

more knowledge of community composition and dynamics would also be needed before any such studies became commonplace. Geological processes have traditionally been measured against a scale conveniently provided by evolutionary biological diversity; it would be fitting that the most rapid geological processes should be measured against ecological diversity responding to catastrophic events.

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Social Dynamics of Mammals: Reproductive Success, Kinship and Individual Fitness

Kenneth B. Armitage

Apparent altruism, in which an individual seemingly decreases its evolutionary fitness by assisting others, can confer benefits if the individual assists kin. Thus, an animal can increase its total or inclusive fitness by producing offspring (direct fitness) and/or helping kin to reproduce (indirect fitness). Although kin selection has been suggested as the mechanism underlying the formation of mammalian societies, many species act as if they attempt to maximize the direct fitness component of their inclusive fitness.

Natural selection favors those individuals that maximize the number of their offspring that become reproductive adults. But in some species of mammals, individuals apparently reduce their own reproductive success while increasing the reproductive success of others¹. Such behavior is called altruism. However, some altruistic traits, which I designate apparent altruism, have not been distinguished from true altruism, which is a loss of individual or direct fitness by the altruist and a gain in individual fitness by the recipient². For example, some individuals (alloparents) postpone their own reproduction and care for the offspring of others¹. Because foregoing reproduction could reduce individual fitness, alloparenting is apparent altruism, but not necess-

arily true altruism. The apparent altruist may gain time and maturity that increase the probability of survival when it disperses or the probability that it will inherit the parental home range and be guaranteed the resources necessary for longer survival and a greater lifetime reproductive success. Thus, apparent altruism may increase rather than decrease individual fitness.

Inclusive fitness, kin selection and nepotism

An alternative explanation for apparent altruism was provided by Hamilton³. Altruism can evolve if the self-sacrificing aid is sufficiently beneficial to relatives. An individual's total or inclusive fitness consists of two components: direct fitness (classical individual fitness) and indirect fitness (derived from effects on non-descendant relatives)³⁻⁵. Indirect fitness is kin selection³⁻⁵. Although an individual should maximize its inclusive fitness^{3,5}, it is unclear to what degree it maximizes the direct or indirect components.

Many mammals live in social groups, and kin selection could thus contribute significantly to fitness⁵. However, the contribution of non-descendant relatives (= kin selection) to inclusive fitness is weighted

according to the degree of relatedness of the kin to the individual affected^{3,5}. Thus, if a female foregoes reproduction to assist her sister, the number of additional offspring produced by a full sib must be double the apparent altruist's loss and must double for each halving of the coefficient of relatedness for more distant kin. Because an individual usually has more control over its own reproductive efforts than over those of its kin and can expect lower variance in the pay-offs of its own efforts, it should generally choose to produce offspring rather than assist kin⁶.

Although lifetime reproductive success should be the measure of fitness, it is difficult to assess. Other measures are generally used: nepotistic social interactions, kinship in groups, sharing of resources and alarm calling are interpreted to support kin selection. Usually, it is implicitly assumed that these measures of social dynamics are directly related to reproductive success.

The relative contribution of kin selection to inclusive fitness is obscured by the use of terms such as altruism² and nepotism. Nepotism, defined as the preferential treatment of kin⁷, does not distinguish between

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Table 1. Population structure and social organization of female ground-dwelling squirrels (genera *Spermophilus*, *Cynomys* and *Marmota*)

Individualistic, daughters settle near mothers to form kin clusters ^{11,12} :		
<i>S. tridecemlineatus</i>	<i>S. parryi</i>	<i>S. franklinii</i> ^a
<i>S. beldingi</i>	<i>S. beechyi</i> ^a	<i>S. elegans</i> ^a
<i>S. richardsonii</i>	<i>S. armatus</i> ^a	<i>C. leucurus</i> ^a
<i>S. tereticaudus</i>		
Individualistic, non-breeding yearlings remain proximate to natal site, female kin clusters formed, daughters may inherit nest sites from their mothers ^{13,16} :		
<i>S. columbianus</i>		
Social, complete overlap of home ranges of closely-related females that form a matriarchy:		
<i>M. flaviventris</i> ¹⁴	<i>M. olympus</i> ^b	<i>C. gunnisoni</i> ^b
<i>C. ludovicianus</i> ¹⁵	<i>M. caligata</i> ^b	

