Methods

Major elements

These were determined using a JEOL JXA 8600 microprobe at IGG-CNR, in Florence. The acceleration voltage was 15 kV, the sample current was 10 nA. The counting times were 40 s for Na and Cl and 10 s for all other elements; the spot size was 10 μm.

H_2O

H_2O content was determined by secondary ion mass spectrometry (SIMS) with a Cameca IMS 4f ion microprobe (at IGG-CNR in Pavia), following a procedure that involves 'energy filtered' secondary ions[27] (emission energies in the range 75–125 eV). Under these experimental conditions, the H background, measured on a sample of quartz, is typically 0.009 wt% H_2O. The values for H_2O in the Supplementary Table are the average of three measurements. The accuracy of analysis is estimated to be 10% relative.

REE

REE concentrations were determined with the Pavia ion microprobe. An optimized energy filtering technique was applied to remove complex molecular interferences in the secondary ion mass spectrum. Light-REE-rich basalts were analysed applying a deconvolution filter to the secondary-ion REE mass spectrum in order to reduce residual oxide interferences (that is, BaO on Eu, CeO and NdO on Gd, GdO on Yb, and EuO on Er). Precision of the measurement is of the order of 10% relative, for REE concentrations in the range 0.1–0.7 p.p.m. Below 0.1 p.p.m., precision is mainly limited by (poissonian) counting statistics and falls to $\sim$30% relative. Accuracy is of the same order of precision. The experimental conditions involved a 9.5 nA, $^{16}O^-$ primary ion beam accelerated through -12.5 kV and focused into a spot 10–15 μm in diameter, and energy-filtered (75–125 eV) positive secondary ions detected under an ion image field of 25 μm.

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Correspondence and requests for materials should be addressed to E.B. (enrico.bonatti@bo.ismar.cnr.it).

Kin selection and cooperative courtship in wild turkeys

Alan H. Krakauer

Department of Integrative Biology and Museum of Vertebrate Zoology, University of California, Berkeley, California 94720-3160, USA

In the few species of birds in which males form display partnerships to attract females, one male secures most or all of the copulations[1,2]. This leads to the question of why subordinate males help in the absence of observable reproductive benefits. Hamilton's concept of kin selection[3], whereby individuals can benefit indirectly by helping a relative, was a crucial breakthrough for understanding apparently altruistic systems. However in the only direct test of kin selection in coordinated display partnerships, partners were unrelated[1], discounting kin selection as an explanation for the evolution of cooperation. Here I show, using genetic measures of relatedness and reproductive success, that kin selection can explain the evolution of cooperative courtship in wild turkeys. Subordinate (helper) males do not themselves reproduce, but their indirect fitness as calculated by Hamilton's rule[3,4] more than offsets the cost of helping. This result confirms a textbook example of kin selection[2] that until now has been controversial[5] and also extends recent findings[6–8] of male relatedness on avian leks by quantifying the kin-selected benefits gained by non-reproducing males.

The observation that cooperation in birds typically occurs between relatives[9] is superficial support for the idea that kin selection is a general explanation for avian helping behaviour. However, most examples of helping or cooperative breeding involve offspring retained in intergenerational family groups[9,10] in which it is difficult to separate the indirect fitness benefits due to kin selection from benefits due to direct fitness[11], even when the dynamics of helping behaviour qualitatively fits the predictions of Hamilton's rule[12]. Species with aggregated male displays are therefore valuable for studying kin selection because it is possible to isolate the role of indirect fitness in the absence of direct benefits stemming from delayed dispersal. Surprisingly, the role of kin selection on leks has only recently been proposed[13], and kin associations of displaying males have now been demonstrated for several species including grouse[6], peafowl[7] and manakins[8]. This kinship facilitates indirect fitness benefits for low-ranked males because female visitation often increases at larger leks, thereby explaining why a male might settle at one lek rather than another[13,14]. No empirical study has yet quantified this kin-selected benefit relative to alternative benefits such as low frequencies of matings or future inheritance of dominant positions.

Wild turkeys (*Meleagris gallopavo*) are among the few species of birds to form male display partnerships within larger display aggregations. Male turkeys form coalitions of two to four same-aged males that court females and defend those females against other groups and solitary males. A previous observational study[2] found that only one male in each coalition mates. The authors of that study believed that coalitions were composed of brothers (sibling nestmates), thereby providing the relatedness necessary to accrue indirect fitness benefits. Although this work was published long before molecular techniques were available to measure relatedness and reproductive success directly and has been questioned on other grounds[5], the story remains a well-cited example of kin selection[15,16].

