

Environmental Constraints
-Predation
-Patchiness
-Length of growing season

Life History
-Body mass
-Length of active season

Social Complexity

Time to 1st Reproduction

% Survival to Age 1

% Adult Females Breeding

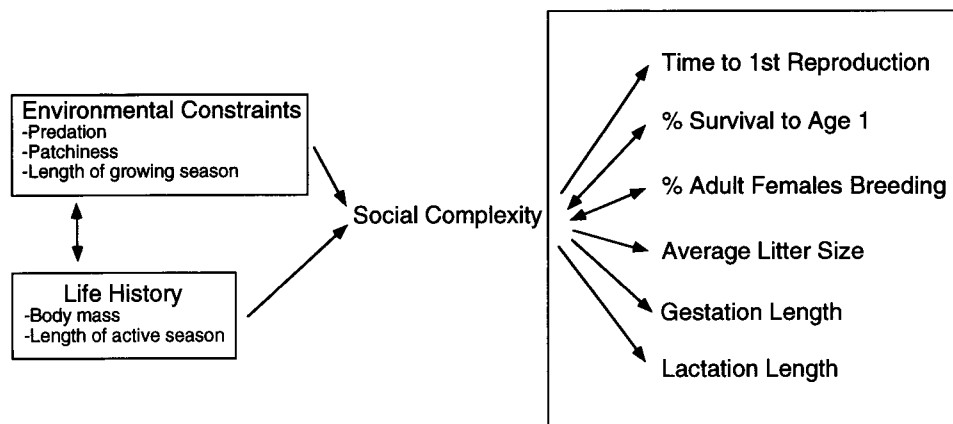Average Litter Size

Gestation Length

Lactation Length

Figure 1
Some causes and consequences
of social complexity. Causality is
justified in text.

tion in complexity. A new metric of social variation is required to specifically quantify complexity.

Social complexity emerges from groups of individuals that interact over some time. Within a group, animals may be described as having certain "roles"—socially expected behavior patterns (Blumstein and Armitage, 1997). For instance, there may be a dominant and a subordinate role. Or, there may be a breeder and a nonbreeder role. An individual's role may change over time. To quantify social complexity, it is crucial to identify roles. Practically, this is quite difficult to do in a comparative study because different studies emphasize different aspects of sociality. However, it is possible to define "demographic roles" (e.g., adult female/adult male, subadult female/male, etc.), and these demographic roles should describe the potential for more complex social behavior.

Social complexity also implies social flexibility, and intraspecific social variation is often adaptive (Lott, 1991). Consider two species with two demographic roles. Each of these roles has the same mean size (e.g., six adult males and six adult females), but the species differ in the variance around these means. Because it requires more information to describe a more variable system than a less variable system, the more variable system is more complex. For instance, if males always aggregate in groups of six (i.e., no variation), then it requires little information to describe male social structure—males aggregate in groups of six. Additional variation requires more information to describe a demographic role. Socially, a species that must be able to adapt to different types and numbers of potential social partners is more complex than one with a fixed number of social partners. Thus, social complexity increases with more demographic roles and when the number of individuals in a given role varies. It is also likely that more precisely defined roles will reveal more variation in social complexity. For instance, the six males may or may not have dominance relationships.

We previously defined social complexity using information theory (Blumstein and Armitage, 1997). We focused on social group structure, where we defined a social group as a group of individuals that remain together and interact more with each other than with other conspecifics (Slobodchikoff and Shields, 1988; Wilson, 1975). For ground-dwelling sciurids, animals in the same social group have extensively overlapping home ranges, and animals may share sleeping burrows during much of the year. In suitable habitat, there may be many contiguous social groups (e.g., a prairie dog "town," or a ground squirrel "colony"). We focus on the individual social units within this higher level aggregation because the number of

contiguous social groups will be influenced strongly by the amount of suitable habitat and by a species' total energetic requirements.

Sciurid demographic roles include adult females/males, 2 year olds, yearlings, and juveniles. Not all species have all five roles. For each role a species had, we summarized the frequency distribution of the numbers of animals (i.e., 0 males in 1 group, 1 male in 20 groups, 2 males in 36 groups, 3 males in 0 groups, etc.). From frequency distributions like these, we quantified the amount of information required to describe each demographic role.

$$H(X)_r = -{\textstyle\sum} p(i) \log_2 p(i) \qquad (1)$$

defines the number of bits of information required to describe a role, $H(X)r$, given the relative frequency, $p(i)$, of each of the discrete counts (i.e., 0, 1, 2, 3, ...) of animals in that role. We summed the $H(X)r$ for each role to get an $H(X)t$, the total number of bits required to describe a species given the number of demographic roles. Because timing of natal dispersal from sciurid social groups varies, we multiplied $H(X)t$ by a number reflecting the time to natal dispersal (1 = dispersed as juveniles, 2 = dispersed as yearlings, 3 = dispersed at age two or older), and log transformed the product to generate a number, SC_d, a value reflecting social complexity. In doing so we are aware that sciurids with more demographic roles also have delayed dispersal. In fact, this multiplication has limited effects on our data set. The multiplication emphasizes the potential importance of kin structure, a key characteristic of sociality and social complexity.

At first glance, our use of social complexity to study life history consequences may appear circular. Our metric of social complexity, SC_d, is largely determined by a species' demographic structure and thus is influenced by variables such as the time to natal dispersal. However, there is no a priori reason that more socially complex species should delay dispersal. The ground-dwelling sciurids we studied increased complexity largely by delaying dispersal, but social complexity could also increase via immigration and not delayed dispersal (e.g., imagine a college dormitory, a very complex "social group," formed exclusively by immigration).

Given our metric of social complexity, we focused on life-history consequences of social complexity and thereby imply causal relationships between social complexity and each of our life-history variables. Studying causal processes is difficult with some comparative analyses of continuous data because the sequence of change is not specified (e.g., Promislow, 1996; Ridley and Grafen, 1996). Figure 1 specifies several potential

causes and consequences of social complexity. Complex social behavior is traditionally expected when there are environmental constraints (e.g., Emlen, 1991; Emlen and Vehrencamp, 1983) that may directly, or indirectly (acting through life history variables) influence social complexity. Direct factors such as predation (Alexander, 1974; Hoogland, 1995), habitat patchiness (e.g., Michener, 1984), and growing season length (e.g., Armitage, 1981) may select for aggregation, leading to an increase in social complexity. Life-history variables such as body mass (Armitage, 1981; Barash, 1989; Bekoff et al., 1981) or the length of the active season for hibernating mammals (Armitage, 1981; Barash 1989) may also influence social complexity. Interestingly, although not the topic of this paper, we found no relationship between active season length (number of months active above ground and not hibernating) or body mass (minimum adult female body mass) on social complexity in phylogenetic analyses.

In this paper we focus on six life history consequences of social complexity. We had a priori expectations that social complexity could influence them all (Armitage, 1981, 1996). However, causality might be symmetric for at least two of these variables: percent survival to age 1 (after controlling for body mass) and the percentage of adult females who bred (after controlling for body mass). If more individuals survive to age 1, and if dispersal is delayed, then social complexity will increase because the number of age/sex classes increases. If more adult females breed, and if these breeding females are in the same social group, then social complexity may increase. Alternatively, if only older adult females breed while younger females remain in the social group, social complexity may increase. For these two variables, a potential unimplemented solution would be to hypothesize specific causal models (e.g., Asher, 1983) and study the independent paths to and from these two variables via social complexity. Currently, skeptics may interpret the results as demonstrating a strong, noncausal relationship between social complexity and these two life-history variables.

METHODS

Comparative data set

To calculate social complexity, we reviewed the literature for studies that reported demographic information. A number of studies did not report litter size distribution. If a mean and standard deviation were reported, we assumed litter size was normally distributed to estimate litter size distribution. We obtained sufficient data to calculate social complexity for 25 species: 7/14 marmots, 5/5 prairie dogs, and 13/38 *Spermophilus* ground squirrels. For these 25 species, we summarized information on the following seven life-history variables, selected both because they are generally available and because they have been used in previous comparative studies (see Appendix for comparative data and associated references):

1. Percent adult females who breed. This was generally calculated as a simple average. It was calculated as a weighted average in a few cases where there was age-specific variation and large sample sizes (e.g., Hoogland, 1995).

2. Time to first female reproduction. This was scored as 1, first reproduced as yearlings (including all species for whom it was usual); 2, first reproduced as 2 year olds; 3, first reproduced as $\geq$ 3 year olds.

3. Gestation time. This was the number of days from fertilization to birth.

4. Average litter size. If there was a choice, we summarized litter size at emergence from the natal burrow rather than at birth. Some *Spermophilus* data include embryo counts and may overestimate emergence litter size. Because birth mass

was generally not available, we could not calculate litter mass—a potentially better estimate of reproductive investment (e.g., Gittleman, 1989; Moehlman and Hofer, 1997).

5. Lactation time. This was the number of days from birth to weaning. Most species are weaned at emergence from their natal burrows, and many estimates were based on emergence date.

6. Percent male/female survival to age 1. We averaged male and female survival to age one. We attempted to not conflate dispersal and mortality when sufficient data were provided. Our average survival value may overestimate mortality for species that disperse in their first year of life.

7. Minimum female body mass. Early-season mean body mass was used when given. If not given, we calculated minimum mass from the first or second month's post-emergence body mass. If a range of values was given, we chose the lowest value in that range.

