KIN SELECTION IN RIO GRANDE TURKEYS: A CRITICAL ASSESSMENT

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ABSTRACT.—Cooperative mating among Rio Grande Turkey (*Meleagris gallopavo intermedia*) brothers on the Welder Wildlife Refuge in southern Texas (Watts and Stokes 1971) is often cited as an example of kin selection. The genetic relatedness of the cooperating birds, however, was never known. We reject the hypothesis ($P < 0.01$) that "sibling groups" of the number and size described contained only brothers. We suggest instead that kin selection could produce cooperative mating by males and cooperative rearing of young by females among birds that are siblings or more distantly related. Several lines of evidence, however, lead us to question whether kin selection occurs at all in Rio Grande Turkeys. We present alternative explanations of the observed behavior without invoking kin selection. *Received 21 March 1980, accepted 5 July 1980.*

WATTS (1968, 1969) reported that Rio Grande Turkeys (*Meleagris gallopavo intermedia*) on the Welder Wildlife Refuge, San Patricio County, Texas exhibited a unique social organization during the breeding season. In winter, the turkeys formed unisexual flocks, with immature and adult males living apart. At the onset of breeding in early spring, the adult male flocks separated into sibling groups of one to four brothers. These groups were permanently closed to outsiders; thus the number of males in a sibling group always was the number of surviving brothers. After the breeding season, the sibling groups joined again to form male flocks.

Stable dominance-subordination relationships existed within and between male sibling groups. The group with the largest number of adult members typically was dominant. During the mating period, this dominant group mingled with large female flocks on display grounds, whereas subordinate groups remained at the periphery. Only the highest-ranking male of a group copulated with females, and the dominant member of the dominant group performed most of the mating. While the dominant male copulated, subordinate members of the group cooperated by fending off any intruding males.

Subsequent descriptions of this work by Watts and Stokes (1971), Wilson (1975: 125–126), Barash (1977: 89–90, 171–172), Alcock (1979: 405–407), and others have promulgated the idea that turkey brothers cooperate in mating and that such behavior probably is a product of kin selection. An examination of Watts' (1968, 1969) original work, however, reveals that important qualifications were omitted from later descriptions. Watts observed some brood mixing soon after hatching, and a majority of females with poults joined to form composite brood flocks. Young of the year were not marked until fall or early winter, when they were cannon-netted in large aggregations at baited areas. Thus, before it was possible to identify individuals as members of particular "sibling groups," most males lived in flocks with males that were not their brothers. Smith (1977), who conducted a follow-up study on the population, emphasized the fact that neither he nor Watts ever knew the genetic relatedness of turkeys on the Refuge. We therefore are left with an interesting story about cooperative mating among brothers that is cited in textbooks as an example of kin selection, yet we have no assurance that the story is true.

The issue we have raised could best be resolved by determining genetic relation-

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ships among the Welder turkeys and relating this information to the birds' behavior (e.g. by observing marked individuals from the time of hatching). Such measures are no longer feasible, however, as the population is now greatly reduced and has virtually ceased reproductive activity on the Refuge. In this paper, therefore, we use data and descriptions already available to us to reevaluate the conclusions drawn from Watts' study. Our first objective is to probe a question, not addressed by earlier workers, that we consider basic to the hypothesis of kin selection among turkey brothers: What is the statistical probability that the "sibling groups" described by Watts were indeed composed entirely of brothers? Our second objective is to seek alternative explanations for the behavior observed by Watts, both with and without invoking kin selection.

METHODS

Watts (1969) reported a particular distribution of the numbers of "sibling groups" of various sizes in his study population. We developed an analytical model based upon Bernoulli trials to produce an expected distribution of group sizes if all members of each group were indeed brothers. If one equates success in the trial to being a male,

$$b(k; n, q) = \binom{n}{k} q^k (1 - q)^{n-k}$$

is the probability of k males in a brood of size n, and q is the fraction of a brood that is male on average. Thus, if $p(n)$ is the probability of a brood of size n,

$$p(n)b(k; n, q)$$

is the probability of a group of k males in a brood of size n. The probability of a male sibling group of size k at hatching is then:

$$\nu_0(k) = \sum_n p(n)b(k; n, q).$$

Survival was modeled as success in another Bernoulli trial. Here, the probability of a male sibling group of size k, given a probability $\nu_i(k)$ of a group of size k at a previous time and a survival of s_i for the interval from i to $i + 1$, is:

$$\nu_{i+1}(k) = \sum_j \nu_i(j)b(k; j, s_i).$$

We made several assumptions in using the model to generate an expected probability distribution of "sibling groups":