Here I show that kin-selected indirect fitness benefits do in fact explain cooperative courtship in wild turkeys. Support for kin selection requires the following three conditions to be met: first, that dominant and subordinate males are related; second, that there is a measurable benefit to the dominant male due to the help of the subordinate; and last, that Hamilton's rule ($rB - C < 0$) must be met, the indirect benefit to the subordinate (rB) outweighing the cost of helping instead of attempting to breed independently (C) (refs 3, 4; Table 1).

First, coalitions are clearly composed of relatives, as shown by the similarity of microsatellite genotypes between dominant and subordinate males (Fig. 1). Six coalitions (five pairs and one four-member group for a total of eight dominant–subordinate male dyads) combined for a mean (±s.e.m.) coalition relatedness, r, of 0.42 ± 0.07, significantly higher than r of males drawn randomly from the population (randomization test, 1,000 iterations, $P < 0.001$). The relatedness within coalitions is equivalent to the mean r calculated for two groups of known genealogical relationship with expected $r = 0.5$ based on pedigree (full siblings, $r = 0.52 \pm 0.05$, $n = 10$; mothers and their offspring, $r = 0.46 \pm 0.03$, $n = 12$, analysis of variance $F_{(2,27)} = 0.947$, $P = 0.40$). It was not possible to test specific genealogical hypotheses for individual coalitions because of an insufficient number of loci[17].

Second, the help provided by subordinate males increases the reproductive success of dominant males compared with non-cooperating solitary males (Fig. 2). Dominant males mated with more females ($\chi^2_{(1)} = 9.0$, $P < 0.005$) and fathered more offspring than solitary males ($\chi^2_{(1)} = 58.3$, $P < 0.001$). The benefit B, as calculated by the difference between the mean fitness of dominant males and the mean fitness of solitary males, was 6.1 offspring per male (Table 1). This value is an underestimate to the extent that high relatedness makes it more difficult to assign paternity to males in coalitions (see Methods).

Table 1 **Calculation of Hamilton's rule, $rB - C < 0$**

Variable	Description	Calculation	Value*
r	Coefficient of relatedness	Mean pairwise relatedness of subordinates to their dominant display partner	0.42
B†	Benefit to dominant	(No. of offspring per dominant male) – (no. of offspring per solo male)	6.1 (9.0)
C†	Cost to subordinate	(No. of offspring per solo male)– (no. of offspring per subordinate male)	0.9 (2.3)
	Net benefit†	$rB - C$	+1.7 (1.5)

Dominant, solo and subordinate refer to dominant coalition males, solitary non-cooperating males and subordinate male helpers, respectively.

*Values in parentheses exclude non-reproducing males from mean fitness calculations.

†In units of offspring per male.

An alternative hypothesis is that the benefit is due to differences in individual quality of dominant males rather than the help provided by their subordinate partner(s). If this were true, one would predict a difference in the distributions of reproductive success between dominant and solitary males, and that there would be little or no difference between the success of presumed high-quality males that successfully reproduce, whether they are in a dominant member of a coalition or display as a solitary individual. Contrary to these predictions, both dominants and solitary males show bimodal distributions of reproductive success, with $n = 3$ dominant males and $n = 10$ solitary males not reproducing at all. When only the presumably high-quality males that reproduce are used to calculate the average fitness of dominant and solitary males, the dominant males father significantly more offspring (49) than do solitary males (13) (Mann–Whitney $U = 0.5$, $P = 0.026$, $n = 4$ for both groups), and the benefit B increases to 9.0 offspring per male rather than decreases (Table 1). Thus kin selection seems to best explain the pattern of relatedness and distribution of reproductive success; the important issue of individual male quality that has been studied in captive settings[18,19] remains to be integrated into the complex mating system of free-living turkeys.

Finally, Hamilton's rule can be evaluated by assuming the cost of helping, C, for subordinate male turkeys is equal to the average fitness of non-cooperative solitary males (0.9 offspring per male). With this assumption, the net benefit to helping is +1.7 offspring per male (Table 1), indicating a clear selective benefit to cooperation for subordinate males. Similar results are obtained if presumably low-quality (non-reproducing) males are excluded from calculations (Table 1). This benefit is calculated on the assumption that all coalitions are dyads. One coalition was initially observed to contain three males and another four males, although these both were reduced to pairs during their first season, presumably by hunting or natural predation events. The fitness benefits for third- or lower-ranked males would require further assumptions, including size-specific coalition productivity, which I could not calculate on the basis of my limited sample size.

