

Nepotism in prairie dogs (*Cynomys ludovicianus*) varies with competition but not with kinship

JOHN L. HOOGLAND*

Department of Biology, Princeton University, Princeton, New Jersey 08544, U.S.A.

Abstract. Behavioural interactions among black-tailed prairie dogs (*Cynomys ludovicianus*) of the same sex clearly show nepotism (the favouring of kin). Males and females consistently interact more amicably with kin than with non-kin. Nepotism in this context is striking for two reasons. First, individuals do not interact more amicably with close kin such as offspring and full-siblings than with more distant kin such as half-siblings, full-nieces, half-nieces, and half-nephews. Second, nepotism varies inversely and dramatically with changes in competition for either oestrous females (among males) or nesting burrows and breeding rights (among females).

Nepotism is the preferential treatment of genetic relatives (Alexander 1974; Sherman 1980a), and parental care is one obvious expression of nepotism. Hamilton (1964) predicted that nepotism beyond parental care should vary directly with the coefficient of genetic relatedness (r) under the appropriate conditions; that is, individuals should cooperate with close genetic relatives more than with distant relatives. Altmann (1979) later pointed out that if the recipient's benefit varies directly with the donor's investment, then individuals should channel all assistance to closest kin only. However, benefits to close kin do not usually vary directly with investment but rather reach a point of diminishing returns, after which individuals will be selected to start helping more distant kin. Patterns of nepotism versus r will also be affected by competition, reciprocity, reproductive value of the beneficiary, and the beneficiary's efficiency at using nepotistic assistance (Alexander 1974; West-Eberhard 1975; Sherman 1980b; Schulman & Rubenstein 1983). While these other factors mean that there will be some exceptions, a positive correlation between nepotism and r is still expected in most cases (Alexander 1979; Schulman & Rubenstein 1983).

Nepotism dispensed to kin other than offspring has been observed in numerous species including lions (*Panthero leo*: Bertram 1976), paper wasps (*Polistes exclamans*: Strassman 1981), and acorn woodpeckers (*Melanerpes formicivorus*: Koenig et al. 1983). However, a direct relationship between nepotism and r , perhaps because it is so difficult to

document, has been reported for only a few species including sweat bees (*Lasioglossum zephyrum*: Greenberg 1979; Buckle & Greenberg 1981), Belding's ground squirrels (*Spermophilus beldingi*: Sherman 1980b), two species of primates (Clutton-Brock & Harvey 1976; Kurland 1977; Massey 1977), and humans (Wilson 1978; Alexander 1979; Chagnon 1979). Nepotism evidently does not correlate with r in carpenter ants (*Camponotus* spp.) or perhaps in other insect species in which individuals live in huge colonies (Wilson 1971; Carlin & Holldobler 1983), but failure of nepotism to correlate with r has not previously been reported for any vertebrate. I report here that black-tailed prairie dogs (*Cynomys ludovicianus*), though nepotistic in the context of behavioural interactions, do not interact more amicably with close kin of the same sex, such as offspring and full-siblings, than with more distant kin such as half-siblings, full-nieces, half-nieces, and half-nephews. Further, intrasexual black-tail nepotism varies inversely in a regular, predictable fashion with competition for either oestrous females (among males) or nesting burrows and the opportunity to successfully wean a litter (among females).

Black-tails are diurnal, colonial, harem-polygynous, cooperatively breeding squirrels (Rodentia: Sciuridae). My study colony in Wind Cave National Park, South Dakota, occupies 6.6 ha and in late spring of each year contains approximately 130 adults (more than 2 years old) and yearlings plus 80 juveniles arranged into approximately 24 family groups known as coteries (Hoogland 1979). A typical coterie contains one adult male, three or four adult females, and several offspring which are either yearlings or juveniles (King 1955). In some years as many as 33% of all coteries contain more

* Present address: Appalachian Environmental Laboratory, The University of Maryland, Gunter Hall, Frostburg, Maryland 21532, U.S.A.

than one adult male, and the males in these multi-male coterie are frequently kin (Hoogland 1981a; Hoogland & Foltz 1982). In South Dakota, black-tails copulate in February and March, and juveniles first emerge from their natal burrows just before or at weaning in May and June. Females usually remain in the natal coterie for life, but males usually depart permanently 12–14 months after weaning (Hoogland 1982); consequently, the females within a coterie are almost always genetically related. Oestrous females usually mate with the adult male(s) resident in the home coterie (Foltz & Hoogland 1981; Hoogland & Foltz 1982) and avoid mating with close kin (Hoogland 1982; Foltz & Hoogland 1983). Coterie members restrict over 99% of foraging and other activities to a well-defined coterie territory which is defended by adults and yearlings of both sexes from individuals of contiguous coterie territories (King 1955; Hoogland 1981a).

