

simple expression for the radius of the inner core

$$c(t) = b \left[\int_0^t f_m(\tau) d\tau / M \right]^{1/2} \quad (8)$$

Specific predictions of $c(t)$ from our model require an estimate of $f_m(t)$. A plausible upper bound on f_m can be inferred from the heat flux measured at the Earth's surface. Given chondritic abundances of radioactive isotopes¹⁹ in the upper mantle, it is unlikely that the total heat flux across the core-mantle boundary exceeds 10^{13} W. It is also unlikely, although not impossible, that the total heat flux is less than that conducted up the adiabat, which is estimated¹² to be 2.7×10^{12} W. As an illustrative example, we consider these two bounds on f_m , along with the midpoint value 6.3×10^{12} W as a typical estimate. Using the parameter values in Table 1, we obtain the growth histories shown in Fig. 2. For the typical value of f_m , we see that the inner core grows to its present radius in 1.6×10^9 years, a value similar to those obtained previously by Stevenson *et al.*¹⁰. The values calculated from the bounds on f_m are 1.0×10^9 and 3.6×10^9 years. These ages span a wide interval, but are roughly consistent with palaeomagnetic data²⁰, which are sometimes used to constrain the age of the inner core under the assumption that the onset of solidification is associated with a rapid increase in the strength of the magnetic field.

The thermal buoyancy flux associated with the cooling of the liquid core depends on the amount by which f_m exceeds the heat flux f_a conducted down the adiabatic gradient. For our typical value of f_m , the thermal buoyancy flux caused by the downwelling of cold dense fluid at the core-mantle boundary dominates that associated with latent heat release at the inner-core boundary. But an additional buoyancy flux of compositional origin is produced at the inner-core boundary by the release of light, residual fluid on solidification. The relative importance of the thermal and compositional contributions can be assessed using our model once $\Delta\rho$ and f_m are known. Seismic estimates of the relative density jump $\Delta\rho/\rho$ vary from 2 to 12% (ref. 21), with typical values of 5% (ref. 22). The actual compositional density jump, however, may be less than these seismic estimates if there is any volume change on solidification. In terms of $\Delta\rho$, the compositional buoyancy flux is $4\pi\Delta\rho g(c)c^2(dc/dt)$. For comparison, the thermal buoyancy flux is given by $4\pi\alpha\sigma g(b)b^2(f_m - f_a)$, where α is the coefficient of thermal expansion. From the range of possible values of f_m , we estimate that these two fluxes are roughly comparable if the seismic estimates of the density jump across the inner core boundary represent a compositional change. □

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Parent-offspring conflict and the recruitment of helpers among bee-eaters

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GENETIC conflicts of interest are to be expected between individuals in any non-clonal society^{1–5}. One well studied form of conflict is that between parents and their offspring over the amount of parental care provided to the offspring³. A very different manifestation of parent-offspring conflict may occur in certain cooperatively breeding species in which parents (breeders) are assisted in the rearing of young by their grown offspring (helpers)^{6–8}. If helpers have a sufficiently large effect on reproductive success, breeders will enhance their own inclusive fitness more by retaining their offspring as helpers than by allowing them to reproduce on their own^{4,5,9}. We report here that older male white-fronted bee-eaters (typically fathers) actively disrupt the breeding attempts of their sons, and that such harassment frequently leads to the sons joining as helpers at the nest of the harassing father. Calculation of fitness costs and benefits to the various participants helps to clarify both why parents engage in such 'recruitment' behaviour and why sons frequently do not resist.

White-fronted bee-eaters (*Merops bullockoides*) are common birds of the savannas of East and Central Africa. They breed both gregariously (in colonies averaging 200 individuals) and cooperatively (with half of all nesting attempts including non-breeding adult helpers)¹⁰. Young remain with their parental group until they pair at one to two years of age, when females (but not males) disperse to join the group of their mate¹¹. The resulting social organization is one of patrilocal extended family groups (clans). Each clan occupies a stable feeding territory, but commutes to roost and nest at the colony site^{11,12}.

During the breeding season, several pairs in each extended family may initiate breeding. Some individuals suffer harassment from other members of their clan and many initial reproductive attempts are abandoned. We examined the frequency, pattern and consequences of these harassments to test the hypothesis that such interference constitutes a form of parental manipulation to recruit grown offspring into becoming helpers.