^a Female kin clusters probable but not verified^{9,11}.
^b Multiple-female matriarchies probable but not verified^{10,12}.

descendant and non-descendant kin. Likewise, altruism and kin selection have been applied to offspring as well as non-descendant relatives; preferential treatment of offspring is classical individual fitness⁸. In my opinion, kin selection and nepotism should refer only to non-descendant kin; parental care or reproductive

investment and individual fitness should be used to refer to offspring.

Social organization of ground-dwelling squirrels

A major requirement for determining the contributions of direct and indirect fitness to inclusive fitness is that the relatedness of individuals

comprising a social group be known. Some of the most extensive long-term studies involve hibernating, ground-dwelling squirrels in North America. These species will be considered in some detail.

In ground-dwelling squirrels, patterns of sociality range from aggregated individual territories to polygynous harems^{9,10}. Females are philopatric; this leads to the close association of female kin (Table 1), while males associate with females for varying periods¹². Among the more social species, female-kin groups may occupy a shared home range; mothers usually bequeath their space to one or more daughters^{14,15}.

Most young males of these species disperse from their natal area, and thus there is little or no opportunity to establish patriline. Yellow-bellied marmots (*Marmota flaviventris*)¹² and black-tailed prairie dogs (*Cynomys ludovicianus*)¹⁷ disperse primarily as yearlings, whereas Belding's ground squirrels (*Spermophilus beldingi*) disperse as young¹⁸. The dispersed Belding's females are not defendable; males disperse from the vicinity of their mates and do not interact socially with their mates or offspring¹⁸. Clumped females are defended by male yellow-bellied marmots¹² and black-tailed prairie dogs¹⁷. Because of the delayed dispersal in these species, males interact with their offspring; interactions between fathers and their yearling sons are primarily agonistic^{17,19}. Some black-tailed coterries contain more than one adult male; behavior between resident males is primarily agonistic, especially during breeding¹⁷.

Male reproductive success stems primarily from the number of females mated^{12,17}; dominant male Belding's squirrels gain most of the matings¹⁸, and territorial yellow-bellied marmots (Fig. 1) and black-tailed prairie dogs attempt to increase the number of females within their territories^{12,17}. Territoriality in these last two species increases the probability of future matings and may also serve to protect current investment¹². Male behavior seems to be directed toward maximizing direct fitness.

The relative importance of direct and indirect fitness is especially relevant to female social organization and behavior. Temporal overlap of female kin produces a genealogy whose members have different degrees of relatedness^{14-16,20}. Most matriline of yellow-bellied marmots eventually become extinct or divide to form daughter matriline (Fig. 1)¹⁴. All matriline originate as