Regression analyses

We regressed our measure of social complexity, SC_d, against life-history variables. To control for possible phylogenetic nonindependence on the life-history variables and on sociality, we examined the relationship using "standardized independent contrasts" calculated for each variable and assuming several phylogenetic hypotheses (see below). We used Purvis and Rambaut's (1995) statistical package, CAIC, to calculate independent contrasts for social complexity and each of the life-history variables. As required by the method, regressions of these standardized contrasts were through the origin. Some of these life-history variables may be influenced by body mass (e.g., Armitage, 1981; Bekoff et al., 1981; Gittleman 1989; Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997; see below). To remove variation in those life-history variables that was a function of body mass, we regressed contrasts of minimum female body mass against contrasts of each variable previously reported to be influenced by mass,- and used the residuals for subsequent analyses (Losos, 1990; Martins and Garland, 1991).

No published phylogenetic hypothesis includes all species of interest. We eagerly anticipate the publication of inclusive and well-supported phylogenies and report the results from five different partial working phylogenetic hypotheses. First, we generally inferred phylogeny from taxonomy (Nowak and Paradiso, 1983), but added additional information where known (Hoffmann and Nadler, 1968; Howell, 1915, for marmots; Hafner, 1984, for sciurid subgenera), and refer to this tree as "tree 1" (Figure 2). Second, because Black (1972) assumed that the genus *Marmota* evolved in the New World from a "woodchuck-like" ancestor, we switched the location of *M. marmota* and *M. monax* to create "tree 2" (Figure 2). Thomas and Martin (1993) questioned the ancestral location of the genus *Marmota*. They suggested the genus *Marmota* evolved recently from *Spermophilus* ancestors. We calculated independent contrasts from "tree 3" (Figure 2), where *Cynomys, Marmota,* and the remaining *Spermophilus* subgroups branch simultaneously, and "tree 4" (Figure 2), which reflected a recent origin of marmots. We generated "tree 5" (Figure 2) to recognize evidence suggesting *Cynomys* is the crown group of the subgenus *Spermophilus* in the currently recognized genus *Spermophilus* (Dobson, 1985, and references therein; Goodwin, 1990). Finally, we calculated independent contrasts with two other possible tree topologies; one suggested by R. S. Hoffmann (personal communication) and the other derived from that where *Marmota* and *Cynomys* were resolved differently. Although we do not illustrate or report results based on those trees here, the independent contrasts
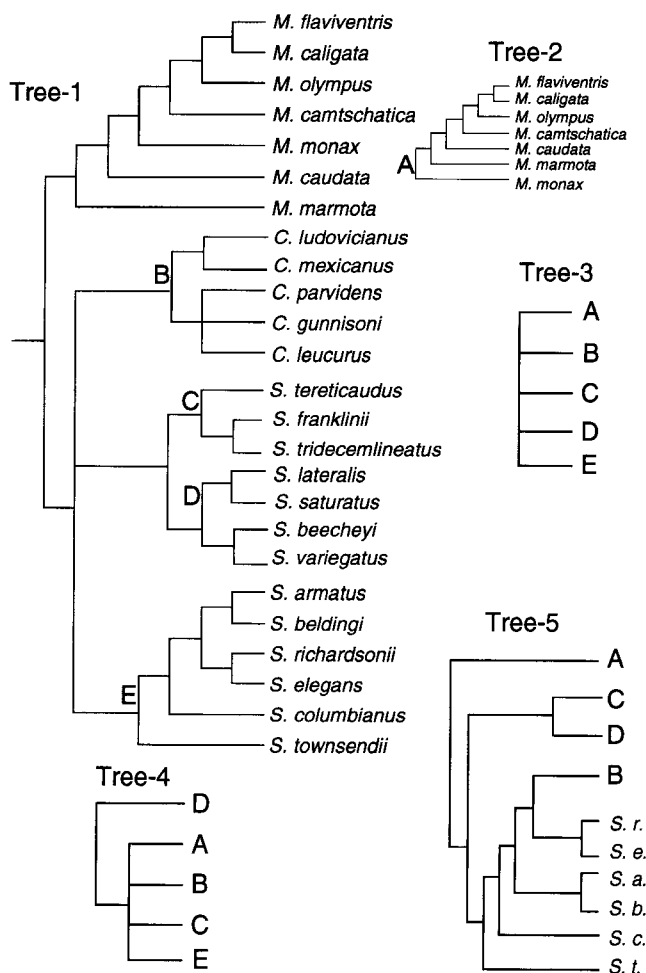
Figure 2

Phylogenetic hypotheses used to calculate contrasts. These are partial working phylogenies of sciurid rodents: recognized genera and species not included in these analyses are not illustrated. Tree 1, a taxonomically derived tree with phylogenetic information added where known. Tree 2, *Marmota monax* was shifted to reflect its possible ancestral location in *Marmota*. Letters marked at higher nodes on tree 1 and tree 2 are used to illustrate structure of the following two trees. Tree 3 illustrates an unresolved origin of *Marmota*. Tree 4 illustrates a recent origin of *Marmota* and other sciurids from a subgroup of species currently classified as *Spermophilus*. Tree 5 illustrates *Cynomys* as the crown group of the subgenus *Spermophilus*.

calculated from them led to the same conclusions as those based on trees 1–5.

To calculate standardized independent contrasts, we set all branch lengths equal and selected the "crunch" option in CAIC. Setting branch lengths equal assumes an underlying evolutionary model of punctuational change (e.g., Harvey and Pagel, 1991). In the absence of information about branch lengths, assuming punctuational change is much more straightforward than estimating an infinite number of possible branch length scenarios. Given no independent measures of branch lengths for our partial phylogenies, we did not calculate contrasts assuming Brownian motion trait evolution.

Each comparative method has strengths and weaknesses (Martins and Hansen, 1996). In addition to calculating independent contrasts, we also analyzed the data with phylogenetic autocorrelation (Cheverud et al., 1985; Gittleman and Kot, 1990; Gittleman and Luh, 1992). Phylogenetic autocorrelation permitted us to estimate and statistically remove the max-

imum amount of variation in each variable (social complexity and each of the life-history variables) that could be explained by phylogenetic similarity. This is admittedly a rough metric that perhaps better quantifies the degree of evolutionary change in a clade; strictly it should not be interpreted (Losos and Miles, 1994) as the amount of adaptive versus nonadaptive trait variation (Cheverud et al., 1985). Phylogenetic autocorrelation assumes explicitly statistical models of trait change that vary according to an autoregressive model (Martins, 1995; Purvis et al., 1994) and, under a Brownian-motion model of evolution, may produce erratic results with sample sizes < 40 (Martins, 1996). We used a single phylogenetic hypothesis, the taxonomy reported in Nowak and Paradiso (1983), to estimate the "phylogenetic distance matrix." The phylogenetic distance matrix is a "weighting matrix" that defines the relative weight that each individual species' trait value will contribute when searching for autocorrelation. The classical taxonomic classification recognizes subgenera in both *Cynomys* and *Spermophilus* and recognizes two subtribes: one containing *Marmota* and the other containing both *Cynomys* and *Spermophilus*. We used the program "P.A." (Luh et al., 1995) to fit phylogenetic autocorrelations.

RESULTS

Does social complexity influence the percentage of adult females who breed?

We had no a priori reason to expect that a species' body mass should influence the proportion of females who breed. Thus, we regressed social complexity against the percentage of adult females who breed to study costs and benefits of social complexity.

No matter how we examined the relationship, more socially complex species had a smaller percentage of adult female breeders (Table 1, Figure 3). Different methods lead to different specific estimates of the amount of variation explained by social complexity (Table 1). Explained variation ranged from 24% (based on contrasts calculated using tree 4), to 58% (calculated using raw data). All methods to adjust for phylogenetic similarity reduced the amount of explained variation.

"Correlograms" (plots of Moran's I, the autocorrelation statistic, versus taxonomic level) suggested significant autocorrelation at certain taxonomic levels that disappeared after we calculated "phylogeny-free" residuals. Phylogenetic autocorrelation results suggest a maximum of 33% of the variation in the percentage of adult females who breed may be attributed to phylogenetic similarity.

Does social complexity influence the time to first reproduction?

Body size may explain variation in the time to reproduction (Gittleman, 1989; Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997). Thus, we analyzed the relationship between social complexity and time to female reproduction after removing variation in time to reproduction explained by minimum female body mass.

There is a significant, positive relationship between social complexity and the time to first reproduction (Table 1, Figure 4). More social species first breed at older ages. Interestingly, after removing variation in the time to reproduction accounted for by body mass, analyses based on independent contrasts and phylogeny-free residuals both explained more variation than the analyses on nonindependent raw data. As much as 75% of the variation in time to first reproduction was explained by social complexity (in the contrasts analysis using tree 3).

Table 1

Variation explained by social complexity

	Trend	Raw data	Raw mass-free data	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5	Autocorrelation
Percent females breed	−	0.58	—	0.41	0.25	0.26	0.24	0.36	0.48
Time to first reproduction	+	0.50	0.20	0.61	0.53	0.75	0.51	0.53	0.67
Gestation time (days)		0.22	0	0.04	0.19	0.10	0.03	0.15	0
Average litter size	−	0.37	0.22	0.14*	0.19	0.28	0.22	0.21	0.21
Lactation time (days)		0	0	0	0	0	0	0	0
Survival to age 1	+	0.34	—	0.32	0.34	0.36	0.30	0.24	0.33

Variation explained by social complexity (adjusted R^2, bold if $p < .05$) for six life-history traits analyzed different ways. Trend is the direction of significant trends (+ or −). Raw data is the variation in the dependent variable explained by social complexity from regressions of the raw data. Raw mass-free data is the variation explained by sociality after variation explained by body mass has been removed from the dependent variable. Tree 1, 2, 3, and 4 are results calculated by regressing independent contrasts of social complexity against the independent contrasts of each dependent variable. The values differ in the phylogenetic hypotheses used to calculate contrasts. Autocorrelation is the result of regressing phylogeny-free residuals of sociality against each dependent variable. If there is a value in the raw mass-free data column, then analyses are conducted on mass-free residuals (see text for details).