The minimum level of relatedness necessary to offset a subordinate's loss of independent reproductive opportunities can be

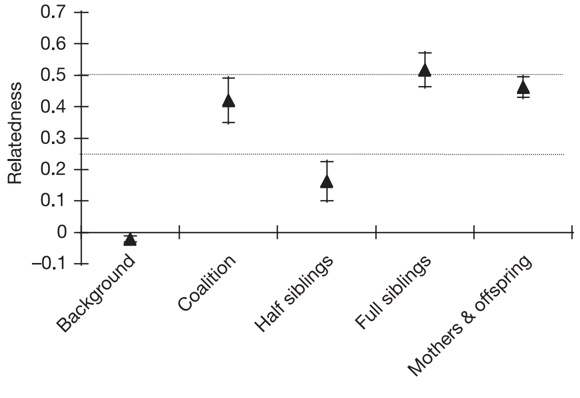

Figure 1 Relatedness values calculated from microsatellite genotypes. The graph shows the background relatedness for all adult males and the relatedness of subordinate males to their dominant partner ('Coalition'). Dotted lines represent expected values for full and half siblings; unrelated individuals should have $r = 0$. Relatedness of three known genealogical relationships, based on parentage analysis, indicate that calculated r values are concordant with their predicted values based on pedigree. These groups were: half siblings sharing either a mother or a father, full sibling nest mates and mothers and their offspring. Values are means ± s.e.m. Sample sizes, from left to right, are $n = 1{,}250$, 8, 10, 10 and 12.

calculated by setting the indirect benefit, rB, equal to the cost C and solving for r. On the basis of the values in Table 1, helping behaviour should be observed as long as coalitions are related at a level of $r > 0.15$. Given that half-brothers have an expected r value of 0.25, processes that produce half-siblings such as multiple paternity, quasiparasitism or crèching of broods fathered by the same male should not reduce relatedness among brood-mates to the point in which cooperative behaviour is no longer favoured. This conclusion is robust to an almost 50% underestimate in relative fitness of solitary males.

How do turkeys compare to other bird species that form male display partnerships? In contrast to reproductive 'sharing' by satellite males in ruff (*Philomachus pugnax*) partnerships[20], I found no evidence of direct reproduction by subordinate male turkeys (Fig. 2). None of eight marked subordinate males fathered any offspring during my study, compared with four out of seven dominant members of coalitions (Fisher exact test, $P = 0.026$).

In cooperative partnerships of *Chiroxiphia* manakins, subordinate males seem to benefit through an increased likelihood of future inheritance of a display perch[1]. Unlike *Chiroxiphia*, wild turkey coalitions do not act as social queues because coalitions change only through attrition. Coalitions form before adulthood (three coalitions were marked as 1-year-old subadults); furthermore, no solitary displaying male was observed to later join a coalition ($n = 14$ males and 24 male-years). This trend cannot be explained by solitary males joining distant coalitions outside the study area, because coalitions and solitary males were observed at similar rates (see Supplementary Table 1). All changes in coalition membership observed were losses rather than gains of individuals ($n = 7$ coalitions across 11 coalition-years; 6 losses, 0 gains, Sign test $P < 0.04$). This pattern indicates that if the dominant male disappears from a cooperative pair, the subordinate is left as a solitary male and does not attract a new display partner. Finally, turkeys do not defend territories either during the breeding season, when several male groups may court a given flock of females, or outside the breeding season, when males are highly social[2,21]. Thus future resource or territory inheritance cannot account for subordinate male cooperation.

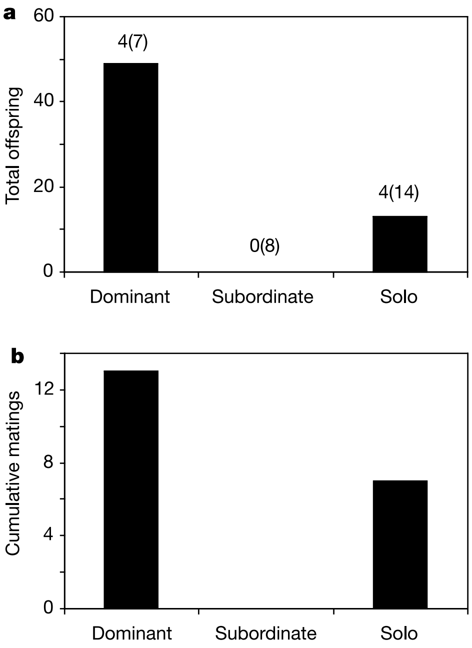

Figure 2 Reproductive success of the three male display strategies in wild turkeys. Males are classified as either dominant coalition member, subordinate coalition helper or non-cooperating solitary male. Reproductive success is shown as total number of offspring (**a**) and total number of mates (**b**). The number of males assigned paternity, with total sampled males in parentheses, are indicated above the bars in **a**. Subordinate males fathered no offspring. Dominant males fathered significantly more offspring than solitary males ($\chi^2_{(1)} = 58.3$, $P < 0.001$) and mated with significantly more females ($\chi^2_{(1)} = 9.0$, $P < 0.005$).