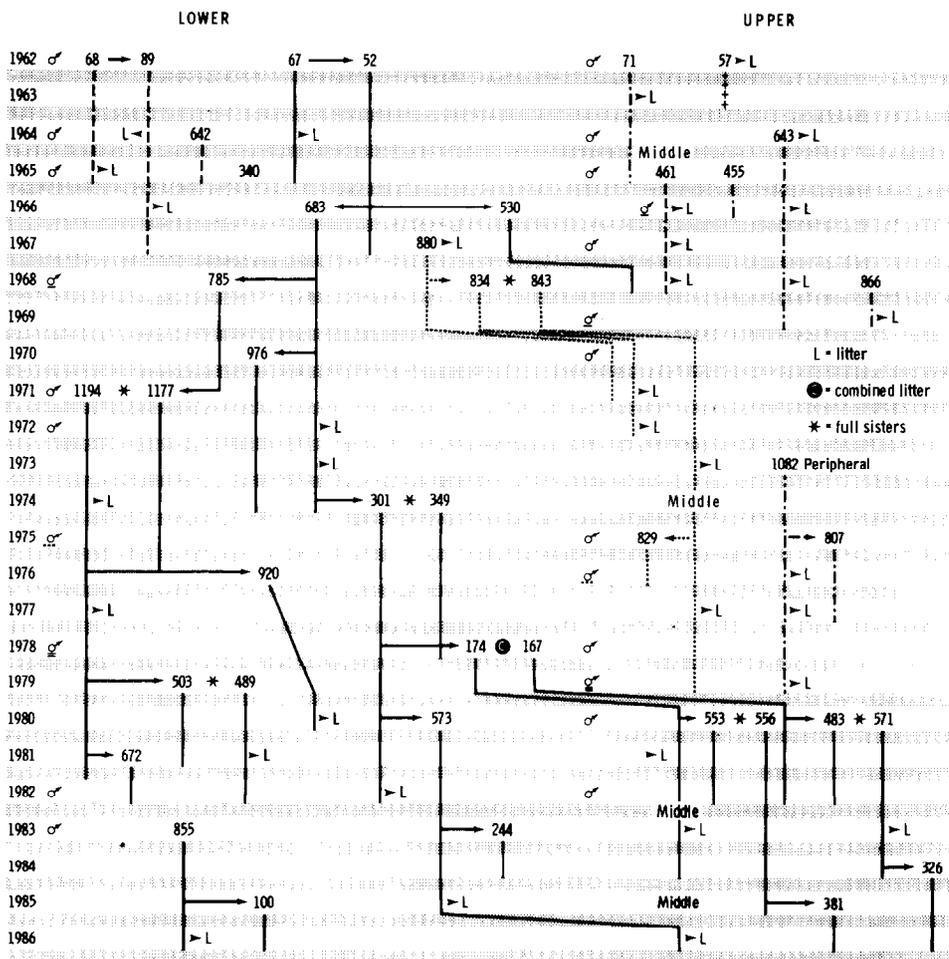


Fig. 1. Patterns of residency, recruitment and immigration in the formation of matriline for yellow-bellied marmots (*Marmota flaviventris*) in Picnic Colony. Lower, Upper and Middle refer to three habitat patches. Each patch is usually inhabited by a separate matriline and sometimes by a separate harem. Each animal is identified by ear-tag number in the year of immigration or birth. Years of residency are indicated by the vertical lines. Matriline are represented by vertical lines of the same pattern. Recruits to a matriline are indicated by a short horizontal arrow in the year of birth. When there was no recruitment, an arrowhead points to L. Resident males are indicated by the male symbol in the first year of residency. Male symbols with the same underline indicate that the same individual defended two or more areas within the colony. Only one male was present from 1983 through 1986. A horizontal arrow that crosses two vertical lines indicates that young were of uncertain maternity because adult females shared the same burrow system, e.g. 1976 and 1978. Modified and up-dated from Ref. 14, by courtesy of University Nebraska Press.

mother/daughter(s) groups; daughters are recruited into the maternal home ranges. Only littermate sisters associate in the same matriline (Fig. 1). The fission of matriline may require several years to complete. Thus, kinships may consist of sister/sister, mother/daughter, grandmother/granddaughter and aunt/niece. Similar patterns of kinship occur in black-tailed prairie dog matrilineal groups¹⁵ and among Belding's ground squirrel kin clusters²⁰.

Two lines of evidence suggest that matriline formation does not represent kin selection, as previously suggested¹⁹, but is an expression of parental investment (= direct fitness). First, matriline are small: the average matriline consists of 1.47 females¹². Fission of large matriline and mortality produce small matriline. Second, matriline begin as mother/daughter associations; sister/sister matriline occur when the mother dies. Sister/sister matriline are the demographic results of parental recruitment of two daughters from the same litter who remain together after their mother's death.

The persistence of sister/sister matriline does not require kin selection. There is no evidence that sisters associating in a matriline lose any direct fitness; matriline size does not affect the per capita production of young or yearlings^{12,14}. Sisters may gain direct fitness by socializing; two females associating in a matriline produce more young, more young per litter, and more recruits (individuals who remain in their natal area) than females living singly or than females who are sole members of a matriline when another matriline is present¹². Indirect fitness (= kin selection) may add to inclusive fitness, but such gain is likely to be a bonus derived from a social organization evolved to maximize an individual's direct fitness through increasing the probability of producing reproductive descendants.