* $p = .0519$.

Correlograms suggested significant autocorrelation at all taxonomic levels that disappeared after we calculated phylogeny-free residuals. Phylogenetic autocorrelation results suggest a maximum of 60% of the variation in the time to first female reproduction may be attributed to phylogenetic similarity.

Does social complexity influence gestation time?

Body size may explain variation in gestation time (Armitage, 1981; Bekoff et al., 1981; Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997). Thus, we analyzed the relationship between social complexity and gestation time after removing variation in gestation time explained by minimum female body mass.

Although there is a significant positive relationship between social complexity and gestation time in the raw data set, after controlling for body mass, social complexity explained no significant variation in gestation time (Table 1, Figure 5). Phy-

logenetically based analyses produced mostly consistent, negative results: 19% of the variation was explained in contrast analysis using tree 2, and 15% using tree 5 (Table 1). All other phylogenetically based analyses found no significant relationship between social complexity and gestation time.

Correlograms suggested significant autocorrelation at subtribe and tribe taxonomic levels, which disappeared after we calculated phylogeny-free residuals. Phylogenetic autocorrelation results suggest that a maximum of 47% of the variation in the gestation time may be attributed to phylogenetic similarity.

Does social complexity influence litter size?

Body size may explain variation in average litter size (Armitage, 1981; Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997). Thus, we analyzed the relationship between social complexity and average litter size after removing variation in litter size explained by minimum female body mass.
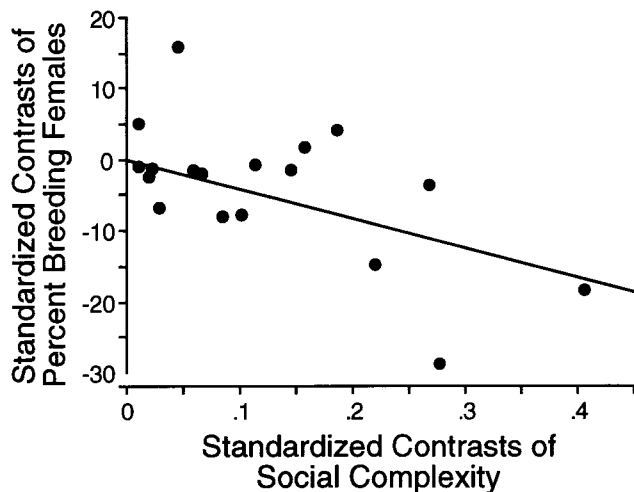

Figure 3
The relationship between standardized contrasts of social complexity and standardized contrasts of the percentage of adult females who breed. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.
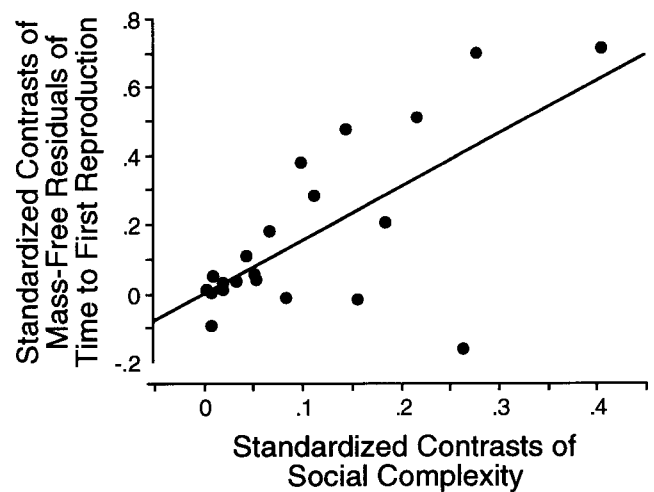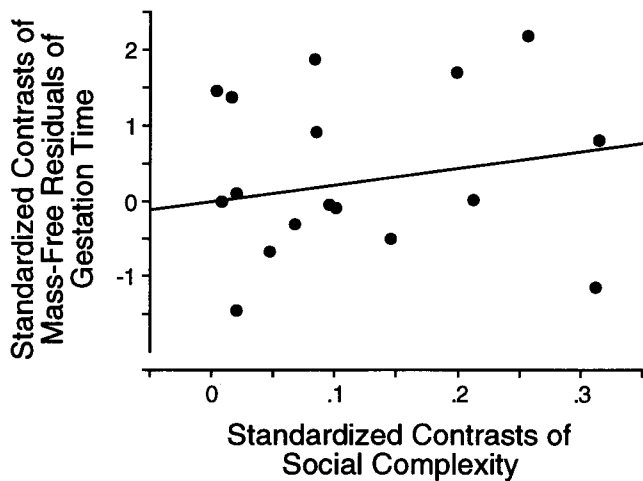

Figure 4
The relationship between standardized contrasts of social complexity and standardized contrasts of the body mass-free residuals of time to first female reproduction. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.

Figure 5
The relationship between standardized contrasts of social complexity and standardized contrasts of the body mass-free residuals of gestation time. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.

Figure 6
The relationship between standardized contrasts of social complexity and standardized contrasts of the body-mass free residuals of the average litter size. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.

There is a significant, negative relationship between social complexity and average litter size (Table 1, Figure 6). More social species have smaller litters. After controlling for variation accounted for by body mass, 14–28% of the variation in litter size was explained by social complexity in contrast-based analyses, and 21% was explained by social complexity after removing the effects of phylogeny in the autocorrelation analysis.

Correlograms suggested significant autocorrelation at all but the subgenus taxonomic level, which disappeared after we calculated phylogeny-free residuals. Phylogenetic autocorrelation results suggest that a maximum of 17% of the variation in average litter size may be attributed to phylogenetic similarity.

Does social complexity influence lactation time?

Body size may explain considerable variation in lactation time (Harvey and Clutton-Brock, 1985; Moehlman and Hofer, 1997). Thus, we analyzed the relationship between social complexity and lactation time after removing variation in lactation time explained by minimum female body mass.

There is no relationship between social complexity and lactation time (Table 1, Figure 7). All analyses produced consistent results: no variation in lactation time was explained by social complexity.

Correlograms suggested no significant autocorrelation at any of the taxonomic levels we examined. Thus, we could not estimate the amount of variation in lactation time explained by phylogenetic similarity.

Does social complexity influence juvenile survival to age 1?

We had no a priori reason to expect that a species' body mass should influence survival to age 1. Thus, we regressed social complexity against overall survival to age 1 to study costs and benefits of social complexity.

No matter how we examined the relationship, more socially complex species had a higher survival rate to age one (Table 1, Figure 8). Different methods lead to different estimates of the amount of variation explained by social complexity (Table
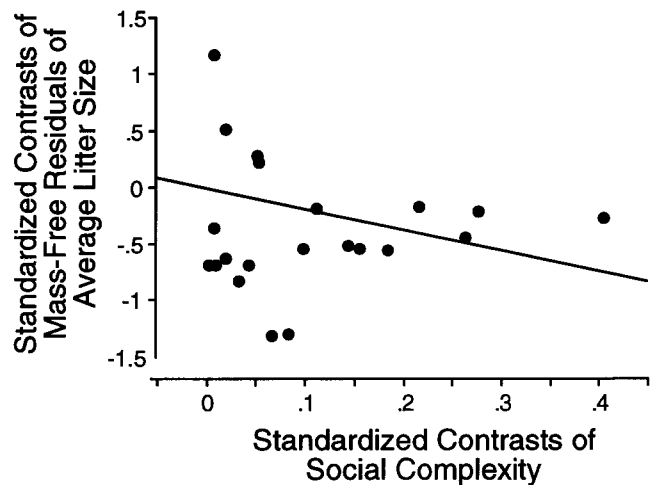
1). About 30% of the variation in survival to age one (range 24–36%) was explained by social complexity.

Correlograms suggested significant autocorrelation at the tribe level, which disappeared after we calculated phylogeny-free residuals. Phylogenetic autocorrelation suggested a maximum of 4% of the variation in survival to age 1 was explained by phylogenetic similarity.

