State-dependent sentinels: an experimental study in the Arabian babbler

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Natural patterns of cooperative sentinel behaviour in Arabian babblers, *Turdoides squamiceps*, have proven consistent with state-dependent models of individually selfish anti-predator strategies. Here we demonstrate experimentally that sentinel effort within groups is determined simply by individual state. The two highest-ranking males in eight groups were separately fed a supplement of mealworms, each for one day at a time. Control days before and after each treatment confirmed that no carry-over effects occurred, and that most normal sentinel activity was carried out by alpha males, then beta males and then by the rest of the group. When supplemented, both alpha and beta males exhibited similar marked increases in sentinel activity, relative to control days. Unsupplemented males and the rest of the group incompletely compensated for these increases with reductions in sentinel effort. Differences in individual body mass within groups reflected natural and experimental variation in sentinel effort. Alpha and beta males weighed more than other group members, and gained mass only when supplementally fed. There was no evidence either for competitive sentinel behaviour, nor for any increased interference between males during the supplementation treatments. These results therefore provide strong evidence in support of the state-dependent approach to cooperative sentinel behaviour.

Keywords: sentinel; state dependent; anti-predation; vigilance; cooperation; Arabian babbler

1. INTRODUCTION

Sentinel behaviour is a cooperative system of vigilance occurring within stable social groups of birds and mammals, usually living in open habitats (Gaston 1977; Rasa 1986, 1989; McGowan & Woolfenden 1989; Zahavi 1990; Bednekoff 1997; Wright *et al.* 2001*a*). Group members take turns to be vigilant, positioning themselves where they can scan the surrounding area and make alarm calls when potential predators are sighted (Wright *et al.* 2001*b*). This allows other individuals to forage in relative safety and presumably makes the whole group more efficient in both types of activity. The key questions are: what maintains such an orderly system, and what prevents individuals from avoiding their sentinel duties whilst still benefiting from the efforts of others?

Kin selection (Hamilton 1964; Maynard Smith 1964) predicts that individuals will maintain sentinel effort in order to preferentially protect relatives. Reciprocal altruism (Trivers 1971) might predict a system of regular rotation and balanced sentinel effort among even un-related individuals by monitoring and score-keeping within the group. Alternatively, being seen to sentinel consistently may gain individuals 'social prestige' and thus associated fitness benefits in terms of access to allies and/or mating opportunities (Zahavi 1989, 1990; Zahavi & Zahavi 1997). However, a recent model by Bednekoff (1997) suggests that cooperative sentinel behaviour based upon individually selfish state-dependent behaviour can be evolutionarily stable. This is achieved by assuming that sentinel behaviour is actually a low cost activity performed only when an individual possesses sufficient

energy reserves. Safe refuges are assumed not to exist, making the sentinel role the safest (if the alternative is to risk foraging without a sentinel). Having just a single sentinel is expected to suffice. Hence, as an extension to the logic of Bednekoff's (1997) model, we propose that greater sentinel effort by one individual will reduce that among the other members of the group.

In contrast to the predictions of alternative explanations, individual state-dependent sentinel behaviour should operate irrespective of relatedness, dominance or past performance as a sentinel. Additionally, we might expect total group sentinel effort to increase with group size or food availability, whilst effort per individual should decrease with group size or reduced foraging success. Many of these predictions are consistent with existing data on sentinel behaviour in a range of systems (e.g. McGowan & Woolfenden 1989; Rasa 1986, 1989), and have been supported by a recent study on meerkats (*Suricata suricatta*; Clutton-Brock *et al.* 1999). Natural data we have collected on sentinel behaviour in Arabian babblers (*Turdoides squamiceps*) also provide excellent support for the assumptions and predictions arising from state-dependent models (Wright *et al.* 2001*a,b*).