Social behavior: direct or indirect fitness?

It is tacitly assumed that social behavior is directly related to fitness; therefore, it should vary directly with the degree of relatedness^{3,15}. Several lines of evidence suggest that amicable behaviors are biased toward closely-related kin.

In the closed matrilineal groups of yellow-bellied marmots and black-tailed prairie dogs (Table 1), amicable behavior occurs among group members, but rarely occurs between members of different matriline (Fig. 2); inter-matrilineal behavior is

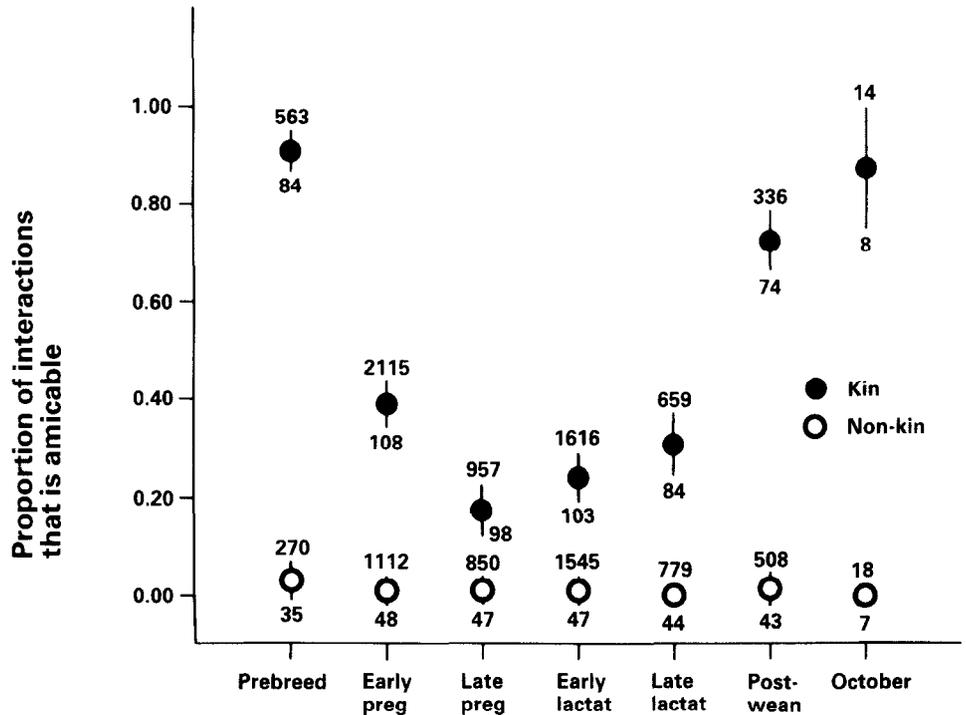


Fig. 2. Social interactions among female black-tailed prairie dogs (*Cynomys ludovicianus*) at different periods during the annual cycle. Circles indicate means; vertical lines indicate one standard error (SE). Numbers above SE lines are the number of observed interactions; numbers below SE lines indicate numbers of dyads. Reproduced from Ref. 15, by courtesy of Baillière Tindall.

almost entirely agonistic^{15,19}. Within matriline, amicable behavior of animals related by 0.5 (both descendant and collateral kin) occurs significantly more frequently among female yellow-bellied marmots than expected from the frequency of these kin groups in the population¹⁹, significantly more often between mother-daughter pairs than among littermate sisters, and among littermate sisters more often than among less-related Belding's ground squirrels (Fig. 3)²⁰. Likewise, a greater number of amicable interactions occur among these close relatives in

black-tailed prairie dog coterie¹⁵. For both marmots and Belding's ground squirrels, agonistic behavior is less frequent among close relatives than among more distant relatives (Fig. 3)^{12,19,20}. However, among black-tailed prairie dogs, amicability does not vary significantly with the degree of relatedness at any stage of the annual cycle¹⁵.