Because subordinate males acquire large indirect fitness benefits, do not themselves gain direct reproduction and are unlikely to increase their future mating opportunities, kin selection seems to provide the best explanation for the evolution of cooperative behaviour in wild turkeys. By contrasting these results with the patterns described for *Chiroxiphia* manakins[1] and ruffs[20], it is evident that although these species independently evolved cooperative courtship as a solution to intensely competitive mating systems, the exact form of fitness benefit maintaining subordinate cooperation can differ greatly. □

Methods

Field methods

From 1999 to 2004 I studied an introduced population of *M. gallopavo* at the Hastings Natural History Reservation in Carmel Valley, Monterey County, California. I captured 126 immature and adult turkeys (51 males, 75 females) by using walk-in traps or drop nets. About 100 μl of blood was taken from the wing vein and stored in blood storage buffer. Adults were tagged with uniquely numbered patagial wing tags, and a subset ($n = 8$ males, $n = 68$ females) were outfitted with backpack-style radiotransmitters. About 50% of the population was marked in any given year. With one or two field assistants each year, I attempted to relocate radio-tagged birds visually at least twice a week in January, February and June, and daily from March to May, to identify female nesting attempts and to observe courtship behaviour and associations. In addition, we regularly drove along about 20 km of roads in and around the reserve, and during the breeding season we hiked at least a 2-km loop at a nearby ranch to search for turkeys without radios. Genetic samples from offspring ($n = 325$) were collected by a combination of capturing flightless young soon after they had hatched, salvaging from failed or abandoned nests, and collecting early nests to incubate and sample eggs. These samples were stored in one or more of the following: blood storage buffer, dimethyl sulphoxide or 100% ethanol. All procedures were approved by the University of California, Berkeley, and the California Department of Fish and Game.

Behavioural definitions

Coalitions were defined as adult males in their third year (2 years old) or older that were seen displaying to females at least twice while within 2 m of each other. Solitary males were males that never met this criterion and either were observed at least twice displaying alone or showed patterns of association that precluded them from having a specific partnership with another male. Within a coalition, the dominant male was the one that performed most of the full strut (stereotyped pulmonary puff) displays. Data on individual coalitions and solitary males are provided in Supplementary Table 1.

DNA extraction and genotyping

DNA was extracted from samples using DNEasy tissue extraction kits (Qiagen) then diluted to a concentration of 20 μg ml^{-1}. All individuals were then genotyped at ten microsatellite loci identified from previous studies of wild or domestic turkeys[22–24]. Using GENEPOP[25], I determined that these loci were unlinked. Additional details such as reaction conditions and allelic diversity are provided in Supplementary Table 2. One primer of each primer pair was fluorescently labelled and loci were multiplexed on an ABI 3730 automated sequencer. Polymerase chain reaction products were run on 96-well plates that contained one negative control and two positive controls (the same two individuals were included with every run). All adults were genotyped at least twice, and genotypes were more than 0.999 complete. Offspring genotypes were 0.98 complete; individuals were rerun if allelic calls were questionable or if they did not match the genotype of the incubating female. Some level of mismatching is to be expected because of both marker mutation and nest parasitism by other females.

Analysis of genetic data

Relatedness was calculated with RELATEDNESS 5.0 (ref. 26). The background allele frequencies were defined as the allele frequencies for adults only. Relatedness values were then calculated for all pairs of males, and coalition values were compared with 1,000 sets of eight randomly selected values. Sets of full siblings, half siblings and mother–offspring pairs were identified during subsequent paternity analyses (see below); r values were calculated for these known genealogical relationships to confirm that the relatedness estimates generated from microsatellite genotypes corresponded to those predicted by pedigree.