DISCUSSION

To our knowledge, this is the first study to specifically examine life-history consequences of social complexity. Moreover, and
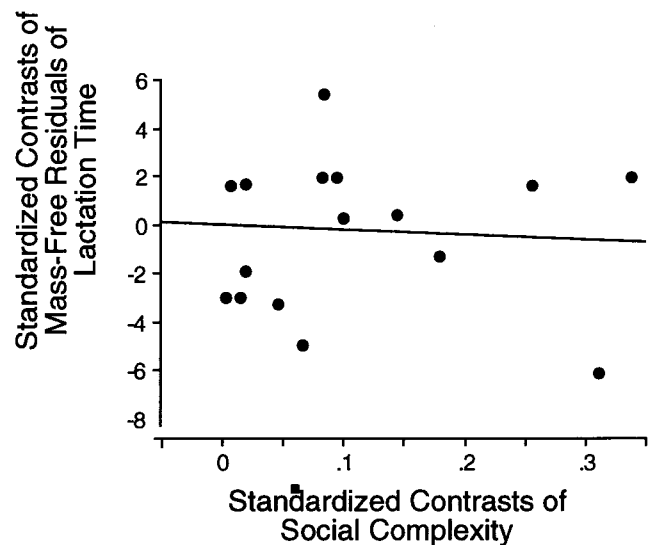

Figure 7
The relationship between standardized contrasts of social complexity and standardized contrasts of the body-mass free residuals of lactation time. Contrasts calculated from tree 1, and the regression is through the origin. Table 1 compares the significance and magnitude of explained variation for this and the other analyses.
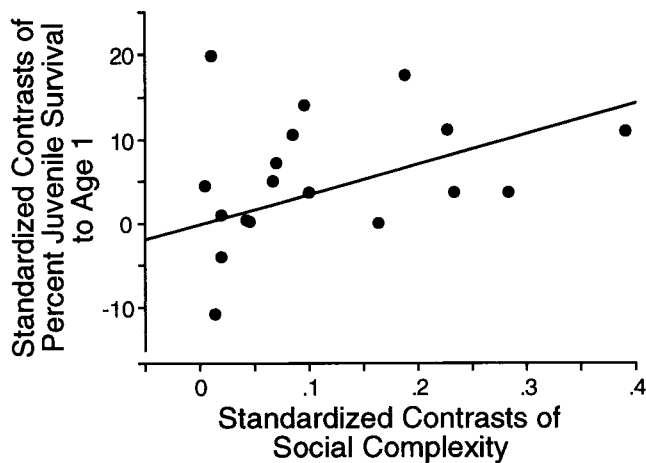
Figure 8
The relationship between standardized contrasts of social
complexity and standardized contrasts of the percent juvenile
survival to age 1. Contrasts calculated from tree 1, and the
regression is through the origin. Table 1 compares the significance
and magnitude of explained variation for this and the other
analyses.

unlike other current studies of complexity, we focused on the
consequences of complexity rather than on the evolution of
complexity itself (e.g., Bonner, 1988; McShea, 1991, 1996;
Szathmáry and Maynard Smith, 1995). As sciurid social com-
plexity increased, a smaller proportion of adult females bred
(Figure 3), age of first reproduction increased (Figure 4), lit-
ter size decreased (Figure 6), and first-year offspring survival
increased (Figure 8). Social complexity influenced neither
gestation time (Figure 5) nor lactation time (Figure 7). Thus,
social complexity has costs in terms of a reduction in the an-
nual per capita number offspring produced, but benefits in
terms of enhanced offspring survival.

It is not surprising that gestation and lactation time were
unaffected by social complexity. The times of gestation and
lactation are correlated with body size in mammals, but the
correlation with lactation is weak (Reiss, 1989). Gestation, but
not lactation, is correlated with body size in ground-dwelling
sciurids (Armitage, 1981). Both of these life-history variables
are more likely dependent on the physiological processes of
converting maternal energy into neonate energy. For exam-
ple, relative birth weight is proportional to adult metabolic
rate and the relative cost of producing an offspring is similar
for large and small mammals (Rahn, 1982). Because milk pro-
duction and energy content of milk can vary widely, the time
of lactation can vary with environmental conditions (Peaker
et al., 1984). Among ground-dwelling sciurids, the period of
lactation was positively correlated with the length of the active
season. For example, M. monax, with an active season of about
8.5 months, has a lactation period of 46 days, whereas M.
flaviventris, with an active season of about 4.5 months, has a
lactation period of 24 days (Armitage, 1981; this study).

The inclusion of phylogenetic information to the compar-
ative study generated remarkably consistent results. Given
some uncertainty about historical relationships, we examined
several phylogenetic hypotheses and two different compara-
tive methods; all led to consistent and interpretable results
which in some cases differed from analyses on raw data (see
Purvis et al., 1994; but also see Ricklefs and Stark, 1996).
While we acknowledge more data and better phylogenetic res-
olution will permit better estimates of the exact relationship
between social complexity and these life-history variables, we

suspect, given the variety of hypotheses examined, they will
not change the major conclusions.

Armitage (1981) first suggested that sociality is a life-history
tactic in sciurid rodents. Both Armitage (1981) and Barash
(1989) noted that increased sociality reduces juvenile mortal-
ity by retention of juveniles in the social groups. Our com-
parative evidence suggests that this pattern is widespread
among ground-dwelling sciurids: more socially complex spe-
cies have a greater percentage of juveniles survive to age 1.
Arnold's (1993b) studies of thermoregulatory helping behav-
ior during hibernation in marmots provides direct evidence
that, by delaying dispersal, offspring can increase the survival
of their younger siblings. We predict that more social species
will have more kin-selected (Hamilton, 1964) mechanisms to
increase offspring survival. We acknowledge that kin selection
may also work on a larger spatial scale, and behaviors such as
alarm calls may benefit relatives not living in the same social
group (e.g., Sherman, 1977; but see Blumstein et al., 1997).

Sociality has its costs in terms of the ability to produce off-
spring. As social complexity increased in sciurid rodents, few-
er females bred. After controlling for variation accounted for
by body size, we found that more socially complex species took
longer to first reproduce and had smaller litters. These pat-
terns suggest that some form of reproductive suppression
should be common in more socially complex sciurid rodents,
and perhaps more generally, in more social species. Certainly,
some of the most remarkable forms of reproductive suppres-
sion occur in highly social species with numerous roles within
a society (e.g., *Heterocephalus glaber.* Faulkes et al., 1991; social
insects: Brockmann, 1984).

Additional demographic evidence exists for reproductive
suppression. Among several marmot species, the percentage
of females breeding increases with age. When older females
are removed from the population, or when the population
density is low, younger females breed (Armitage, 1996). In the
biennial breeding *M. caligata,* a female skips an additional
year when her co-resident breeds (Wasser and Barash, 1983).
In *M. flaviventris,* weaning success is lower for females living
in proximity to other adult females than in those living with
no other adult females (Armitage, 1986).

The reproductive costs of sociality raise the question of why
reproductively suppressed females remain in social groups.
Several possibilities come to mind. First, survivorship of dis-
persers is likely to be less than those who become reproductive
on their natal home range because dispersers are more sus-
ceptible to predation than are residents (Hoogland, 1995; Van
Vuren and Armitage, 1994). Second, dispersers must either
colonize new habitat or invade an established group. Immi-
grants encounter resistance and may receive wounds inflicted
by residents (Garrett and Franklin, 1988). Consequently, im-
migration rates may be low (Sherman and Morton, 1984), and
immigration into "higher-quality" habitat patches may not oc-
cur annually (Armitage, 1984, 1991). For most *M. flaviventris*
social groups, recruitment (retention of individuals in their
natal social group) greatly exceeds immigration; immigration
is likely to occur only when resident mortality is high and
unoccupied areas are available for settlement (Armitage,
1988). In those species with low social complexity and high
rates of population turnover (e.g., *S. beldingi.* Sherman and
Morton, 1984; *S. richardsonii.* Michener and Michener, 1977),
individuals that survive hibernation have a high probability of
finding vacant space and breeding. However, some species
with high social complexity have a low rate of population turn-
over, thus *M. flaviventris* (Armitage, 1988, 1991), *C. ludovi-
cianus* (Hoogland, 1995), and *M. olympus* (Barash, 1973) hab-
itats may approach saturation (Armitage, 1996). For socially
complex species, an individual's probability of future repro-
duction may increase by remaining in its natal habitat rather

than dispersing in an attempt to reproduce at a younger age. However, individuals should disperse when the costs of remaining in their natal group are greater than the costs of dispersing. If nonbreeding residents can gain indirect fitness, delayed dispersal may be favored (e.g., Arnold, 1993). Dispersal should be delayed to an age when the probability of successful colonization is greater than that of dispersing at a younger age (Armitage, 1992).

Several factors should enter into the decision-making process of whether to disperse or to remain philopatric. Decisions may differ between the sexes depending on which sex normally disperses. In most species of ground-dwelling squirrels, natal dispersal is male biased and males typically disperse in the season before attaining reproductive maturity (Holekamp, 1984). Female dispersal is more variable, and, in squirrels, females tend to be philopatric or to disperse shorter distances than males (Armitage, 1981; Holekamp, 1984; Michener, 1983). Thus, conspecific density may serve as an important cue to the likelihood of successful settlement and eventual reproduction. However, the timing of dispersal should depend on an individual's expected life span; individuals of species with longer life spans and older ages at reproductive maturity are better able to delay dispersal. The probability of finding and being capable of occupying a vacant habitat should, on average, increase as an animal becomes older. But for any particular individual, that probability will be affected by the demographic events occurring in its social group in the years before its birth, which will affect the likelihood of becoming resident, and by demographic events in other social groups, which will effect the likelihood of immigration. Furthermore, each individual's residual reproductive value, which initially increases, will begin to decline at some point. When residual reproductive value declines, individuals should attempt to maximize their remaining reproductive value. Whether individuals remain in their natal group will depend on the level of inbreeding tolerance, the presence of dominant conspecifics, and the distance to neighboring groups. If groups are widely dispersed such that the probability of finding a group with a vacancy is low, the potential fitness cost of inbreeding and/or further loss of residual reproductive value may be less than the costs of dispersing. Where groups are contiguous or closely spaced individuals may easily and inexpensively determine vacancies in neighboring groups. Individuals should disperse if the expected fitness of moving is greater than the expected fitness from remaining at home for 1 or more additional years before breeding. Finally, when residual reproductive value is declining, animals that disperse should make a greater effort to invade and displace a resident; conversely, an animal that remains in its natal social group should attempt to become reproductive.