These differences in social behavior cannot be attributed to dispersion. In Belding's ground squirrel, close and distant kin nest in about equal proximity; neither reciprocity nor age account for the differences in

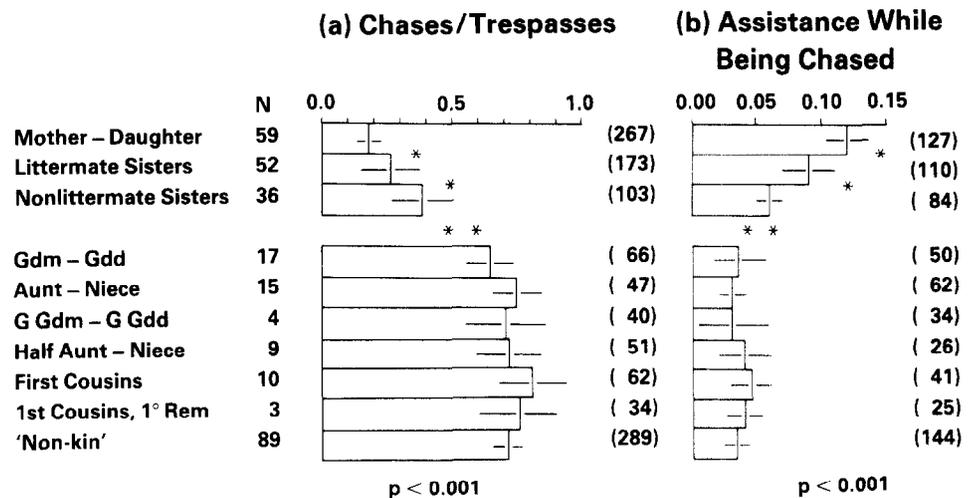


Fig. 3. Aggression (a) and cooperation (b) among female Belding's ground squirrels (*Spermophilus beldingi*). (a) Proportion of times pregnant and lactating females chased various relatives and non-kin from their territories when the resident was present above ground during the trespass. Numbers in parentheses are the total number of trespasses for each kin category. (b) Proportion of chases in which the chassee was joined by various relatives and non-kin. Numbers in parentheses are the number of chases that occurred when both focal animals were present. N is the number of different dyads observed. For both (a) and (b), means and standard deviations are presented. Stars indicate that sequential means differed significantly; the p value beneath each figure indicates the likelihood that there is no difference among means. Modified from Ref. 20, by courtesy of Springer-Verlag.

social behavior²⁰. Among yellow-bellied marmots, close and distant kin are members of the same matriline and their space use overlaps sufficiently to permit social interactions^{12,14}. Social behaviour among sisters is far more amicable and less agonistic, whereas aunt/niece behavior is more agonistic and less amicable, than expected¹². Although Sherman suggested that nepotism is limited by demography²⁰, the sharp step-like difference in Belding's ground squirrel behaviors between mothers, daughters, sisters and all other kin pairs (Fig. 3), and the virtual absence of amicable behaviors among marmot aunt-niece pairs¹², suggest that there is a reproductive strategy favoring mother/daughter and sister/sister relationships. The mother/daughter relationships are as expected, i.e. parental investment to enhance direct fitness, but the relationships among other kin groups requires further analysis.

These relationships are produced by demography. For example, yellow-bellied marmot ♀683 first reproduced at age two in 1968 (Fig. 1). She lived to be eight years old; four daughters and two granddaughters were added to the matriline during her residency. The daughters were fathered by three different males. Thus, relatedness varied from 0.125 to 0.5 ($\bar{x} = 0.3$) by 1974. By 1974, the matriline was undergoing fission into three matriline; mortality resulted in two matriline in 1975, and the average relatedness of each matriline increased to 0.5 (Fig. 1). Similarly, demography produces black-tailed prairie dog matrilineal groups that consist of mothers, daughters, sisters, nieces, half-sisters, half nieces, etc.¹⁵ and produces patterns of proximity among resident Belding's ground squirrels ranging from mother/daughter to cousin pairs among kin to non-kin neighbors²⁰.