Reproductive success was determined by assigning parentage to sampled offspring. Maternity of an offspring was assigned to the female incubating that nest if she had no more than one locus mismatching the offspring. Paternity was calculated by a combination of maximum likelihood assignment with CERVUS 2.0 (ref. 27) and genotypic exclusion, meaning that a male could be assigned paternity only if he met the strict 95% assignment level and was the only perfect genotypic match among sampled males. Details of the CERVUS analysis are given in Supplementary Table 3.

This set of conservative criteria lead to the assignment of 75 of 325 offspring to a known, sampled male. Although many of the unassigned offspring were probably fathered by unsampled males, others were fathered by known males but could not be assigned to them. CERVUS generates a test statistic (Δ) based on the difference in LOD scores (cumulative log-likelihood ratio of parentage compared with non-parentage) between the two most likely sampled males. The program then compares this value with a user-defined critical value based on the percentage of simulations (here, 95%) that correctly assigned an offspring to the actual parent. The more genotypically similar that two candidate parents are, the more likely they are to have similar LOD scores and therefore to generate a smaller Δ score. Given the wild turkey's unique kin structure, coalition males were handicapped by necessarily having close relatives among the set of candidate males.

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Correspondence and requests for materials should be addressed to the author (krakauer@berkeley.edu).

Disruptive coloration and background pattern matching

Innes C. Cuthill[1], Martin Stevens[1], Jenna Sheppard[1], Tracey Maddocks[1], C. Alejandro Párraga[2] & Tom S. Troscianko[2]

[1]*School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK*
[2]*Department of Experimental Psychology, University of Bristol, Woodland Road, Bristol BS8 1TN, UK*

Effective camouflage renders a target indistinguishable from irrelevant background objects. Two interrelated but logically distinct mechanisms for this are background pattern matching (crypsis[1,2]) and disruptive coloration: in the former, the animal's colours are a random sample of the background[1,2]; in the latter, bold contrasting colours on the animal's periphery break up its outline. The latter has long been proposed as an explanation for some apparently conspicuous coloration in animals[3,4], and is standard textbook material. Surprisingly, only one quantitative test[5] of the theory exists, and one experimental test of its effectiveness against non-human predators[6]. Here we test two key predictions: that patterns on the body's outline should be particularly effective in promoting concealment and that highly contrasting colours should enhance this disruptive effect. Artificial moth-like targets were exposed to bird predation in the field, with the experimental colour patterns on the 'wings' and a dead mealworm as the edible 'body'. Survival analysis supported the predictions, indicating that disruptive coloration is an effective means of camouflage, above and beyond background pattern matching.

The pioneers of modern military camouflage were both artists and keen observers of nature[7]. For example, the work of Thayer, who proposed the theory of countershading[8] and developed Bates's ideas on disruptive coloration in animals[3], was influential in persuading

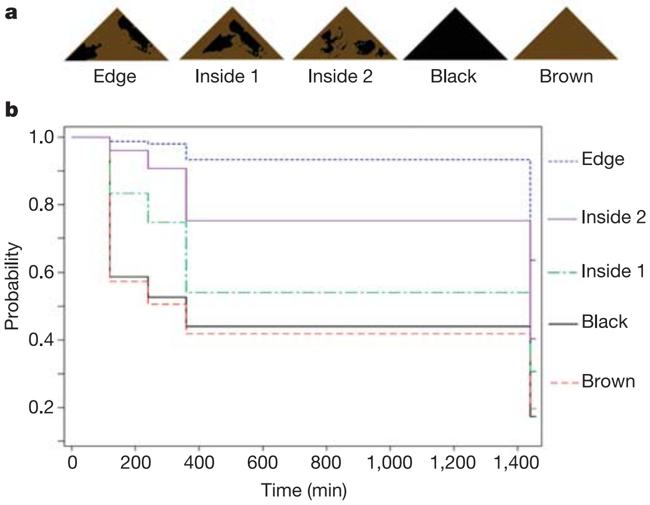

Figure 1 Patterns placed on the body's outline enhance survival. **a**, Examples of 'moth' targets in experiment 1; **b**, survival curves. The differences between treatments were significant (Wald = 138.92, d.f. = 4, $P < 0.001$) in the order Edge > Inside 2 (Wald = 16.03, d.f. = 1, $P < 0.001$) > Inside 1 (Wald = 11.01, d.f. = 1, $P = 0.001$) > Black or Brown (Inside 1 versus Black, Wald = 13.33, d.f. = 1, $P < 0.001$; Inside 1 versus Brown, Wald = 13.11, d.f. = 1, $P < 0.001$); there was no difference between the latter monochrome treatments (Wald = 0.00, d.f. = 1, $P = 0.992$).