We do not envision social complexity as a direct target of selection. Social complexity, per se, does not evolve; we envision no "complexity genes." Rather, social complexity emerges following the evolution of social roles and social behaviors (sensu Hinde, 1975). Social complexity is a descriptive concept that allows us to study broad relationships and compare species-specific adaptations with a common currency. Detailed study of each species is required to document mechanisms of increased offspring survival and mechanisms of reproductive suppression. Here and elsewhere (Blumstein and Armitage, 1997) we compared the social complexity among species. Our method of quantifying social complexity also can be used to quantify intraspecific variation in social complexity, and thus may be useful in intraspecific socioecological studies (Lott, 1991).

APPENDIX

Social complexity and life history variables summarized from the sciurid literature

Species	Social complexity	Minimum female mass (g)	% Females breeding	Time to first female reproduction (years)	Gestation time (days)	Lactation time (days)	Average litter size	References[a]
M. flaviventris	1.06	2560	48	2	29	24	4.3	1–12
M. caligata	1.35	3300	45	3	30	28	3.0	13–18
M. olympus	1.46	1400	45	3	nd	nd	4.0	19
M. camtschatica	1.10	nd	nd	3	nd	nd	4.3	20–22
M. monax	0.27	3314	95	1	34	46	4.0	23–31
M. caudata	1.22	1400	14	3	30	nd	4.2	32–33
M. marmota	1.41	2811	48	3	37	45	2.4	23, 34–38
C. ludovicianus	1.12	525	75	1	34	41	3.1	39–41
C. mexicanus	1.05	756	nd	1	nd	40	4.4	42–43
C. parvidens	1.23	703	80	1	nd	nd	3.9	44–45
C. gunnisoni	1.03	600	66	1	29	39	4.6	46–51, 127
C. leucurus	0.84	575	88	1	30	35	5.6	52–56, 128
S. tereticaudus	0.48	100	90	1	28	28	6.5	57–63
S. franklinii	0.41	333	63	1	28	28	7.5	64–66
S. tridecemlineatus	0.50	105	95	1	28	32	7.3	67–74
S. lateralis	0.38	120	nd	1	31	35	5.0	75–77
S. saturatus	0.27	184	100	1	28	43	4.1	23, 78–80
S. beecheyi	0.26	486	90	1	28	38	7.5	81–86
S. variegatus	0.43	546	74	1	30	49	4.8	87–90
S. armatus	0.44	180	90	1	24	21	5.4	91–94
S. beldingi	0.40	211	95	1	27	25	4.2	95–99

APPENDIX

Continued

Species	Social complexity	Minimum female mass (g)	% Females breeding	Time to first female reproduction (years)	Gestation time (days)	Lactation time (days)	Average litter size	References[a]
S. richardsonii	0.39	269	95	1	22	29	6.8	23, 100–107
S. elegans	0.43	189	nd	1	22	32	5.9	108–111
S. columbianus	0.65	376	75	2	24	28	3.7	112–123
S. townsendii	0.41	93	86	1	24	38	8.6	124–126

nd, no data. All variables defined in text.

[a] 1, Armitage, 1965; 2, Armitage, 1974; 3, Armitage, 1975; 4, Armitage, 1984; 5, Armitage, 1991; 6, Armitage and Downhower, 1974; 7, Armitage and Johns, 1982; 8, Armitage et al., 1979; 9, Brody AK, and Melcher J, personal communication; 10, Frase and Hoffmann, 1980; 11, Schwartz et al., unpublished data; 12, Thompson, 1979; 13, Barash, 1974; 14, Barash, 1980; 15, Barash, 1981; 16, Holmes, 1979; 17, Holmes, 1984b; 18, Holmes, 1984a; 19, Barash, 1973; 20, Kapitonov, 1963 cited in Rausch and Rausch, 1971; 21, Mosolov and Tokarsky, 1994; 22, Ognev, 1947; 23, Arnold, 1993a; 24, Meier, 1985; 25, Meier, 1992; 26, Davis et al., 1964; 27, de Vos and Gillespie, 1960; 28, Ferron and Ouellette, 1989; 29, Grizell, 1955; 30, Snyder, 1962; 31, Snyder and Christian, 1960; 32, Blumstein DT, unpublished data; 33, Blumstein and Arnold, in press; 34, Arnold, 1990; 35, Arnold, 1993a; 36, Barash, 1976; 37, Perrin et al., 1993b; 38, Perrin et al., 1993a; 39, Hoogland, 1995; 40, King, 1955; 41, Knowles, 1987; 42, Ceballos-G. and Wilson, 1985; 43, Trevino -Villarreal, 1990; 44, Pizzimenti and Collier, 1975; 45, Wright-Smith, 1978; 46, Fitzgerald and Lechleitner, 1974; 47, Longhurst, 1944; 48, Pizzimenti and Hoffmann, 1973; 49, Rayor, 1985; 50, Rayor, 1988; 51, Rayor and Armitage, 1991; 52, Clark, 1977; 53, Clark et al., 1971; 54, Cooke L, personal communication; 55, Stockard, 1929; 56, Tileston and Lechleitner, 1966; 57, Dunford, 1977b; 58, Dunford, 1977c; 59, Dunford, 1977a; 60, Ernest and Mares, 1978; 61, Neal, 1965a; 62, Neal, 1965b; 63, Reynolds and Turkowski, 1972; 64, Iverson and Turner, 1972; 65, Murie, 1973; 66, Sowls, 1948; 67, Armstrong, 1972; 68, McCarley, 1966; 69, McCarley, 1970; 70, Rongastad, 1965; 71, Schwagmeyer, 1980; 72, Schwagmeyer and Brown, 1983; 73, Streubel and Fitzgerald, 1978; 74, Wistrand, 1974; 75, Bartels and Thompson, 1993; 76, Bronson, 1979; 77, Hatt, 1927; 78, Kenagy and Barnes, 1988; 79, Trombulak, 1987; 80, Trombulak, 1988; 81, Dobson and Davis, 1986; 82, Dobson, 1979; 83, Dobson, 1983; 84, Evans and Holdenried, 1943; 85, Fitch, 1948; 86, Holekamp, 1989; 87, Oaks et al., 1987; 88, Ortega, 1990a; 89, Ortega, 1990b; 90, Shriner and Stacey, 1991; 91, Balph, 1984; 92, Balph and Stokes, 1963; 93, Sauer and Slade, 1987; 94, Slade and Balph, 1974; 95, Jenkins and Eshelman, 1984; 96, Morton, 1975; 97, Morton and Gallup, 1975; 98, Morton and Parmer, 1975; 99, Sherman and Morton, 1984; 100, Michener, 1979a; 101, Michener, 1979c; 102, Michener, 1979b; 103, Michener, 1980; 104, Michener and Koeppl, 1985; 105, Michener and Locklear, 1990; 106, Michener and Michener, 1977; 107, Yeaton, 1972; 108, Faggerstone, 1982 cited in Zegers, 1984; 109, Pfeifer, 1982; 110, Zegers, 1984; 111, Zegers and Williams, 1977; 112, Balfour, 1983; 113, Boag and Murie, 1981; 114, Elliot and Flinders, 1991; 115, Festa-Bianchet, 1981; 116, Festa-Bianchet and Boag, 1982; 117, Festa-Bianchet and King, 1984; 118, Festa-Bianchet and King, 1991; 119, Betts, 1976; 120, Murie and Harris, 1978; 121, Murie and Harris, 1982; 122, Young, 1990; 123, Zammuto and Millar, 1985; 124, Smith and Johnson, 1985; 125, Rickart, 1986; 126, Rickart, 1987; 127, Hoogland, in press; 128, Dobson S, and Hadlock T, personal communication.

REFERENCES

Abbott DH, 1987. Behaviourally mediated supression of reproduction in female primates. J Zool 213:455–470.

Alexander RD, 1974. The evolution of social behavior. Annu Rev Ecol Syst 5:325–383.

Armitage KB, 1965. Vernal behaviour of the yellow-bellied marmot (Marmota flaviventris). Anim Behav 13:59–68.

Armitage KB, 1974. Male behaviour and territoriality in the yellow-bellied marmot. J Zool, London 172:233–265.

Armitage KB, 1975. Social behavior and population dynamics of marmots. Oikos 26:341–354.

Armitage KB, 1981. Sociality as a life-history tactic of ground squirrels. Oecologia 48:36–49.

Armitage KB, 1984. Recruitment in yellow-bellied marmot populations: kinship, philopatry, and individual variability. In: The biology of ground-dwelling squirrels (Murie JO, Michener GR, eds). Lincoln: University of Nebraska Press; 377–403.

Armitage KB, 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies. In: Ecological aspects of social evolution (Rubenstein DI, Wrangham RW, eds). Princeton, New Jersey: Princeton University Press; 303–331.

Armitage KB, 1988. Resources and social organization of ground-dwelling squirrels. In: The ecology of social behavior (Slobodchikoff CN, ed.). San Diego: Academic Press; 131–155.

Armitage KB, 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. Annu Rev Ecol Syst 22: 379–407.

Armitage KB, 1992. Social organization and fitness strategies of marmots. In: Proceedings of 1st international symposium on alpine marmot (Marmota marmota) and on genus Marmota (Bassano B, Durio P, Gallo Orsi U, Macchi E, eds). Torino, Italy: Dipartmento di Produzioni Animali, Epidemiologia ed Ecologia; 89–94.

Armitage KB, 1996. Social dynamics, kinship, and population dynamics of marmots. In: Biodiversity in marmots (Le Berre M, Ramousse R, Le Guelte L, eds). Moscow-Lyon: International Marmot Network; 113–128.

