BLACK-TAILED PRAIRIE DOG COTERIES ARE COOPERATIVELY BREEDING UNITS

Black-tailed prairie dogs (Sciuridae: *Cynomys ludovocianus*) live in polygynous social groups called coteries which typically contain 1 adult male, 3–4 genetically related adult females, and several yearling and juvenile offspring of the adult females (King 1955; Hoogland 1979, 1981*a*, 1982, 1983; Foltz and Hoogland 1981; Hoogland and Foltz 1983). Because several adult females and all the yearlings within a coterie typically do not breed each year but do behave parentally in some contexts toward juvenile nondescendant genetic relatives of the home coterie, I recently classified black-tails as cooperative breeders (Hoogland 1981*b*). I pointed out that black-tail helpers (breeders or nonbreeders who behave parentally toward nondescendant juveniles) "do not assist breeders to the same degree as do helpers in most avian cooperative breeders" (p. 285) and "Of Brown's (1978) list of diagnostic behaviors, black-tail helpers show only defense of the territory" (p. 285). Michener and Murie (1983, p. 272) have challenged my classification: "Because pregnant and lactating females nested in isolation, were hostile to their own group members, received no direct or umambiguous assistance with rearing young from group members, and had lower reproductive success in larger units containing many supposed helpers, we question Hoogland's designation of black-tailed prairie dog coteries as cooperative breeding units." I have several comments in response to Michener and Murie's challenge.

Most importantly, none of the conclusions in Hoogland (1981*b*) depend on whether black-tails are "cooperative breeders." Whether they are designated as cooperative breeders, competitive breeders, or anything else, my three main conclusions remain unaffected: (*a*) The adult females, yearling females, and yearling males within a coterie are almost always close genetic relatives. (*b*) Behavioral interactions, alarm calling, communal sleeping patterns, excavation and maintenance of burrow systems, nestbuilding, and two variations in social organization all emphasize the importance of nepotism (i.e., the preferential treatment of genetic relatives) to black-tails. (*c*) The annual reproductive success (ARS) of adult females varies inversely with coterie size.

In their critique, Michener and Murie (1983, p. 267) assert that ". . . a case for nonbreeders *relinquishing* the opportunity to breed was not established" (emphasis theirs). The problem here is semantic, and I now see that my usage of the term "relinquish" (Hoogland 1981*b*, p. 283) may be misleading. "Relinquish" means "to withdraw from" or "to give up" (Webster's New Collegiate Dictionary 1977); although "relinquish" may imply self-initiated rather than forced withdrawal, this is not necessarily so. The real issue is whether certain adult females in a coterie do successfully breed while other adult females in the same coterie, for whatever reason, do not successfully breed. This issue is clearly resolved in figure 18-10a of Hoogland 1981*b*, which shows that the mean number of litters weaned per adult

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female was lower than 1.0 for 24 of the 25 coteries (96%) at my study site in 1976–1978. Some nonbreeding adult females do not copulate, others copulate but do not conceive, others conceive but do not give birth, and still others give birth but lose their offspring during lactation.

Later in their critique, Michener and Murie (1983, p. 268) ask: "Do nonbreeders help breeders?" All black-tail nonbreeders help defend the home coterie territory, most also help with the excavation and maintenance of burrow systems, nest-building, and the grooming of and playing with juveniles, and a few may help in other ways as well (King 1955; Hoogland 1981*b* and below). Although helping behaviors such as these are usually assumed to increase the ARS of breeding individuals, the demonstration of either increased ARS of breeders or any other favorable effect is not a requirement in theory or in practice for the designation of species as cooperative breeders (Skutch 1935, 1961; Brown 1974, 1978; Emlen 1978, 1981, 1982*a*, 1982*b*; Ligon and Ligon 1978*a*, 1978*b*; Ligon 1981*a*, 1981*b*; Koenig 1981; Koenig and Pitelka 1981; Brown and Brown 1981; Brown et al. 1982). If individuals within a species help rear nondescendant juveniles, then, contrary to Michener and Murie's (1983) argument, designation of that species as a cooperative breeder does not require demonstration for members of cooperatively breeding units of either (*a*) increased availability of resources, (*b*) reduced parental load, (*c*) increased survivorship, or (*d*) increased ARS of breeders. These are all predictions from, but not prerequisites for, the designation of cooperative breeding; these predictions have been rigorously tested for fewer than 10% of the 150 species of cooperatively breeding birds and for none of the cooperatively breeding species of other taxa. For black-tails, I presented preliminary tests for all four of Michener and Murie's (1983) predictions (Hoogland 1981*b*).