1. We assumed a mean brood size at hatching of 11.4. We relied upon information available in Mosby (1967) to arrive at this figure, as Watts collected no data on clutch sizes or on brood sizes at hatching. We assumed a standard deviation equal to that for clutch size (i.e. 2.4; see Mosby 1967); we consider this assumption reasonable, as hatching success in clutches that escape total loss appears very high (see Mosby 1967). We further assumed a normal distribution of brood sizes at hatching. We performed simulations using uniform, concentrated, and bimodal distributions as well but found that they produced no appreciable difference in our results.
2. In the absence of evidence to the contrary, we assumed an even sex ratio at hatching. Smith (1977) makes a similar assumption, and Watts (1969) noted no significant disparity in the sex ratio of 180 poults in late summer.
3. We conservatively assumed an annual mortality rate of 60% for the first 4 months (Mosby 1967), 50% for the next 2 months (our interpolation), and 40% thereafter (Watts 1969, Smith 1977). Remarks by Knowlton (1964) and Smith (1977) suggest that mortality among young poults could be considerably higher than the figure we used.
4. We assumed an age at first breeding of 2 yr for males on the basis of Watts' (1969) data and descriptions.
5. We assumed that the distribution of adult male group sizes reported by Watts (1969) was representative for the Welder population. Watts (1969) identified "sibling groups" and recorded their sizes by observing the behavior of marked individuals while they were still in winter flocks, prior to the mating

TABLE 1. Observed and expected distribution of adult male "sibling groups" of various sizes.

	Group size			
	1	2	3	4
Observed	59	40	9	7
Expected	71.3	28.7	12.0	3.0

season (virtually the entire local population of adult males). He states that there were no subsequent changes in group membership except through mortality (Watts 1968, 1969).

6. Finally, we assumed the survivorship of individual males to be independent of group size. Certain potential benefits of flocking might favor the survival of group members relative to isolates during the breeding season, although this difference should be lessened by the fact that all males roosted communally (see Smith 1977). Moreover, adult males were particularly vulnerable to predation during courtship displays (Knowlton 1964, Glazener 1967); dominant males (i.e. members of the larger groups) gobbled and strutted more frequently than subordinates (Smith 1977) and so may have suffered higher predation losses. We therefore believe that our assumption of independence should, if anything, make our test conservative.

RESULTS AND DISCUSSION

Watts (1969) observed 115 adult male groups of turkeys on the Refuge that ranged in size from one to four members. A comparison of this distribution with the expected distribution (Table 1) generated by the analytical model leads us to reject the hypothesis that these groups were composed entirely of brothers ($P < 0.01$; exact Chi-square test, Radlow and Alf 1975). Mortality among brothers appears to have been too high to expect the distribution of group sizes reported by Watts. It would seem even less likely that adult male groups of up to seven members on the Refuge described by Knowlton (1964) contained brothers only.

If, as our results suggest, the "sibling groups" studied by Watts were not what Watts thought they were, is kin selection still a possibility? Kin selection might indeed occur if members of groups were more closely related to one another than to others in the population (see West Eberhard 1975). Watts (1969) describes an observation that we believe could indirectly support the notion of genetic relatedness among group members: Toward the end of the mating season, female flocks separated into small groups containing up to five birds (much as males had done earlier) and moved toward nesting areas. Soon after the hatching of young, members of these female groups and their respective broods often joined together to form composite brood flocks. Although Watts does not discuss the implications of this finding, we speculate as follows: Perhaps surviving young from composite brood flocks became male and female groups during subsequent reproductive seasons. One male usually bred all members of a female group. Thus, groups of either sex were likely to consist of some full siblings and some partial siblings (related through common fathers and through mothers that were likely to be closely related to one another). Male group members cooperated in mating as a result of kin selection. Female group members cooperated in raising broods, also as a result of kin selection, because the greater the number of male poults reared in a brood flock, the larger the male group should be at adulthood and the greater the likelihood that the group would be dominant and hence secure copulations. Although a particular female group member may not have been the mother of the dominant male that ultimately copulated, she nevertheless was likely to be closely related to him through his mother. Close genetic relationships among the member broods virtually eliminated any need for poults to discriminate between "siblings" and "nonsiblings" within the flock—a potentially important advantage over the system described by Watts, as changes in the appearance of young caused by rapid growth and frequent molts (see Lewis 1967) might make the tracking of identities difficult and kin imprinting within broods unlikely.