In all three species, females defend their nest burrows^{12,17,18}. But successful defense requires assistance. All members of the black-tailed prairie dog coterie cooperate to defend their territory against incursion by conspecifics¹⁷. Yellow-bellied marmot matrilineal groups defend against incursion by members of other matriline, even when the intruders are distant kin¹². Among Belding's ground squirrels, close kin cooperate in defending their territories and young¹⁸. Cooperation is not based on proximity, but on relatedness; kin more distant than nonlittermate sisters are treated as non-kin. Because aunts/nieces and nonlittermate sisters have the same average

relatedness, relatedness does not account for the differences in behaviour (Fig. 3). Nonlittermate sisters behave significantly more amicably when their mother is present than when she is absent¹⁸. The mother may enhance her direct fitness by reducing conflict among her direct descendants (she is related to daughters by 0.5 but to nieces by only 0.25) and this influence may affect subsequent social relationships among her descendants.

Similarly, in marmots a large matrilineal group arises while the matriarch is alive, but divides when she dies (Fig. 1, Lower Picnic: 1966–1975). When the mother dies, her daughters act to enhance their own direct fitnesses. Because cooperative defense is necessary to maximize direct fitness, cooperation with close kin increases inclusive fitness by adding some measure of indirect fitness. Apparently the level of benefit that would be required for cooperation among more distant kin is too high for an evolutionary pay-off.

Social dynamics are also characterized by competition. Among yellow-bellied marmots, females may suppress the reproduction of kin. When her mother or other kin was present, a two-year-old female was significantly less likely to reproduce than if no other adults were present¹². Within black-tailed prairie dog coterie, conflict predominated during the reproductive season (Fig. 2). This conflict represents defense of direct fitness investments as females defend against possible infanticide²¹. Female black-tailed prairie dogs kill the offspring of close kin²¹ and female yellow-bellied marmots expel the offspring of their sisters¹². At first thought, such behaviors would appear to reduce inclusive fitness. However, when only a limited number of adults can achieve access to limited resources, a female may increase her direct fitness to a much greater extent than her losses of indirect fitness if her behavior increases the probability that her daughters rather than more distant kin will inherit the resources.

Annual reproductive output decreases as coterie size of prairie dogs¹⁷ or harem size of marmots¹² increases. The effect of group size in marmots is a consequence of inter-matrilineal competition; there is no effect of group size on annual reproductive output of matriline. It is most likely that the reason there are few large matriline is that an individual gains more inclusive fitness by reducing competition by forming her own matriline. Kin selection does not explain why large prairie dog

coterie occur when smaller groups have a larger annual reproductive output. Possibly, lifetime reproductive output is similar in small and large groups.

The size of large groups can be reduced by dispersal. Although poorly documented, it is widely believed that survival and reproduction of dispersers is much lower than that of recruits²². The mortality rate of intercolony dispersers was significantly greater than resident black-tailed prairie dogs (M.G. Garrett, MSc thesis, Iowa State University, 1982). However, many of these were males, most of whom disperse independently of density. Because females are the philopatric sex, we must consider their alternatives. If a young female disperses, she must enter hostile social and/or physical environments while seeking residency. The daughter who remains, even though losing some reproductive output, may have greater fitness than the daughter who disperses and fails to reproduce. Therefore, a female increases her direct fitness if she retains her daughters in her natal area. However, not all daughters can be recruited, so a female can increase her direct fitness by eliminating the direct competitors of her offspring by infanticide²¹ or by expelling young of other females¹² or by limiting access to resources and mates¹². Thus, individuals in large social groups may have greater inclusive fitness than they would have if they socially restricted group size. These animals can only choose between available alternatives; in effect, they must make the best of the situation they encounter. Social dynamics may not be optimal but may only reflect the possible.

The examination of social dynamics in the best studied ground-dwelling squirrels reveals a pattern of cooperation and competition within female kin groups^{12,15,18}. Cooperation increases the direct fitness of those individuals that cooperate. Cooperation probably increases indirect fitness because only mother/daughter and sister/sister kin groups are highly cooperative. If indirect fitness were not increased, then any set of individuals should cooperate and there should be no relationship between kinship and cooperation.

Philopatry, direct fitness and the evolution of social groups

Do the social dynamics of ground-dwelling squirrels constitute a special case, or can the concept that behavior acts to maximize direct fitness be generalized to other mammalian species?