METHODS

Interactions between two black-tails can be categorized as either amicable or hostile. Amicable interactions involve a kiss, anal sniff, or allogrooming in the absence of any aggression (King 1955; Hoogland 1981a). Hostile interactions frequently begin with a kiss or anal sniff followed by a fight, chase, or territorial dispute (King 1955; Hoogland 1979, 1981a). Combinations of amicable (e.g. kiss + kiss or kiss + allogrooming) or hostile (e.g. fight + fight or chase + territorial dispute) interactions were scored as single interactions. Fights can lead to serious injury or death, chases sometimes involve more than 500 m of hard running, and territorial disputes can persist for as long as 3 h (Hoogland 1979, unpublished data). Thus, because hostile interactions are evidently costly to individual black-tails, it seems likely that interacting more amicably with kin than with non-kin (i.e. reducing aggression towards kin) would be an important expression of nepotism in this species.

Because black-tail females nurse only their own young, except perhaps just before weaning (Hoogland 1983a), nepotism in this context clearly favours close kin. In this report I only consider nepotism among adults and yearlings as it applies to behavioural interactions. A dyad is a pair of reproductive or potentially reproductive individuals of the same sex. Because females frequently copulate as yearlings while males almost never

copulate until they reach 2 years of age (Hoogland 1982; Hoogland & Foltz 1982), numerous yearling females, but only those yearling males known to copulate, were included in dyads.

To show that nepotism does or does not vary with r in the context of behavioural interactions requires detailed genealogies and observations of numerous interactions. To investigate this question for the black-tails of known ages and genetic relationships at my study colony, field assistants and I recorded interactions from three 5-m observation towers in February through June of 1979 through 1984. Analyses have been completed for male data from all years, but, because of the large sample sizes involved (Table I, Fig. 1), analyses have been completed for female data through 1981 only. We were at the study colony each day for over 99% of the daylight hours when the prairie dogs were above ground. Sibling genetic relationships were determined by marking all young from a litter before they mixed with young from other litters (Hoogland 1981a, 1982). Lactating females defend the burrow containing their young from all conspecifics during the day and sleep there alone with their young at night (King 1955; Hoogland 1983a), so that maternities could be determined by observing defensive and sleeping patterns of individual females. Paternities were inferred from behavioural observations of oestrous females in combination with an electrophoretic analysis of blood samples (Foltz & Hoogland 1981; Hoogland & Foltz 1982). In each coterie each year, interactions were classified according to stage of the annual cycle: 'pre-breeding' if before the first copulation in that coterie; 'early pregnancy (breeding)' if during the first 3 weeks following the first copulation; 'late pregnancy' if during the fourth and fifth weeks after the first copulation; 'early lactation' if during the first 4 weeks after the first parturition (as determined from changes in behaviour (Hoogland & Foltz 1982) or by counting either the number of days after copulation or the number of days before the first juvenile emergence); 'late lactation' if during the fifth and sixth weeks after the first parturition; and 'postweaning' if during the first 6 weeks after the first juvenile emergence. In 1979, limited data for females were also available from October. Females within a coterie usually breed synchronously (Hoogland 1981b), so that all copulations in each coterie occurred during the stage labelled early pregnancy (breeding) in Table I and Fig. 1.

Although almost all reproductively mature females at the study colony copulate each year, many do not successfully wean a litter (King 1955; Hoogland 1981a; Hoogland & Foltz 1982); some unsuccessful females never conceive, others abort their young sometime during pregnancy, and still others lose their young during lactation (Hoogland

1983a, in press). Because interactions between two non-reproductive females are almost always amicable and show little variation with stage of the annual cycle, I only analysed data from dyads for which at least one of the females successfully weaned a litter. For some male and female dyads, data were available for more than 1 year; in these

Table 1. Nepotism for different types of dyad at different stages of the black-tail annual cycle for (A) females and (B) males