Armitage KB, Downhower JF, 1974. Demography of yellow-bellied marmot populations. Ecology 55:1233–1245.

Armitage KB, Johns DW, 1982. Kinship, reproductive strategies and social dynamics of yellow-bellied marmots. Behav Ecol Sociobiol 11: 55–63.

Armitage KB, Johns D, Andersen DC, 1979. Cannibalism among yellow-bellied marmots. J Mammal 60:205–207.

Armstrong DM, 1972. Distribution of mammals in Colorado. Lawrence: University of. Kansas.

Arnold W, 1990. The evolution of marmot sociality: I. Why disperse late? Behav Ecol Sociobiol 27:229–237.

Arnold W, 1993a. Energetics of social hibernation. In: Life in the cold: ecological, physiological, and molecular mechanisms (Carey C, Florant GL, Wunder BA, Horwitz B, eds). Boulder, Colorado: Westview Press; 65–80.

Arnold W, 1993b. Social evolution in marmots and the adaptive value of joint hibernation. Verh Dtsch Zool Ges 86:79–93.

Asher HB, 1983. Causal modeling, second ed. Beverly Hills: Sage Publications.

Balfour D, 1983. Infanticide in the columbian ground squirrel, Spermophilus columbianus. Anim Behav 31:949–950.

Balph DF, 1984. Spatial and social behavior in a population of Uinta ground squirrels: interrelations with climate and annual cycle. In: The biology of ground-dwelling squirrels (Murie JO, Michener GR, eds). Lincoln: University of Nebraska Press; 336–352.

Balph DF, Stokes AW, 1963. On the ethology of Uinta ground squirrels. Am Midl Nat 69:106–126.

Barash DP, 1973. The social biology of the Olympic marmot. Anim Behav Mon 6:173–245.

Barash DP, 1974. The social behavior of the hoary marmot (Marmota caligata). Anim Behav 22:256–261.

Barash DP, 1976. Social behaviour and individual differences in free-living alpine marmots (Marmota marmota). Anim Behav 24:27–35.

Barash DP, 1980. The influence of reproductive status on foraging by hoary marmots (*Marmota caligata*). Behav Ecol Sociobiol 7:201–205.

Barash DP, 1981. Mate guarding and gallivanting by hoary marmots (*Marmota caligata*). Behav Ecol Sociobiol 9:187–193.

Barash DP, 1989. Marmots: social behavior and ecology. Stanford, California: Stanford University Press.

Bartels MA, Thompson DP, 1993. *Spermophilus lateralis*. Mammal Sp 440:1–8.

Bekoff M, Diamond J, Mitton JB, 1981. Life-history patterns and sociality in canids: body size, reproduction, and behavior. Oecologia 50:386–390.

Benz JJ, 1993. Food-elicited vocalizations in golden lion tamarins: design features for representational communication. Anim Behav 45:443–455.

Bernstein IS, 1981. Dominance: the baby and the bathwater. Behav Brain Sci 4:419–457.

Betts BJ, 1976. Behaviour in a population of Columbian ground squirrels, *Spermophilus columbianus columbianus*. Anim Behav 24:652–680.

Bibikow DI, 1996. Die murmeltiere der welt. Heidelberg: Spektrum Akademischer Verlag.

Black CC, 1972. Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). Evol Biol 6:305–322.

Blumstein DT, Armitage KB, 1997. Does sociality drive the evolution of communicative complexity? A comparative analysis with ground-dwelling sciurid alarm calls. Am Nat 150:179–200.

Blumstein DT, Arnold W, in press. Ecology and social behavior of golden marmots (*Marmota caudata aurea*). J Mammal.

Blumstein DT, Steinmetz J, Armitage KB, Daniel JC, 1997. Alarm calling in yellow-bellied marmots: II. Kin selection or parental care? Anim Behav 53:173–184

Boag DA, Murie JO, 1981. Population ecology of Columbian ground squirrels in southwestern Alberta. Can J Zool 59:2230–2240.

Bonner JT, 1988. The evolution of complexity. Princeton, New Jersey: Princeton University Press.

Brockmann HJ, 1984. The evolution of social behaviour in insects. In: Behavioural ecology an evolutionary approach (Krebs JR, Davies NB, eds). Sunderland, Massachusetts: Sinauer Associates Inc.; 340–361.

Bronson MT, 1979. Altitudinal variation in the life-history of the golden mantled ground squirrel (*Spermophilus lateralis*). Ecology 60:272–279.

Brown CR, Brown MB, 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). Ecology 67:1206–1218.

Brown JL, 1987. Helping and communal breeding in birds. Princeton: Princeton University Press.

Ceballos-G. G, Wilson DE, 1985. *Cynomys mexicanus*. Mammal Sp 248:1–3.

Cheverud JM, Dow MM, Leutenegger W, 1985. The quantitative assessment of phylogenetic constraints in comparative analyes: sexual dimorphism in body weight among primates. Evolution 39:1335–1351.

Clark TW, 1977. Ecology and ethology of the white-tailed prairie dog (*Cynomys leucurus*). Publ Biol Geol Milwaukee Pub Mus 3:1–97.

Clark TW, Hoffmann RS, Nadler CF, 1971. *Cynomys leucurus*. Mammal Sp 7:1–4.

Davis DE, Christian JJ, Bronson F, 1964. Effect of exploitation on birth, mortality, and movement rates in a woodchuck population. J Wildlife Mgmt 28:1–9.

de Vos A, Gillespie DJ, 1960. A study of woodchucks on an Ontario farm. Can Field-Nat 74:130–145.

Dobson FS, 1979. An experimental study of dispersal in the California ground squirrel. Ecology 60:1103–1109.

Dobson FS, 1983. Agonism and territoriality in the California ground squirrel. J Mammal 64:218–225.

Dobson FS, 1985. The use of phylogeny in behavior and ecology. Evolution 39:1384–1388.

Dobson FS, Davis DE, 1986. Hibernation and sociality in the California ground squirrel. J Mammal 67:416–421.

Dunford CJ, 1977a. Behavioral limitation of round-tailed ground squirrel density. Ecology 58:1254–1268.

Dunford C, 1977b. Kin selection for ground squirrels alarm calls. Am Nat 111:782–785.

Dunford C, 1977c. Social systems of round-tailed ground squirrels. Anim Behav 25:885–906.

Eisenberg JF, 1981. The mammalian radiations. Chicago: University of Chicago Press.

Elliott CL, Flinders JT, 1991. *Spermophilus columbianus*. Mammal Sp 372:1–9.

Emlen ST, 1991. Evolution of cooperative breeding in birds and mammals. In: Behavioural ecology, 3rd ed. (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific Publications; 301–335.

Emlen ST, Oring LW, 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–222.

Emlen ST, Vehrencamp SL, 1983. Cooperative breeding strategies among birds. In: Perspectives in ornithology (Bush AH, Clark GA, eds). Cambridge: Cambridge University Press; 93–120.

Ernest KA, Mares MA, 1987. *Spermophilus tereticaudus*. Mammal Sp 274:1–9.

Evans FC, Holdenreid R, 1943. A population study of the Beechey ground squirrel in Central California. J Mammal 24:231–260.

Faulkes CG, Abbott DH, Liddell CE, George LM, Jarvis JUM, 1991. Hormonal and behavioral aspects of reproductive suppression in female naked mole-rats. In: The biology of the naked mole-rat (Sherman PW, Jarvis JUM, Alexander RD, eds). Princeton, New Jersey: Princeton University Press; 426–445.

Ferron J, Ouellet JP, 1989. Temporal and intersexual variation in the use of space with regard to social organization in the woodchuck (*Marmota monax*). Can J Zool 67:1642–1649.

Festa-Bianchet M, 1981. Reproduction in yearling female Columbian ground squirrels *Spermophilus columbianus*. Can J Zool 59:1032–1066.

Festa-Bianchet M, Boag DA, 1982. Territoriality in adult female Columbian ground squirrels. Can J Zool 60:1060–1066.

Festa-Bianchet M, King WJ, 1984. Behavior and dispersal of yearling Columbian ground squirrels. Can J Zool 62:161–167.

Festa-Bianchet M, King WJ, 1991. Effects of litter size and population dynamics on juvenile and maternal survival in Columbian ground squirrels. J Anim Ecol 60:1077–1090.

Fitch HS, 1948. Ecology of the California ground squirrel on grazing lands. Am Midl Nat 39:513–596.

Fitzgerald JP, Lechleitner RR, 1974. Observations on the biology of Gunnison's prairie dog in central Colorado. Am Midl Nat 92:146–163.

Frase BA, Hoffmann RS, 1980. *Marmota flaviventris*. Mammal Sp 135:1–8.

Garrett MG, Franklin WL, 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. J Mammal 69:236–250.

Gittleman JL, 1989. Functions of communal care in mammals. In: Evolution: essays in honour of John Maynard Smith (Greenwood PJ, Harvey PH, Slatkin M, eds). Cambridge: Cambridge University Press; 187–205.

Gittleman JL, Kot M, 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. Syst Zool 39:227–241.

Gittleman JL, Luh H-K, 1992. On comparing comparative methods. Annu Rev Ecol Syst 23:383–404.

Goodall J, 1986. The chimpanzees of Gombe. Cambridge, Massachusetts: Belknap Press.

Goodwin HT, 1990. Systematics, biogeography, and evolution of fossil prairie dogs (genus *Cynomys*) (PhD dissertation). Lawrence: University of Kansas.

Grizzell RA, Jr., 1955. A study of the southern woodchuck, *Marmota monax monax*. Am Midl Nat 53:257–293.