Widespread natal philopatry among solitary and gregarious mammals²² suggests that a common factor underlies mammalian societies. Because dispersal imposes heavier costs on daughters than on sons (through reduced survivorship or delayed reproduction) than does philopatry²³, the female whose daughter remains in or near her natal home range is more likely to reproduce. Intraspecific competition is probably a major factor selecting for group formation²⁴; the proximity of female kin creates the conditions for the formation of social groups based on kinship. Because mammalian social groups commonly consist of related females^{12,25-28}, these groups are probably derived evolutionarily from mother/daughter lineages that maximized direct fitness.

Various ecological and demographic factors affect group formation and composition²⁴. Social groups in ground squirrels⁹ and canids²⁹ are associated with delayed dispersal of juveniles in those species whose large size requires more time for juveniles to reach maturity. Hence, juvenile retention in the natal home range forms the basis of group living.

Although juvenile retention causes relatedness in mammalian societies to be higher than that of a random sample of the population, demographic processes reduce average relatedness. In the common vampire bat (*Desmodus rotundus*) relatively high juvenile mortality, low adult mortality, male immigration and female recruitment produce social groups with a low level of relatedness³⁰. Similarly, demography produces lion prides of relatively low average relatedness²⁶. This pattern probably characterizes relatively long-lived mammals. Because average relatedness decreases over time, matrilineal should split, as they do in marmots¹⁴ and rhesus monkeys (*Macaca mulatta*)³¹. In rhesus monkeys, a subordinate female and her daughters is the group most likely to split off. This genealogical splitting suggests that each female attempts to maximize her direct fitness.

Each member of the society should act to maximize its inclusive fitness; I suggest that maximizing inclusive fitness most likely occurs by maximizing direct fitness. Individuals should cooperate or compete depending on the effects of those behaviors on its direct fitness. Older adult vervet monkey females maintain affiliative and supportive relationships with their adult daughters. The daughters produce significantly more surviving offspring than com-

parable adult females without mothers³². Female yellow baboons affiliate with unrelated females when they enter lactation together³³. Such behavior increases the direct fitness of the females in the affiliation as cooperation increases the likelihood that their infants will survive.

Competition appears to be directed at improving the likelihood of offspring survivorship and reducing the probability that other offspring will succeed. Female yellow baboons attack other females to inhibit their reproduction³³ and female macaques attempt to deny other females access to resources necessary for reproductive success³⁴. Reproductive suppression of competing females is widespread among mammals³⁵, as is infanticide²¹. Although these behaviors support the hypothesis that mammalian social dynamics primarily enhance direct fitness, the widespread occurrence of kin groups suggests an important contribution from indirect fitness to inclusive fitness. Instances of shifting alliances, reproductive suppression of kin, infanticide of close kin and expulsion of kin from social groups, that appear to reduce inclusive fitness, are all explicable if gains in direct fitness exceed losses in indirect fitness.

Conclusions

Analysis of social dynamics of the well-studied ground-dwelling squirrels, plus evidence from several mammalian orders, suggest that kin selection (= indirect fitness) is less important than direct fitness in the evolution of mammalian social groups and behavior. Demography confounds interpretations of the relative significance of direct and indirect fitness in inclusive fitness, and further long-term studies embracing several generations of animals of known relatedness are required to test the interpretation presented here. The currency of fitness should be the number of reproductive descendants produced by an individual over its lifetime. Because social behavior may be directly related to lifetime reproductive success³⁶, social behavior must be quantitatively described over the lifetime of each individual. The ecological conditions associated with group living and the demography of the population must also be described²⁴. Ultimately, experimental manipulation of social structure and environment should directly test hypotheses about the relative importance of kin selection and direct fitness in mammalian societies.

Acknowledgements

Preparation of this review was supported partially by NSF Grant BSR 8614690. My thanks to John Hoogland and Paul Sherman who provided original copies of figures for my use.