Dyad	Stage						
	Prebreeding	Early pregnancy (breeding)	Late pregnancy	Early lactation	Late lactation	Post-weaning	October
(A) Female dyads							
Mother-daughter	0.87 ± 0.05 216 35	0.43 ± 0.04 784 48	0.19 ± 0.04 335 44	0.31 ± 0.05 656 45	0.36 ± 0.07 235 38	0.83 ± 0.05 122 32	0.67 ± 0.33 3 3
Full sisters	0.94 ± 0.03 143 14	0.28 ± 0.08 537 15	0.08 ± 0.05 194 15	0.13 ± 0.06 268 15	0.20 ± 0.07 160 13	0.62 ± 0.08 105 12	1.0 ± 0.0 3 2
Half-sisters	0.90 ± 0.07 74 15	0.40 ± 0.08 351 20	0.32 ± 0.09 259 19	0.28 ± 0.09 314 18	0.39 ± 0.12 136 15	0.65 ± 0.10 62 14	1.0 ± 0.0 2 1
Full aunt-niece	0.95 ± 0.05 50 10	0.26 ± 0.05 298 13	0.13 ± 0.09 125 12	0.18 ± 0.09 262 13	0.32 ± 0.12 86 11	0.66 ± 0.14 35 10	1.0 ± 0.0 6 2
Half-aunt-niece	0.96 ± 0.03 60 9	0.52 ± 0.10 125 11	0.04 ± 0.04 44 8	0.13 ± 0.08 111 11	0.04 ± 0.04 36 6	0.77 ± 0.15 9 5	— 0 0
Full first cousins	0.85 ± 0.0 20 1	0.40 ± 0.0 20 1	— 0 0	0.0 ± 0.0 5 1	0.0 ± 0.0 6 1	0.33 ± 0.0 3 1	— 0 0
(B) Male dyads							
Father-son	0.49 ± 0.38 230 6	0.17 ± 0.21 135 6	0.25 ± 0.43 21 5	0.25 ± 0.38 67 6	0.36 ± 0.50 29 6	0.46 ± 0.30 24 5	— 0 0
Full brothers	0.57 ± 0.44 270 6	0.29 ± 0.41 229 6	0.60 ± 0.55 27 5	0.67 ± 0.44 106 5	0.78 ± 0.44 82 5	0.67 ± 0.47 39 6	— 0 0
Half-brothers	0.07 ± 0.12 131 4	0.20 ± 0.21 127 3	0.30 ± 0.51 25 3	0.21 ± 0.42 103 4	0.25 ± 0.43 34 3	0.56 ± 0.62 15 2	— 0 0
Full uncle-nephew	— 0 0	— 0 0	— 0 0	— 0 0	— 0 0	— 0 0	— 0 0
Half-uncle-nephew	0.29 ± 0.40 11 2	0.0 ± 0.0 20 1	0.65 ± 0.21 25 2	1.0 ± 0.0 239 2	1.0 ± 0.0 76 2	0.83 ± 0.24 32 2	— 0 0
Full first cousins	0.0 ± 0.0 35 1	0.0 ± 0.0 48 1	0.0 ± 0.0 3 1	0.0 ± 0.0 10 1	0.0 ± 0.0 6 1	0.0 ± 0.0 12 1	— 0 0

For each dyad, at each stage, figures are given for the proportion of interactions that were amicable (mean ± 1 SE), the total number of observed interactions, and the number of observed dyads. Amicability of interactions did not vary significantly with *r* at any stage for either sex; see text for details.