To illustrate how the system we have proposed might operate: If one begins with p_1 genetically unrelated females bred by a single male and if each female on average produces n offspring, the average relatedness (ar) of the np_1 young satisfies

$$\tfrac{1}{2} \geqslant ar_1 \geqslant \tfrac{1}{4},$$

where the upper limit corresponds to $p_1 = 1$ and the lower limit to $n = 1$. Under the social system we have described, the average relatedness of the np_q young of the q^{th} generation satisfies

$$\tfrac{1}{2} \geqslant ar_q \geqslant \tfrac{1}{2} - (\tfrac{1}{2})^{q+1},$$

where, again, the extremes of the range correspond to $p_q = 1$ and $n = 1$. In the limit as the number of generations becomes large, the average genetic relatedness of poults in a composite brood flock approaches that of full siblings, i.e. ½.

Our alternative model of kin selection, like the system described by Watts, depends strongly upon competition among males for females, such that only the highest-ranking member of the dominant male group in an area accomplishes most or all of the breeding. If subordinate members of male groups could secure copulations easily, there should be little value in their forgoing reproduction to help a dominant male to breed. Moreover, if males from any group could copulate, there would be no reason for females to cooperate in promoting the survival of large, hence dominant, male groups. Observations by Watts (1969) and Smith (1977) suggest that monopolization of females by the highest-ranking male in an area depends in turn upon the maintenance of visual contact among males during the mating period. When the alpha male of a dominant group disappeared (even momentarily) from view, a subordinate member of the dominant group (Watts 1969) and a dominant member of a subordinate group (Smith 1977) immediately mounted females. Such behavior suggests that an environment free of visual barriers may be necessary for either of the proposed kin-selected social systems to operate as described.

Open habitat facilitating visual contact in mating areas did exist where Watts conducted his research. Prior to and during Watts' study, the Welder Wildlife Refuge was subject to a brush control program and to moderate grazing by cattle (Box and Chamrad 1966). Watts made most of his observations in several areas that had been cleared of visual obstructions to protect turkeys from predation when they flew down from their roosts. Watts and Stokes (1971) apparently did not consider these environmental conditions atypical for the birds' evolutionary past. They describe the Rio Grande Turkey as a grassland form with a lek mode of polygamy and liken it to other lekking galliforms of the prairie. Our search of the literature on this point, however, suggests a somewhat different picture. Aldrich (1967) places the original distribution of the Rio Grande Turkey primarily in mesquite grasslands, oak savanna, stream-bordered woods and scrub, and pine-oak forests. Early accounts of the subspecies in upland areas of Texas describe the birds as living in small, scattered groups in rough, brushy country (see Bent 1932). Prior to modern settlement, southern Texas is believed to have been a tall-grass prairie maintained by periodic fires, with trees and brush along watercourses (Box et al. 1980). To the extent that such habitats might restrict visual contact among male turkeys during the mating period, social systems such as Watts or we have outlined should be less likely to develop. Characterization of the Rio Grande Turkey as a lekking form also seems inappropriate (see Smith 1977), as male turkeys in Watts' study neither displayed communally (in the strict sense) nor defended territories and as males followed females both on and off mating areas.

Other considerations pose further problems for the kin-selection hypothesis, whether Watts' version or ours. Watts' (1969) findings indicate an inverse association between age and dominance status among reproductively mature male groups due to the larger average size of younger groups; thus one might expect strong selective pressure for early maturation in males. The males in Watts' study, however, did not attempt to breed (even when opportunities arose) until they were 2 yr of age, similarly to most races of this species (see Bailey and Rinell 1967). One also might expect female parental investment to favor male offspring, but there is no evidence to suggest that such was the case in Watts' population, as the sex ratio of 180 poults in early September was insignificantly biased in favor of *females* (Watts 1969). Finally, adult females that lost their clutches or broods did not join another brood flock, but instead associated with other unsuccessful females (Watts 1969), whereas our model of kin selection predicts that a female without young should cooperate in rearing the young of others in her female group.