The part of Michener and Murie's (1983, p. 269) critique entitled "*Cooperation or competition?*" contains several misinterpretations and misrepresentations. (*a*) Michener and Murie (1983) imply throughout this section that I did not consider the importance of competition in the evolution of black-tail cooperative breeding. However, I discussed the possible importance of aggression and competition in numerous places in Hoogland (1981*b*; e.g., see pp. 294, 296, 304, 305, 307). On page 306, I specifically pointed out that the inverse relationship between coterie size and ARS of adult females might result from increased competition in larger coteries (see also Hoogland 1979). (*b*) Michener and Murie's (1983) table 1 is extracted from figure 18–4 of Hoogland (1981*b*), and shows that within-coterie interactions between adult females and between adult females and yearlings are more hostile during the stages of late breeding and lactation than during the stages of prebreeding, early breeding, and postweaning; from table 1 Michener and Murie (1983) concluded that helpers do not promote the successful reproduction of breeding females. However, theories of cooperation and cooperative breeding do not predict that behaviors should always be cooperative: When competition is extreme within a cooperatively breeding unit, as is competition for food, mates, and nesting burrows within a black-tail coterie during breeding through lactation (Hoogland 1979, 1981*b*), then cooperation should be less evident than during periods of less extreme competition (Hamilton 1964; Alexander 1974; Emlen 1978, 1982*b*; Sherman 1980). Seasonal variation in aggression similar to what I observed

in black-tails has been observed in cooperatively breeding species of both birds (Emlen 1978, 1982*b*; Trail et al. 1981) and insects (West-Eberhard 1969; Wilson 1971). (*c*) Michener and Murie's (1983) table 2, which is also extracted from figure 18-4 of Hoogland (1981*b*), shows that, for interactions between adult females and between adult females and yearlings, the number of within-coterie hostile interactions was greater than the number of between-coterie hostile interactions during the stages of late breeding and lactation. From table 2 Michener and Murie (1983) again concluded that helpers do not promote the successful reproduction of breeding females. However, the number of within-coterie amicable interactions between adult females and between adult females and yearlings was also greater than the number of between-coterie amicable interactions during late breeding and lactation. In Hoogland (1981*b*, pp. 287–288) I specifically examined proportions of interactions that were amicable rather than absolute numbers of amicable (or hostile) interactions in order to account for differences in sample size. I found that between-coterie interactions were almost always hostile, and that within-coterie interactions ranged from mostly amicable (during prebreeding, early breeding, and postweaning) to mostly hostile (during late breeding and lactation). At each stage, even during late breeding and lactation, within-coterie interactions were significantly more amicable than were between-coterie interactions. (*d*) Because the number of helpers increases directly with coterie size, "I predicted at the outset of my study that ARS of adult females would increase directly with coterie size" (Hoogland 1981*b*, p. 300). I was surprised to find that female ARS varies inversely with coterie size, and devoted 10 of 26 text pages (38%) to possible explanations for this paradox. I pointed out that the paradox might be explained by either (*a*) unnatural or disturbed conditions at the study colony (pp. 300–301), (*b*) an inverse relationship between coterie size and territory quality (p. 306), or (*c*) shortage of suitable habitat (pp. 306–307). I also pointed out in several places the importance of examining lifetime reproductive success (LRS) of females for a thorough understanding of black-tail cooperative breeding. Despite the opposite trend in female ARS, I predicted that female LRS might vary directly with coterie size if either (*a*) longevity of adult females and their offspring varies directly with coterie size (p. 303), or (*b*) individuals in large coteries are somehow better able than individuals in smaller coteries to take over those coterie territories that rarely become vacant within the home colony (pp. 306–307). Another way that female LRS might vary directly with coterie size would involve individuals in large coteries being less vulnerable to territorial take-overs by invading prairie dogs that otherwise might kill juveniles and evict adults and yearlings (see example in Hoogland 1981*b*, p. 288). Michener and Murie (1983) ignored my prediction and suggested that female LRS varies inversely with coterie size (p. 272); their suggestion is based on no new information and seems premature. As with ARS of females, the demonstration of a direct relationship between coterie size and LRS of females is a prediction from, but not a prerequisite for, the designation of black-tails as cooperative breeders.