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Species Introductions

Ecology of Biological Invasions

edited by R.H. Groves and J.J. Burdon, *Cambridge University Press*, 1986. £25/\$42.50 (ix + 166 pages) ISBN 0 521 30355 9

Ecology of Biological Invasions of North America and Hawaii

edited by H.A. Mooney and J.A. Drake, *Springer-Verlag (Ecological Studies 58)*, 1986. DM 148 (xvii + 321 pages) ISBN 0 387 96289 1

These two books correspond to meetings held in 1984 in Canberra and Asilomar respectively. The meetings were part of an international program on biological invasions, but each book is strictly regional. Groves and Burdon deal with Australia, whilst Mooney and Drake deal with North America and Hawaii.

The books represent an important consolidation of what we know about the biology of species introduced from one region to another. The main reason for this is that many of the authors have earnestly tried to collect and assess data sets on substantial numbers of introductions. Also, some of the best papers set out to test alternative hypotheses about the species or ecosystem characteristics which may affect the entry and success of species introduced from elsewhere. As all the authors recognized, there are intractable problems with such data. The most notable is that introductions that failed are very poorly documented. Nevertheless, using large data sets to assess explicit questions is clearly an advance on using examples piecemeal to support whatever argument an author cares to make.

By the same token, even those authors who used large data sets often reached different conclusions in these books. Some of these differences may have come about because the same raw material has been analysed in different ways. This should be resolved over the next few years as people reanalyse each other's data. In other cases con-

clusions may have been different because different groups of organisms were being considered.

Most authors agreed that invaders are only likely to be successful if introduced to environments physically similar to those from which they came. The strongest claim along these lines is by Nix and Wapshere (in Groves and Burdon). They calculated a measure of climatic similarity between source and target regions for introduced birds, for invertebrate control agents of weeds, and for biocontrol agents of insects. This measure accounted for 80–90% of the variance in establishment success in each of the three groups. This was a poster at the meeting, and unfortunately only a one-page abstract is published with few details of this very striking result.

It remains far from clear to what extent some ecosystems offer stronger 'biotic resistance' to invasion than others. Simberloff (in Mooney and Drake) found little evidence in insects for lowered resistance in island faunas. On the other hand Moulton and Pimm (in Mooney and Drake) showed that birds introduced to Hawaii were more likely to succeed when their bill morphology was more different from the nearest congener already present.

All authors agreed that the great majority of invaders were successful only in 'disturbed' environments. This implies that such environments do show lowered biotic resistance. Unfortunately many authors did not define what they meant by 'disturbed'. In the case of agricultural or urban environments the idea is clear enough, but in more marginal cases definitions of disturbance will need to be made consistent between authors, and measurable, if synthesis of the data sets is to go further.

Overall it is clear that most introductions have not succeeded, and most of those which have succeeded have only penetrated disturbed environments. Nevertheless, the few successes have had big impacts. We are certainly not in a position to predict in advance which ones will

succeed and which will not. What do we do next? No clear programme emerges. Ehrlich (in Mooney and Drake) consoles us that even the laws of physics are probabilistic where individual particles are concerned. This analogy suggests that introductions cannot be assessed or managed on a species-by-species basis – we can only choose a mean rate of introduction. In contrast, Simberloff remains 'convinced that the reasons for success or failure of any attempt can be determined by extensive field study but that these reasons will reside in aspects of the particular species and system that are so idiosyncratic that they will defeat any attempt at concise generalization'.

Regal (in Mooney and Drake) makes the excellent point that virtually all issues about the ecology of introduced species apply also to the ecology of genetically engineered organisms. Ecologists have been arguing for caution and further research on each particular case before any genetically engineered organism is released. The problem is, how much research, of what kind, will allow us to be confident that we understand the consequences of release? The state of play in introduced-species research, as reflected in these books, is that we do not know what information would be sufficient for a confident prediction. Indeed, if Ehrlich's analogy is right, the risk that an introduction or genetically-engineered organism will become a success where it is not wanted may be inherently probabilistic. In that event it would not be possible to manage releases by attempting to predict the outcome of each release on a case-by-case basis. It would be necessary to ask instead, what is the probability that a release will become a disaster, how many disasters are acceptable, and therefore how many genetically engineered releases should be made in total?

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