Is it necessary to invoke kin selection to explain Watts' (1968, 1969) account of turkey reproductive behavior? We believe not. Perhaps the most parsimonious interpretation is that the turkeys Watts observed were responding to conditions not representative of their evolutionary past. Watts conducted his study at a time when the turkey population on the Refuge was exceptionally dense, and (as noted earlier) he observed the birds in areas cleared of tall vegetation. The turkeys' behavior thus could have reflected the birds' attempt to cope with high population densities in an artificially open habitat, rather than the selective forces that shaped their evolution (see Rowell 1979 for a discussion of such problems). Indeed, Smith (1977) found that, when the density of the Welder turkey population was reduced by about half, the highest-ranking male group no longer controlled access to females.

Another possible explanation that does not rely upon kin selection is that Rio Grande Turkeys are inherently gregarious. One could suppose that the male groups in Watts' study were survivors of brood flocks and that wintering male flocks were loose associations of these groups. As the reproductive season approached, intolerance among groups broke up the winter flocks. Social bonds established within broods or composite brood flocks early in life, however, were strong enough to keep the members of male groups together. Several observations attest to the sociality of turkeys on the Refuge even during the reproductive season. First, as noted earlier, females as well as males associated with conspecifics of the same sex throughout the year. Second, Smith (1977) indicates that, when population densities were reduced, small male groups or single males sometimes joined to form "pairings" and remained together for considerable periods during the mating season.

The proximate and ultimate advantage to turkeys of associating with conspecifics throughout the year could reside in certain benefits of flocking (reviewed by Orians 1971), such as increased efficiency in exploiting food supplies, in escaping from predators, or in finding ways to and from roosting and foraging sites (see also discussion by Smith 1977). Beyond this, permanent membership in a group appears to enhance the dominance status of individual males in a winter flock (see Watts 1969). Constancy of group membership also might promote stable social relationships, which in turn could function to reduce aggression within groups (see Balph 1979), a supposition that we find consistent with Watts' (1969) and Smith's (1977) behavioral descriptions. Flocking could, it is true, impose costs as well as benefits. In particular, subordinate males may incur a reproductive cost by remaining in groups rather than living as isolates during the breeding season. Watts (1969) notes that, when females departed in small groups from the display ground, male groups and single males followed them to nesting areas, where some further insemination probably occurred. Watts (1969) speculates that subordinate members of male groups were less likely than isolates to secure copulations at this time. Such a cost, however, probably was not great, particularly for subordinate members of dominant groups. Watts (1969) emphasizes his belief that a few high-ranking males sired the vast majority of offspring. Mortality among adult males in the breeding season was relatively high (Knowlton 1964, Glazener 1967) and was perhaps even higher for dominant males during copulation (see Smith 1967). Subordinate members of a group thus had a reasonable chance to succeed a dominant male during the mating season, a point also made by Watts and Stokes (1971).

A question remains as to why subordinate males should cooperate by warding off intruders while the dominant male copulated. We think it possible that what appeared to be altruistic behavior was no more than the maintenance of a distance of intolerance from outsiders, a common activity for all members of a male group in a variety of contexts. On some occasions in Smith's (1977) study, resident male groups even formed temporary "coalitions" during courtship and chased away foreign males. By our interpretation, the sight of a nearby dominant male inhibited subordinates from copulating with females but did not prevent them from continuing to defend an individual distance. Watts (1969) and Smith (1977) also note that subordinate males regularly mock-copulated (sometimes to ejaculation) while the dominant copulated with females; this behavior, together with the apparent readiness of subordinates to mate with females as soon as the dominant male was out of sight, further suggests to us that the "cooperation" Watts observed may not have been motivated by altruism.

In conclusion, we believe our reassessment of kin selection in Rio Grande Turkeys raises questions that only further research can answer. Unfortunately, there now are fewer than 100 (largely nonreproducing) turkeys on the Welder Wildlife Refuge, as compared to about 700 birds during Watts' study. As suggested earlier, it may be difficult or impossible under present circumstances to determine kinship patterns within this population. Future investigations elsewhere within the subspecies' range might help to resolve some of the problems discussed here.

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