Since Hoogland (1981*b*), field assistants and I have observed black-tails during four additional breeding seasons (1979–1982, involving over 12,000 additional man-hours of observation of marked individuals under natural conditions). Some

of our new findings make the term cooperative breeding seem less appropriate for black-tails, while other new findings make the term seem more appropriate. On the negative side, we have found that lactating females sometimes kill the unweaned offspring of other lactating females of the home coterie. Similar killing, involving the destruction of eggs laid by other females of the cooperatively breeding unit, has been observed in several cooperatively breeding species of both birds (Vehrencamp 1977, 1978; Emlen 1978, 1982*b*; Trail et al. 1981) and insects (Hamilton 1964; West-Eberhard 1969; Wilson 1971). Killing of this sort emphasizes once again that cooperative breeding involves both cooperation and competition. On the positive side, there are two new lines of evidence. First, we have found that mothers with newborn young frequently spend as much as 75% of daylight hours underground with their young, during which time defense of the home coterie territory by nonbreeding helpers (who typically spend less than 10% of daylight hours underground during lactation) seems especially important. Second, we have found that there may be limited communal nursing similar to that reported for numerous carnivore species (e.g., Bertram 1976; Rood 1978, 1980; MacDonald and Moehlman 1982). When black-tail young first emerge from the natal burrow approximately 5 wk after birth, I have assumed to this point that they are weaned (e.g., see Hoogland 1981*a*, 1981*b*, 1982). Recent circumstantial evidence based on sleeping patterns indicates that young probably are not weaned at first emergence, and that following first emergences mothers will frequently nurse not only their own offspring but also the offspring of other females of the home coterie.

The number of "helping behaviors" that have been described among cooperatively breeding species is large. Some species show numerous helping behaviors, while others show only a few. In other words, cooperative breeders form a continuum regarding the range of cooperation shown by helpers (Brown 1978; Emlen 1978; Woolfenden 1975, 1981). No objective criteria exist which dictate how many helping behaviors must be detected before a species can be appropriately classified as a cooperative breeder. Classification is especially difficult for mammals since, as correctly pointed out by Michener and Murie (1983, p. 266), helping mammals may be more limited than helpers in other taxa in the number of ways that they can assist breeders since so much parental care in mammals occurs inside the mother's uterus before birth. Michener and Murie (1983, p. 266) listed four types of helping that have been observed among cooperatively breeding mammals. Of these four, black-tails show at least two (grooming of young and active defense of young against predators and aggressive conspecifics), probably one other (a variation of "babysitting," in which helpers defend the home coterie territory while the mother nurses her offspring underground), and possibly the fourth as well (food to nondescendant young via communal nursing; Hoogland 1981*b* and above). Thus, Michener and Murie's (1983) own list of helping behaviors seems to argue that black-tails should be classified as cooperative breeders.

The black-tailed prairie dog is probably the most colonial as well as the most cooperative of all the squirrel species (King 1955; Hoogland 1979, 1981*a*, 1981*b*, 1983). Here I have argued that black-tails can legitimately be designated as cooperative breeders. When compared to helping and competition within the

social units of other cooperatively breeding species, helping within the black-tail coterie may be less extreme and competition within the coterie may be more extreme. Thus, black-tails should probably be ranked at the lower extreme in the continuum of cooperative breeders.

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