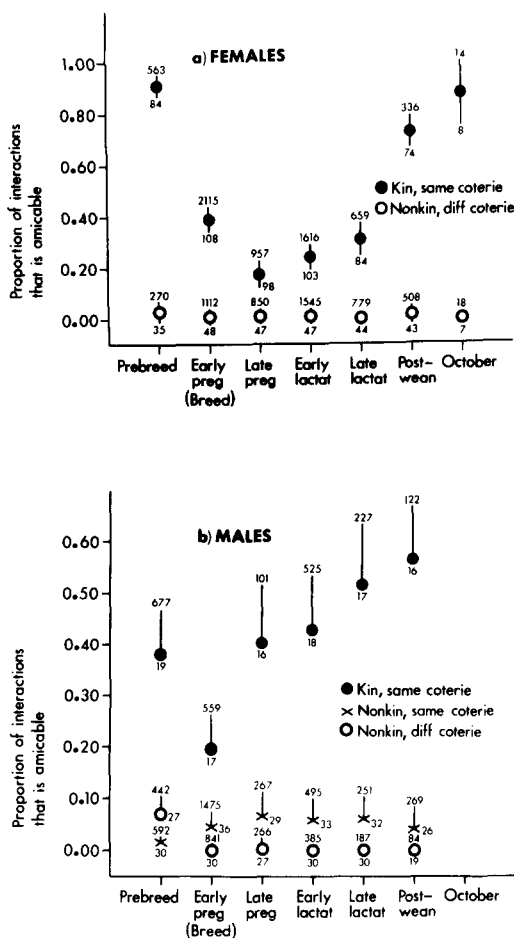


Figure 1. Nepotism versus competition for (a) females and (b) males. Symbols indicate means; lines indicate one standard error (SE); numbers above SE lines indicate numbers of observed interactions; numbers below SE lines indicate numbers of dyads. Note that vertical axes of (a) and (b) differ.

cases, data from the different years were combined so that each dyad was represented one time only in all statistical analyses. The number of observers often differed among different stages of the annual cycle, and consequently the number of dyads for which data were available also differed among different stages (Table I). Dyads containing individuals of the same and different ages were considered equivalent since, to this point, there is no evidence that amicability of interactions among adults and yearlings varies systematically with age for either sex. For males we observed 7765 interactions involving 85 different dyads, and for females

we observed 11 342 interactions involving 156 different dyads (Table I).

I use the terms close kin, for two individuals for which r is equal to or greater than 0.50 (parent-offspring, full siblings), distant kin, for two individuals for which $0.50 > r > 0.00$ (half-siblings, full aunt-niece, half-aunt-niece, full uncle-nephew, half-uncle-nephew, full first cousins), and non-kin, for two individuals for which there is no known kinship. Because of male and female dispersal patterns, individual black-tails only rarely interact with kin of the same sex that belong to a different coterie (Hoogland 1981a, 1982); for all male and female dyads involving kin in this report, individuals were always of the same coterie. In all female dyads, non-kin were always from different coterie; in male dyads, non-kin were either from the same (multi-male) or from different coterie. All significance levels are for two-tailed statistical tests.

RESULTS

Nepotism among black-tail females extends to distant kin such as half-sisters, full nieces, and half-nieces, and nepotism among black-tail males extends to distant kin such as half-brothers and half-nephews (Table I). Whereas many of the interactions for the single set of female full first cousins were amicable, all of the interactions for the single set of male full first cousins were hostile. For an investigation of amicability of intrasexual interactions versus r for males and females, data were available for three levels of r : $r = 0.50$ (parent-offspring and full siblings), $r = 0.25$ (half-siblings, full aunt-niece or full uncle-nephew), and $r = 0.125$ (half-aunt-niece or half-uncle-nephew, full first cousins). Amicability of interactions did not vary significantly with r at any stage of the annual cycle for either males or females ($P > 0.050$ for all stages, Kruskal-Wallis ANOVA). Thus, Hamilton's hypothesis that nepotism should vary directly with r is not supported by data from black-tails.

Numerous authors have pointed out that nepotism should vary inversely with competition (Hamilton 1964; Alexander 1974; West-Eberhard 1975). While several studies have demonstrated nepotism under conditions of reduced competition (Rowley 1965; Woolfenden 1975; Brown 1978) and several others have demonstrated an apparent lack of nepotism under conditions of extreme competition (Ingram 1959; Hamilton 1972; Eickwort

1973), no previous study has specifically examined how nepotism among the same individuals varies with changes in competition. For black-tail males, as for males of mammalian species in general (Darwin 1871; Trivers 1972), the major source of intrasexual competition is almost certainly oestrous females. It follows that competition among black-tail males should be most extreme, and that nepotism should therefore be least extreme, during the stage labelled early pregnancy (breeding), when all copulations occur. Data in Fig. 1 support this prediction.

Although coterie territories typically contain 30–50 burrow systems (King 1955; Hoogland 1981b), only some of these systems are evidently suitable for rearing offspring since in each territory only a small subset of systems consistently produces weaned juveniles over the years (unpublished data). Further, perhaps because a colony's resources can support only a limited number of offspring each year, lactating females sometimes try to kill the unweaned offspring of other lactating females of either the home coterie or adjacent coterie (Hoogland 1983a, in press). It follows that competition among black-tail females should be most extreme, and that nepotism should therefore be least extreme, during the stages of early pregnancy (when females first begin to defend nesting burrows) through late lactation. Data in Fig. 1 support this prediction. The patterns of nepotism versus competition for males and females shown in Fig. 1 are evident year after year for both sexes, and can also be seen in the analyses of the same dyads in different years (unpublished data).

