

GROUND SQUIRREL ALARM CALLS:
NEPOTISM OR PARENTAL CARE?

Recently, Sherman (1977) and Dunford (1977) independently reached the conclusion that the alarm calling of two ground squirrel species (*Spermophilus beltingi* and *S. tereticaudus*) was altruistic nepotism, and therefore was better explained through kin, than through individual, selection. Though their analyses differed in detail, both were able to show that a variety of alternative individual selection hypotheses (e.g., Trivers 1971; Charnov and Krebs 1975) were improbable explanations of squirrel alarm calling. Sherman was also able to show that hypotheses of group benefit and reciprocity were less consistent with his data than the nepotism hypothesis. Though neither stated it explicitly, both implied that benefits to any and all nearby kin were important in shaping the behavior.

I agree that they have demonstrated that alarm calls benefit listeners more directly than callers. However, they also failed to distinguish between classes of potential beneficiaries, which might have a bearing on the necessity of citing kin selection as the primary force in the evolution of alarm calling. If benefits to collateral (nondescendant) kin are necessary to explain calling, then kin selection, in its normal usage, is necessary to explain donor behavior. If the primary, or sole, beneficiaries are lineal descendants of the caller, especially young of the year, then donor behavior could be considered parental care. Since offspring are kin, costly parental care could be considered altruism, and thus within kin selection's domain (e.g., Hamilton 1964; Alexander 1974; Dawkins 1976). Since individual selection has always been defined in terms of personal reproductive success, others place parental care in its domain, limiting altruism to cases when collateral kin are primary beneficiaries (e.g., Williams 1966; Wilson 1975; Brown 1975). Perhaps parental care's ambiguity can be reduced by following West Eberhard's (1975) definition of inclusive fitness as the combined effects of (1) a "classical individual component," tied to personal reproduction and corresponding to the target of classical individual (in the context of parental care, lineal kin?) selection, and (2) a "kinship component," tied to the reproduction of collateral relatives and corresponding to the traditional target of kin (collateral?) selection. In this framework, a conceptual dichotomy between individual and kin selection is not necessary. Rather one can ask, What is the relative importance of each component in shaping a particular character? This would still permit a distinction between selfish social behavior, "contributing primarily to the personal fitness component," and altruistic behavior, "contributing primarily to the kinship component" (West Eberhard 1975). Parental care would be considered selfishness owing to its immediate effects on personal reproductive success. As an explanation of alarm calling, then, it would be a testable alternative to the broader