We collected observations ad lib during 5 and 1 breeding seasons, respectively, from two individually marked and genealogically known populations of white-fronted bee-eaters at Lake Nakuru National Park, Kenya. We defined harassment as involving one or more of the following. (1) Prolonged aggressive chasing of a resident bird on the latter's territory. (2) Repeated interference by males in the courtship feeding of another pair. Such behaviour took the form of either physically preventing the transfer of food to the female, or of begging (but not taking food) from the allofeeding male. Similar begging was also directed towards single birds. Because begging females accepted allofed insects, alternative nutritional explanations for their behaviour could not be discounted. Consequently, cases based only on begging evidence by females were excluded. (3) Blocking a pre-breeding pair from access to its nest chamber. In this behaviour the harassing individual would position itself at a nest entrance and either chase or deny access to the occupants as they attempted to enter. (4) Repeated visits, typically accompanied by begging or other vocalizations, to the nest chamber of another pair during the period before egg laying or hatching at the nest of the harasser. (5) In some analyses we also included cases ($N=9$) in which harassment was implied but not directly observed: one member of an incubating pair abandoned its nest and began helping elsewhere while its mate continued to tend the clutch alone.

Harassment was often directed towards both members of pre-breeding or breeding pairs, yet only males (the natal members of each pair) became helpers at the nests of harassers. We therefore considered males to be the ultimate targets of the harassment attempts.

We directly observed 47 cases of harassment, of which 16 resulted in recruitment (defined when the harasser joined the breeding effort of the harasser as a helper). Among pairs, harassed individuals were more than twice as likely to become helpers as were individuals for which harassment was not observed; statistically this difference was of borderline significance ($P = 0.034$ by simple univariate contingency test, but, $P = 0.12$ by logistic regression analysis controlling for relatedness and age of the harasser). When cases of implied harassment (see 5 above) were included, the difference in likelihood of recruitment became highly significant ($P < 0.01$; logistic regression).

The social and demographic profile of observed harassers fits that predicted if the function of the behaviour were to obtain the services of helpers (Table 1). All were members of breeding pairs and thus in a position to benefit by gaining a helper. Virtually all (91%) were male, and three-quarters (72%) were older than the individuals they harassed. Dominance is age- and sex-related in most species of avian cooperative breeders^{6,13,14}. Assuming the same to be true of *M. bullockoides*, old males would have the greatest leverage to influence the behaviour of younger individuals. These findings support the hypothesis that harassment is a form of coercion that increases a breeder's chances of obtaining helpers.

Harassers preferentially selected close genetic kin as targets of their harassment ($P < 0.01$; chi-square test of null hypothesis of random targeting). Parents were involved in 36–45% of all harassment attempts (omitting and including inferred cases, respectively; see criterion 5), brothers in 16–19%, and other kin (grandparents, uncles and a half-sibling) in 16–17% (Table 1).

The likelihood of harassment leading to successful recruit-

ment increased with the difference in age and with the closeness of genetic relatedness between harasser and harassee (Table 1). The highest success rates were achieved by parents with their grown sons (75–84%). Viewed a different way, 69–76% of successful recruitment attempts involved a parent and its offspring, and 62–68% involved father and son.

We estimated the risk of being recruited for different categories of paired birds. Each paired male having an equally aged or older paired relative present in its clan was classified as a potential recruit. Risk was defined as the per cent of such individuals recruited. In one estimate, only cases based on the five criteria described were included. This presumably underestimates true risk, because some instances of harassment are not observed, and because some uncounted observations of female begging might actually be harassments. A second estimate included all cases where a potential recruit failed to breed and helped elsewhere in its clan. This presumably overestimates risk, because some pairs may help rather than breed for reasons unrelated to harassment. The true recruitment risk lies somewhere in between.