Hafner DJ, 1984. Evolutionary relationships of the nearctic sciuridae. In: The biology of ground-dwelling squirrels (Murie JO, Michener GR, eds). Lincoln: University of Nebraska Press; 3–23.

Hamilton WD, 1964. The genetical evolution of social behavior, I, II. J Theor Biol 7:1–52.

Hart BL, Hart LA, 1992. Reciprocal allogrooming in impala (*Aepyceros melampus*). Anim Behav 44:1073–1083.

Harvey PH, Clutton-Brock TH, 1985. Life history variation in primates. Evolution 39:559–581.

Harvey PH, Pagel MD, 1991. The comparative method in evolutionary biology. Oxford: Oxford University Press.

Hatt RT, 1927. Notes on the ground squirrel *Callospermophilus*. Occ Pap Mus Zool Univ Michigan 185:1–22.

Hauser MD, 1996. The evolution of communication. Cambridge, Massachusetts: MIT Press.

Hinde RA, 1975. Interactions, relationships and social structure in non-human primates. In: Proceedings from the symposia of the fifth congress of the international primatological society, Nagoya, Japan, August 1974 (Kondo S, Kawai M, Ehara A, Kawamura S, eds). Tokyo: Japan Science Press; 13–24.

Hoffmann RS, Nadler CF, 1968. Chromosomes and systematics of some North American species of the genus Marmota (Rodentia: Sciuridae). Experientia 24:740–742.

Holekamp KE, 1984. Dispersal in ground-dwelling sciurids. In: The biology of ground-dewelling squirrels (Murie JO, Michener GR, eds). Lincoln: University of Nebraska Press; 297–320.

Holekamp KE, 1989. Seasonal variation in body weight, fat, and behavior of California ground squirrels (Spermophilus beecheyi). Can J Zool 67:1425–1433.

Holmes WG, 1984a. The ecological basis of monogamy in Alaskan hoary marmots. In: The biology of ground-dwelling squirrels (Murie JO, Michener GR, eds). Lincoln: University of Nebraska Press; 250–274.

Holmes WG, 1984b. Predation risk and foraging behavior of the hoary marmot in Alaska. Behav Ecol Sociobiol 15:293–301.

Hoogland JL, 1995. The black-tailed prairie dog: social life of a burrowing mammal. Chicago: University of Chicago Press.

Hoogland JL, in press. Duration of gestation and lactation for Gunnison's prairie dogs. J Mammal.

Howell AH, 1915. Revision of the American marmots. N Am Fauna 37:4–80.

Iverson SL, Turner BN, 1972. Natural history of a Manitoba population of Franklin's ground squirrels. Can Field Nat 86:145–149.

Janson CH, Goldsmith ML, 1995. Predicting group size in primates: foraging costs and predation risk. Behav Ecol 6:326–336.

Jenkins SH, Eshelman BD, 1984. Spermophilus beldingi. Mammal Sp 221:1–8.

Kenagy GJ, Barnes BM, 1988. Seasonal reproductive patterns in four coexisting rodent species from the Cascade mountain, Washington. J Mammal 69:274–292.

King JA, 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contrib Labor Vert Biol Mich 67:1–123.

Knowles CJ, 1987. Reproductive ecology of black-tailed prairie dogs in Montana. Great Basin Nat 47:202–206.

Kruuk H, 1964. Predators and anti-predator behaviour of the black-headed gull (Larus ridibundus L.). Behaviour (supplement) 11:1–129.

Longhurst W, 1944. Observations on the ecology of the Gunnison prairie dog in Colorado. J Mammal 25:24–36.

Losos JB, 1990. Concordant evolution of locomotor behaviour, display rate and morphology in Anolis lizards. Anim Behav 39:879–890.

Losos JB, Miles DB, 1994. Adaptation, constraint, and the comparative method: phylogenetic issues and methods. In: Ecological morphology: integrative organismal biology (Wainwright PC, Reilly SM, eds). Chicago: Univeristy of Chicago Press; 60–98.

Lott DF, 1991. Intraspecific variation in the social systems of wild vertebrates. Cambridge: Cambridge University Press.

Luh H-K, Gittleman JL, Kot M, 1995. Phylogenetic autocorrelation: a manual. Knoxville: Department of Zoology, University of Tennessee.

Martins EP, 1995. Phylogenies and comparative data: a microevolutionary perspective. Phil Trans Biol Sci 349:85–91.

Martins EP, 1996. Phylogenies, spatial autoregression, and the comparative method: a computer simulation test. Evolution 50:1750–1765.

Martins EP, Garland T, Jr., 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. Evolution 45:534–557.

Martins EP, Hansen TF, 1996. The statistical analysis of interspecific data: a review and evaluation of phylogenetic methods. In: Phylogenies and the comparative method in animal behavior (Martins EP, ed). New York: Oxford University Press; 22–75.

McCarley H, 1966. Annual cycle, population dynamics and adaptive behavior of Citellus tridecemlineatus. J Mammal 47:294–316.

McCarley H, 1970. Differential reproduction in Spermophilus tridecemlineatus. Southwest Nat 14:293–296.

McShea DW, 1991. Complexity and evolution: what everybody knows. Biol Phil 6:303–324.

McShea DW, 1996. Metazoan complexity and evolution: is there a trend? Evolution 50:477–492.

Meier PT, 1985. Behavioral ecology, social organization and mating system of woodchucks (Marmota monax) in southeast Ohio (PhD dissertation). Athens: Ohio University.

Meier PT, 1992. Social organization of woodchucks (Marmota monax). Behav Ecol Sociobiol 31:393–400.

Michener GR, 1979a. The circannual cycle of Richardson's ground squirrels in southern Alberta. J Mammal 60:760–768.

Michener GR, 1979b. Spatial relationships and social organization of adult Richardson's ground squirrels. Can J Zool 57:125–139.

Michener GR, 1979c. Yearly variations in the population dynamics of Richardson's ground squirrels. Can Field Nat 93:363–370.

Michener GR, 1980. Differential reproduction among female Richardson's ground squirrels and its relation to sex ratio. Behav Ecol Sociobiol 7:173–178.

Michener GR, 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In: Advances in the study of mammalian behavior (Eisenberg JF, Kleiman DG, eds). Spec Pub Am Soc Mammal 7:528–572.

Michener GR, 1984. Age, sex, and species differences in the annual cycles of ground-dwelling sciurids: implications for sociality. In: The biology of ground-dwelling squirrels (Murie JO, Michener GR, eds). Lincoln: University of Nebraska Press; 81–107.

Michener GR, Koeppl JW, 1985. Spermophilus richardsonii. Mammal Sp 243:1–8.

Michener GR, Locklear L, 1990. Differential costs of reproductive effort for male and female Richardson's ground squirrels. Ecology 71:855–868.

Michener GR, Michener DR, 1977. Population structure and dispersal in Richardson's ground squirrels. Ecology 58:359–368.

Moehlman PD, Hofer H, 1997. Cooperative breeding, reproductive suppression, and body mass in Canids. In: Cooperative breeding in mammals (Solomon NG, French JA, eds). Cambridge: Cambridge University Press; 76–128.

Mooring MS, Hart BL, 1992. Animal grouping for protection from parasites: selfish herd and encounter-dilution effects. Behaviour 123:173–193.

Morton ML, 1975. Seasonal cycles of body weights and lipids in Belding ground squirrels. Bull S California Acad Sci 74:128–143.

Morton ML, Gallup JS, 1975. Reproductive cycle of the Belding ground squirrel (Spermophilus beldingi beldingi): seasonal and age differences. Great Basin Nat 35:427–433.

Morton ML, Parmer RL, 1975. Body size, organ size, and sex ratios in adult and yearling Belding ground squirrels. Great Basin Nat 35:305–309.

Mosolov VI, Tokarsky VA, 1994. The black-capped marmot (Marmota camtschatica Pall.) in the Kronotsky Reserve. In: Actual problems of marmots investigation (Rumiantsev VY, ed). Moscow: ABF; 98–110.

Murie JO, 1973. Population characteristics and phenology of a Franklin ground squirrel (Spermophilus franklinii) colony in Alberta, Canada. Am Midl Nat 90:334–340.

Murie JO, Harris MA, 1978. Territoriality and dominance in male Columbian ground squirrels (Spermophilus columbianus). Can J Zool 56:2402–2412.

Murie JO, Harris MA, 1982. Annual variation of spring emergence and breeding in Columbian ground squirrels (Spermophilus columbianus). J Mammal 63:431–439.

Murie JO, Michener GR (eds), 1984. The biology of ground-dwelling squirrels. Lincoln: University of Nebraska Press.

Neal BJ, 1965a. Reproductive habits of round-tailed and Harris antelope ground squirrels. J Mammal 46:200–206.

Neal BJ, 1965b. Seasonal changes in body weights, fat depositions, adrenal glands, and temperatures of Citellus tereticaudus and Citellus harrisii (Rodentia). Southwest Nat 10:156–166.

Nowak RM, Paradiso JL, 1983. Walker's mammals of the world, 4th ed. Baltimore, Maryland: The Johns Hopkins University Press.

Oaks EC, Young PJ, Kirkland GL, Jr., Schmidt DF, 1987. Spermophilus variegatus. Mammal Sp 272:1–8.

Ognev SI, 1947 (1963). Mammals of the U.S.S.R. and adjacent countries: rodents. Jerusalem: Israel Program for Scientific Translations.

Ortega JC, 1990a. Home-range size of adult rock squirrels (Spermophilus variegatus) in southeastern Arizona. J Mammal 71:171–176.