For females, amicability of interactions among kin of the same coterie was significantly greater during the combined stages of prebreeding, postweaning, and October (when competition for nesting burrows and breeding rights was minimal) than during the combined stages of early pregnancy through late lactation (when competition for nesting burrows and breeding rights was maximal; $P < 0.001$, Wilcoxon matched-pairs signed-ranks test). Amicability of interactions among female non-kin of different coterie did not vary similarly with stage ($P > 0.300$, Wilcoxon matched-pairs signed-ranks test). Further, female interactions involving kin of the same coterie were significantly more amicable than interactions involving non-kin of different coterie for all stages ($P < 0.001$ for each stage, Mann–Whitney *U*-test). For males, amicability of interactions among kin of the same

coterie was significantly greater during the combined stages of prebreeding and late pregnancy through postweaning (when competition for oestrous females was minimal) than during the stage of breeding–early pregnancy (when competition for oestrous females was maximal; $P < 0.001$, Wilcoxon matched-pairs signed-ranks test). Amicability of interactions among male non-kin of both types did not vary similarly with stage ($P > 0.300$ for each type, Wilcoxon matched-pairs signed-ranks test). Further, male interactions among kin of the same coterie were significantly more amicable than interactions among both types of non-kin for all stages ($P < 0.010$ for each stage, Mann–Whitney *U*-test). Male interactions involving non-kin of the same coterie were not significantly more amicable than interactions involving non-kin of different coterie for any stage ($P > 0.100$, Mann–Whitney *U*-test).

DISCUSSION

Figure 1 shows that competition reduces, but does not eliminate, nepotism. Thus, even when competition is maximal for black-tail males during early pregnancy (breeding), individual males still interact more amicably with kin than with non-kin. Similarly, when competition is maximal for females during pregnancy and lactation, individual females still interact more amicably with kin than with non-kin.

Changes in black-tail nepotism are sometimes dramatic. For example, hostile interactions typically begin, abruptly, the day after a female copulates and end, abruptly, the day that her offspring first emerge from the natal burrow 11 weeks later; before copulation and after the first emergence of her juveniles, a female almost always interacts amicably with other coterie females. Similarly, in one multi-male coterie containing a father and his son and in another multi-male coterie containing two half-brothers, the two males started interacting amicably, following at least 2 weeks of almost constant antagonism, on the day after the last female in the home coterie copulated.

Unrelated adult males of the same multi-male coterie do not interact significantly more amicably than unrelated adult males of different coterie (Fig. 1). Thus, for males at least, observed patterns of nepotism seem to result ultimately from kinship rather than from familiarity resulting from mem-

bership in the same coterie. A similar comparison is not possible for females, since female patterns of dispersal and recruitment preclude interactions with female non-kin in the home coterie (Hoogland 1982, 1983b). Data on intrasexual interactions among male and female kin from different coterie are needed for further investigation of the effects of kinship and familiarity on amicability of interactions. Such data sometimes result after a male from one coterie disperses to an adjacent coterie and sires offspring there, and are only now beginning to accumulate as my long term study of black-tails continues.

Patterns of amicability of intrasexual interactions versus r might be biased for black-tails if individuals avoid interacting with close kin during periods of extreme competition. Females, for example, might consistently nest closer to distant kin rather than close kin, which would lead to more interactions with distant kin during pregnancy and lactation. Biases of this sort evidently do not occur, since the number of observed interactions does not vary systematically with r for either males or females at any stage ($P > 0.050$ for all comparisons, Kendall rank correlation test). Further, analysing the proportion of interactions that are amicable (Table I, Fig. 1) rather than the absolute numbers of amicable and hostile interactions would remove any biases related to partial avoidance of close kin during periods of intense competition.