Figure 1 plots recruitment risk as a function of the age of the potential recruit and its relatedness to the potential recipients of its help (the offspring of the harassing pair). A yearling paired male (pooling across r values) has a 26–40% probability of having its nesting attempt disrupted. For the subset of such males with breeding parents present in the clan, this risk

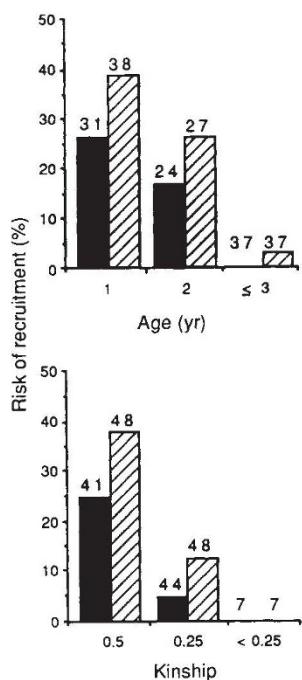


FIG. 1 The effects of age (top) and kinship (bottom) on the probability of paired male bee-eaters being recruited. Kinship is defined as the coefficient of relatedness to the offspring of the harasser pair (the potential recipients of help). Black bars indicate minimum estimate of recruitment risk; hatched bars indicate maximum estimate (see text). Numbers above bars refer to number of potential recruit pairs in each category. Both age and kinship are significant predictors (both $P < 0.01$) in a logistic regression analysis of recruitment risk.

TABLE 1 Social and demographic characteristics of harassers

	Number of attempts*	Number of successful attempts†	Success rate (%) of successful attempts‡
Mating status			
Paired	47 (56)	16 (25)	38 (49)
Single	0 (0)	—	—
Age (relative to harasser)			
Older	34 (42)	15 (23)	52 (62)
Same	6 (6)	1 (1)	17 (17)
Younger	7 (8)	0 (1)	0 (0)
Sex§			
Males	43 (51)	15 (23)	39 (50)
Females	4 (5)	1 (2)	25 (40)
Relationship (to harasser) ¶			
Father (+ mother)	13 (20)	9 (16)	75 (84)
Father (+ non-kin)	3 (3)	1 (1)	50 (50)
Mother (+ non-kin)	1 (2)	1 (2)	100 (100)
Brother (+ non-kin)	9 (9)	3 (3)	33 (33)
Grandparent (+ grandparent)	2 (2)	1 (1)	50 (50)
Other kin (+ non-kin)	6 (7)	0 (1)	0 (14)
Nonkin (+ kin)	4 (4)	1 (1)	25 (25)
Nonkin (+ non-kin)	9 (9)	0 (0)	0 (0)
Kinship (to offspring of harasser) ¶			
0.5	13 (20)	9 (16)	75 (84)
0.25	21 (23)	7 (9)	35 (41)
0.125	4 (4)	0 (0)	0 (0)
0.0	9 (9)	0 (0)	0 (0)

First number in each cell represents cases directly observed (criteria 1–4; see text); numbers in parentheses include criterion 5 as well, with harasser defined as the male member of the pair that receives help.

* Includes 16 cases of single harassers.

† Includes 9 cases of single harassers.

‡ Success could not be assigned for five attempts, because the harasser nest failed shortly after the disruption attempt. These cases are omitted in the success rate calculations.

§ These values may overestimate male harassers because of the exclusion of females from category (2) evidence (see text). Cases from category (5) evidence were arbitrarily assigned to male kin if present in the harasser pair.

|| The identity of the harasser's mate is identified in parentheses.

¶ Kinship assignments assume breeders to be genetic parents of the young they rear.

increases to 42–63%. Risk falls off rapidly as an individual ages and as older close relatives die. By the time an individual is 3 years old, it is virtually immune from harassment, and typically has become a harasser itself (average life expectancy from age of first breeding in this species is 3.7 years).

Continued association between parents and grown offspring (or other close relatives) entails various costs and benefits to both parties^{1–6}. One potential benefit to parents is receipt of help in the rearing of subsequent broods of young. Parents are predicted to encourage such helping whenever they gain more in direct (individual) fitness¹⁵ through the services of the helper than they would in indirect fitness if the potential helper bred independently^{5,9,16}. Among most cooperatively breeding species, opportunities to reproduce independently are severely constrained and both parent and offspring mutually benefit from the continued retention and helping of the latter^{6,7,17–20}. Under certain circumstances, however, fitness payoffs from the two alternative reproductive strategies (helping versus breeding) will be such that the parent benefits, but the offspring loses, by the latter's continued helping (modelled by Emlen³). It is under such conditions of genetic conflict that parents are predicted to use their behavioural dominance in an attempt to retain helpers⁵.