Ortega JC, 1990b. Reproductive biology of the rock squirrel (Sper-

mophilus variegatus) in southeastern Arizona. J Mammal 71:448–457.

Packer C, Collins DA, Sindimwo A, Goodall J, 1995. Reproductive constraints on aggressive competition in female baboons. Nature 373:60–63.

Peaker M, Vernon RG, Knight C (eds), 1984. Physiological strategies in lactation. London: The Zoological Society of London.

Perrin C, Allaine D, Le Berre M, 1993a. Socio-spatial organization and activity distribution of the alpine marmot Marmota marmota: preliminary results. Ethology 93:21–30.

Perrin C, Coulon J, Le Berre M, 1993b. Social behavior of alpine marmots (Marmota marmota): seasonal, group, and individual variability. Can J Zool 71:1945–1953.

Pfeiffer SR, 1982. Variability in reproductive output and success of Spermophilus elegans ground squirrels. J Mammal 63:284–289.

Pienkowski MW, Evans PR, 1982. Breeding behaviour, productivity and survival of colonial and non-colonial shelducks (Tadorna tadorna). Ornis Scand 13:101–116.

Pizzimenti JJ, Collier GD, 1975. Cynomys parvidens. Mammal Sp 52:1–5.

Pizzimenti JJ, Hoffmann RS, 1973. Cynomys gunnisoni. Mammal Sp 25:1–4.

Promislow DEL, 1996. Using comparative approaches to integrate behavior and population biology. In: Phyogenies and the comparative method in animal behavior (Martins EP, ed.). New York: Oxford University Press; 288–323.

Purvis A, Gittleman JL, Luh H-K, 1994. Truth or consequences: effects of phylogenetic accuracy on two comparative methods. J Theor Biol 167:293–300.

Purvis A, Rambaut A, 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. Comp Appl Biosci 11:247–251.

Rahn H, 1982. Embryonic development in birds and mammals. In: A companion to animal physiology (Taylor CR, Johansen K, Bolis L, ed). Cambridge: Cambridge University Press; 124–137.

Rausch RL, Rausch VR, 1971. The somatic chromosomes of some North American marmots (Sciuridae), with remarks on the relationships of Marmota broweri Hall and Gilmore. Mammalia 35:85–101.

Rayor LS, 1985. Effects of habitat quality on growth, age of first reproduction, and dispersal in Gunnison's prairie dogs (Cynomys gunnisoni). Can J Zool 63:2835–2840.

Rayor LS, 1988. Social organization and space-use in Gunnison's prairie dog. Behav Ecol Sociobiol 22:69–78.

Rayor LS, Armitage KB, 1991. Social behavior and space-use of young ground-dwelling squirrel species with different levels of sociality. Ethol Ecol Evol 3:185–205.

Reiss MJ, 1989. The allometry of growth and reproduction. Cambridge: Cambridge University Press.

Reynolds HG, Turkowski F, 1972. Reproductive variations in the round-tailed ground squirrel as related to winter rainfall. J Mammal 53:893–898.

Rickart EA, 1986. Postnatal growth of the Piute ground squirrel (Spermophilus mollis). J Mammal 67:412–416.

Rickart EA, 1987. Spermophilus townsendii. Mammal Sp 268:1–6.

Ricklefs RE, Stark JM, 1996. Applications of phylogenetically independent contrasts: a mixed progress report. Oikos 77:167–172.

Ridley M, Grafen A, 1996. How to study discrete comparative methods. In: Phyogenies and the comparative method in animal behavior (Martins EP, ed). New York: Oxford University Press; 76–103.

Rongstad OJ, 1965. A life history study of thirteen-lined ground squirrels in southern Wisconsin. J Mammal 46:76–87.

Sauer JR, Slade NA, 1987. Uinta ground squirrel demography: is body mass a better categorical variable than age? Ecology 68:642–650.

Schwagmeyer PL, 1980. Alarm calling behavior of the thirteen-lined ground squirrel, Spermophilus tridecemlineatus. Behav Ecol Sociobiol 7:195–200.

Schwagmeyer PL, Brown CH, 1983. Factors affecting male-male competition in thirteen-lined ground squirrels. Behav Ecol Sociobiol 13:1–6.

Shannon CE, Weaver W, 1949. The mathematical theory of communication. Urbana: University of Illinois Press.

Sherman PW, 1977. Nepotism and the evolution of alarm calls. Science 197:1246–1253.

Sherman PW, Morton ML, 1984. Demograpy of Belding's ground squirrels. Ecology 65:1617–1628.

Shriner WM, Stacey PB, 1991. Spatial relationships and dispersal patterns in the rock squirrel, Spermophilus variegatus. J Mammal 72:601–606.

Slade NA, Balph DF, 1974. Population ecology of Uinta ground squirrels. Ecology 55:989–1003.

Slobodchikoff CN, Shields WM, 1988. Ecological trade-offs and social behavior. In: The ecology of social behavior (Slobodchikoff CN, ed). San Diego, California: Academic Press; 3–10.

Smith GW, Johnson DR, 1985. Demography of a Townsend ground squirrel population in southwestern Idaho. Ecology 66:171–178.

Snyder RL, 1962. Reproductive performance of a population of woodchucks after a change in the sex ratio. Ecology 43:506–515.

Snyder RL, Christian JJ, 1960. Reproductive cycle and litter size of the woodchuck. Ecology 41:647–656.

Sowls LK, 1948. The Franklin ground squirrel, Citellus franklinii (Sabine), and its relationship to nesting ducks. J Mammal 29:113–137.

Stockard AH, 1929. Observations on reproduction in the white-tailed prairie dog (Cynomys leucurus). J Mammal 10:209–212.

Streubel DP, Fitzgerald JP, 1978. Spermophilus tridecemlineatus. Mammal Sp 103:1–5.

Szathmáry E, Maynard Smith J, 1995. The major evolutionary transitions. Nature 374:227–232.

Thomas WK, Martin SL, 1993. A recent origin of marmots. Mol Phyl Evol 2:330–336.

Thompson SE, 1979. Socioecology of the yellow-bellied marmot (Marmota flaviventris) in central Oregon (PhD dissertation). Berkeley: University of California.

Tileston JV, Lechleitner RR, 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in North-Central Colorado. Am Midl Nat 75:292–316.

Trevino-Villarreal J, 1990. The annual cycle of the Mexican prairie dog (Cynomys mexicanus). Occ Pap Mus Nat Hist Univ Kansas 139:1–27.

Trombulak SC, 1987. Life history of the Cascade golden-mantled ground squirrel (Spermophilus saturatus). J Mammal 68:544–554.

Trombulak SC, 1988. Spermophilus saturatus. Mammal Sp 322:1–4.

Van Vuren D, Armitage KB, 1994. Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? Oikos 69:179–181.

Walters JR, Seyfarth RM, 1986. Conflict and cooperation. In: Primate societies (Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, eds). Chicago: University of Chicago Press; 306–317.

Wasser AK, Barash DP, 1983. Reproductive supression among female mammals: implications for biomedicine and sexual selection theory. Q Rev Biol 58:513–538.

Wilson EO, 1975. Sociobiology. Cambridge, Massachusetts: Belknap Press.

Wistrand H, 1974. Individual, social, and seasonal behavior of the thirteen-lined ground squirrel (Spermophilus tridecimlineatus). J Mammal 55:329–347.

Wrangham RW, 1981. Drinking competition in vervet monkeys. Anim Behav 29:904–910.

Wrangham RW, 1983. Social relationships in comparative perspective. In: Primate social relationships: an integrated approach (Hinde RA, ed.). Oxford: Blackwell; 325–334.

Wrangham RW, Gittleman JL, Chapman CA, 1993. Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. Behav Ecol Sociobiol 32:199–209.

Wright-Smith MA, 1978. The ecology and social organization of Cynomys parvidens (Utah prairie dog) in south central Utah (MA thesis). Bloomington: Indiana University.

Yeaton RI, 1972. Social behavior and social organization in Richardson's ground squirrel (Spermophilus richardsonii) in Saskatchewan. J Mammal 53:139–147.

Young PJ, 1990. Hibernating patterns of free-ranging Columbian ground squirrels. Oecologia 83:504–511.

Zammuto RM, Millar JS, 1985. Environmental predictability, variability, and Spermophilus columbianus life history over an elevational gradient. Ecology 66:1784–1794.

Zegers DA, 1984. Spermophilus elegans. Mammal Sp 214:1–7.

Zegers DA, Williams O, 1977. Seasonal cycles of body weight and lipids in Richardson's ground squirel, Spermophilus richardsonii elegans. Acta Theriol 22:380–383.

A column was left out of the appendix to the article by Daniel T. Blumstein and Kenneth B. Armitage in the January/February 1998 issue, pages 15–16. The missing column, "% Juvenile survival to age 1," is printed below. The publisher regrets the error.

Species	% Juvenile survival to age 1
M. flaviventris	53.5
M. caligata	—
M. olympus	53.5
M. camtschatica	—
M. monax	24.0
M. caudata	41.0
M. marmota	78.0
C. ludovicianus	50.5
C. mexicanus	—
C. parvidens	—
C. gunnisoni	45.5
C. leucurus	17.5
S. tereticaudus	53.0
S. franklinii	8.5
S. tridecemlineatus	9.0
S. lateralis	18.0
S. saturatus	—
S. beecheyi	36.0
S. variegatus	—
S. armatus	35.0
S. beldingi	33.0
S. richardsonii	27.0
S. elegans	19.0
S. columbianus	37.5
S. townsendii	22.5