When two black-tails interact aggressively, it is usually difficult to determine, from an observation tower, which individual initiates the aggression. Also, rather than recording interactions among a small subset of colony residents, field assistants and I always attempted to record interactions for all colony residents with less attention to detail. Further, in my analyses, I did not distinguish among the different types of aggressive and amicable interactions (e.g. fight versus chase and kiss versus allogroom). Even though frequency and amicability of interactions do not vary systematically with r for either sex, it is possible that other aspects of behavioural interactions (e.g. mean length of each aggressive interaction, ratio of fights to chases) do vary systematically with r , but this seems unlikely.

Among squirrels, preferential treatment of kin in the context of behavioural interactions has been reported for round-tailed ground squirrels (*S. tereticaudus*; Dunford 1977), Richardson's ground squirrels (*S. richardsonii*; Yeaton 1972; Michener

1973; Davis 1982), arctic ground squirrels (*S. parryi*; Holmes & Sherman 1982, 1983; McLean 1982), yellow-bellied marmots (*Marmota flaviventris*; Armitage & Johns 1982; Armitage 1984, 1985), and Belding's ground squirrels (Sherman 1977, 1980b, 1981). Only for yellow-bellied marmots and Belding's ground squirrels has nepotism been documented to the extent reported here and elsewhere (Hoogland 1983b) for black-tails. Nepotism among black-tails differs from nepotism among yellow-bellied marmots and Belding's ground squirrels in at least three important ways. First, male-male nepotism is evident among black-tail adults but absent among yellow-bellied marmot (Armitage 1984) and Belding's ground squirrel adults (Sherman 1981). This difference probably results because black-tail males (Hoogland 1982), unlike yellow-bellied marmot (Armitage & Downhower 1974) and Belding's ground squirrel males (Sherman 1981; Holekamp 1983), sometimes disperse together with a father, son, full brother, or half-brother into the same new area, resulting in frequent interactions among these kin. Second, whereas female-female nepotism in yellow-bellied marmots (Armitage 1984, 1985) and Belding's ground squirrels (Sherman 1980b, 1981) is limited to mother-daughter, full sister, and half-sister dyads, in black-tails it also extends to more distant kin such as full aunt-niece and half-aunt-niece. Female yellow-bellied marmots (Armitage & Downhower 1974) and female Belding's ground squirrels (Sherman 1981; Holekamp 1983) are more likely to disperse away from the natal area than female black-tails (Hoogland 1982). Thus, dispersal is less likely to separate distant female kin for black-tails, and this difference would presumably lead to stronger selection for nepotism among such distant kin. Third, whereas nepotism in Belding's ground squirrels (Sherman 1980b, 1981) and possibly also in yellow-bellied marmots (Armitage 1984, 1985) seems to be most pronounced in mother-daughter dyads, less pronounced in full-sister dyads, and least pronounced in half-sister dyads, there is no evidence in black-tails for similar consistent variation among the same or other female dyads. In other words, even though genetic relationships among coterie females vary extensively (Table I), black-tail females do not seem to discriminate among the various types of kin but rather only between kin (members of the home coterie) and non-kin (members of different coterie). Similar patterns of nepotism are evident in

black-tail alarm calling; individual males and females with offspring in the home coterie do not call significantly more often than individuals with only non-descendant kin in the home coterie (Hoogland 1983b). These surprising results for behavioural interactions and alarm calling do not necessarily imply that black-tails do not or cannot discriminate between close kin and distant kin in other contexts, and an investigation of nepotism versus r in other contexts is in progress.

As my study of black-tails continues, I am becoming more able to determine distant genetic relationships for which I previously had no information. For example, data for both males and females are now beginning to accumulate for interactions between full first cousins once removed, half first cousins, full second cousins, etc. For females, the new data continue to indicate that a female interacts equally amicably with all members of the home coterie, regardless of the magnitude of r . For males, on the other hand, the new data suggest that individuals interact with full first cousins (as suggested in Table I), full first cousins once removed, half first cousins, and full second cousins of the home coterie as though they are non-kin. More data are needed, especially for males, on interactions among distant kin of the home coterie.

Few hypotheses in behavioural ecology and sociobiology have generated as much theoretical (e.g. Orlove 1975; Milinski 1978; Weigel 1981) and empirical (e.g. Kurland 1977; Greenberg 1979; Sherman 1980b; Woolfenden & Fitzpatrick 1984) research as Hamilton's (1964) hypothesis that nepotism should vary directly with r . Definitive field studies are rare, and have uncovered evidence both for and against Hamilton's (1964) hypothesis. Further investigations involving long term field study seem crucial for a better understanding of nepotism versus r under natural conditions.

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