White-fronted bee-eaters fulfill these conditions. Breeders benefit greatly from the activities of helpers. The average number of young fledged by unassisted, unrecruited pairs at Nakuru was 0.51; this increased linearly by 0.47 (± 0.06 s.e.) offspring with each helper added²¹. A grown offspring thus contributes far more to its parent's inclusive fitness by helping than if it bred, unaided, on its own (0.47 versus 0.26 offspring equivalents, respectively).

Why don't sons more forcefully resist the recruitment attempts of their parents? The answer presumably lies in the near equity of the inclusive fitness payoffs of the two options available to them. Previous work has demonstrated that the fitness benefit accrued by helpers in this species derives from increasing the production of non-descendant relatives²². By helping rear full sibs, a son will accrue, on average, 0.47 offspring equivalents; by breeding unaided, 0.51. Incorporating probabilistic future fitness gains²³, the values become 0.52 versus 0.58. Thus there is little fitness cost to a son associated with abandoning an early breeding effort and instead helping both parents to rear full sibs.

If this fitness accounting is correct, it predicts that the success of harassment attempts will be much lower when the potential recruits are non-offspring (because the recruit's payoff from helping, in terms of indirect fitness, drops precipitously as relatedness to the nestling recipients decreases). This is confirmed in Table 1.

This same reasoning explains the apparent paradox that the individuals most targeted for harassment are one's closest kin. For more distant relatives (and non-kin), the payoff of continuing to breed will far outweigh that gained through helping. Selection should favour increased resistance to harassment by such individuals (Table 1). Breeders thus will have their greatest behavioural leverage in interactions with their close kin and, in particular, with their own offspring^{5,16}. □

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Clustering of voltage-dependent sodium channels on axons depends on Schwann cell contact

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IN myelinated nerves, segregation of voltage-dependent sodium channels to nodes of Ranvier is crucial for saltatory conduction along axons^{1–4}. As sodium channels associate⁵ and colocalize with ankyrin at nodes of Ranvier⁶, one possibility is that sodium channels are recruited and immobilized at axonal sites which are specified by the subaxolemmal cytoskeleton, independent of glial cell contact^{7–10}. Alternatively, segregation of channels at distinct sites along the axon may depend on glial cell contact^{11–14}. To resolve this question, we have examined the distribution of sodium channels, ankyrin and spectrin in myelination-competent cocultures of sensory neurons and Schwann cells by immunofluorescence, using sodium channel-, ankyrin- and spectrin-specific antibodies. In the absence of Schwann cells, sodium channels, ankyrin and spectrin are homogeneously distributed on sensory axons. When Schwann cells are introduced into these cultures, the distribution of sodium channels dramatically changes so that channel clusters on axons are abundant, but ankyrin and spectrin remain homogeneously distributed. Addition of latex beads or Schwann cell membranes does not induce channel clustering. Our results suggest that segregation of sodium channels on axons is highly dependent on interactions with active Schwann cells and that continuing axon-glial interactions are necessary to organize and maintain channel distribution during differentiation of myelinated axons.

We cultured dorsal root ganglion neurons (DRGs) in the presence or absence of Schwann cells^{15–17}. DRGs and accompanying Schwann cells were cultured in a chemically defined medium and were arrested in a basal-lamina-free premyelination stage¹⁵. After plating, associated Schwann cells proliferated, adhered tightly to axons, and made extensive contact with the axonal surface. Formation of basal lamina and myelination were initiated by the addition of serum and ascorbic acid to the medium¹⁵. In the second method, dissociated DRGs were treated with antimitotic reagents to remove associated Schwann cells and fibroblasts, leaving isolated neurons free from Schwann cells. These neurons were later reseeded with pure Schwann cells^{15–18}. Within one week of reseeding, Schwann cells migrated onto axons and made extensive contact but were restrained from forming myelin by withholding ascorbic acid^{15,17}.

The distribution of sodium channels, ankyrin and spectrin were examined under each of these culture conditions by