This study aims to build upon these results, using an experimental design that incorporates appropriate controls to provide the first evidence in birds for an effect of individual state upon cooperative sentinel effort. Targeted supplemental feeding of the two highest-ranking males in each group was used to produce changes in sentinel activity and individual body mass, which were compared with control days before and after each treatment. State-dependent models would predict an increase in sentinel effort of supplemented individuals, irrespective of dominance rank and relatedness. Unlike explanations

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involving reciprocity or social prestige, any increase in individual effort should be unimpeded and have no effect on subsequent levels of sentinel effort or social behaviour within the group beyond the immediate stomach contents of the supplemented bird.

2. METHODS

(a) *The study population*

The Arabian babbler is a group-territorial, communally breeding, thrush-like bird occurring in the Arabian and Sinai deserts. In most years groups consist of between 3 and 12 birds, and are of mixed sex with age-related linear dominance hierarchies within each sex class (see Zahavi (1988, 1989, 1990), for further details). Each group usually contains only one breeding pair and its offspring, although subordinate males may reproduce if they are unrelated to the dominant female (Lundy *et al.* 1998; Wright *et al.* 1999).

The study site at Hazeva is a $25 \, km^2$ area of desert, located 30 km south of the Dead Sea in the Arava rift valley in southern Israel. The habitat is very open; sparse vegetation lines the bottom of dry river-beds, comprising well-spaced trees (*Acacia* sp.) and a few low shrubs and annual plants. Since 1971, Professor Amotz Zahavi and students from Tel Aviv University have studied 20 groups of Arabian babblers at Hazeva. Between 1992 and 1997, up to 40 groups were monitored on a weekly basis and habituated to human observers by hand-feeding. All birds in the present study were individually colour-ringed and their family histories known.

(b) *Experimental design*

Eight groups were each observed for two control days, but on the third day either the dominant (alpha) male or the subdominant (beta) male was fed supplementary mealworms (*Tenebrio* sp.) *ad libitum* during the whole observation period. All groups had previously been trained to take mealworms and unfed birds quickly returned to natural foraging. Supplementations therefore caused no additional feeding competition that might have disrupted normal sentinel behaviour. Days 4 and 5 were used for control observations (i.e. with no supplementation), whilst on day 6 the other of the two most dominant males in the group was supplementally fed. Days 7 and 8 were used as final controls. In four groups the alpha male was fed on day 3 and the beta male on day 6, whilst in the remaining four groups the reverse order was used.

(c) *Data collection*

Data were collected between 30 September 1996 and 30 December 1996, during the non-breeding season. Observations were carried out for 3 h in the morning (commencing at sunrise as the group left the roost tree) and for 2 h in the afternoon (terminating at sunset as the group went to roost). Observers remained within 20 m of the group and recorded the identity of any bird acting as a sentinel, and the start and end times of each sentinel bout (to the nearest second). For evidence that observer presence did not affect babbler behaviour, see Wright (1997) and Wright *et al.* (2001*a*). Sentinel behaviour in this species is very conspicuous and almost always involves one group member perching in a prominent and elevated location with its head up, being vigilant for a number of minutes at a time and providing alarm calls upon sighting potential predators (see Wright *et al.* (2001*a*,*b*), for further details).

The body mass of each bird was also measured for as many individuals as possible at the end of each morning and afternoon observation session (totalling 52% of possible occasions). Birds had been trained to stand on electronic top-pan balances (Shekel, (Tel Aviv, Israel) model B-2-P, accuracy 0.1 g) using small crumbs of bread as bait. Mass data were recorded only when the value given by the balance remained constant for 2.5 s (i.e. when the bird was standing still), thereby providing accurate body mass estimates.

(d) *Analysis*

For each bird on each day the mean period of sentinel behaviour was calculated per hour of observation. The sample comprised 42 individuals from eight groups, which ranged in size from three to eight birds. Therefore the effects of the experimental treatment were analysed by reducing the data to mean values per day per group, treating the 'alpha male' and 'beta male' separately, but combining the data for the 'rest of the group' (i.e. providing a mean value per individual, calculated from between one and six birds). These data were then analysed using repeated-measures ANOVA. Two-tailed *p*-values are provided throughout.

3. RESULTS

When comparing the six control days, no significant difference occurred in the amount of sentinel behaviour observed on different days during the experiment (figure 1; $F_{5,105} = 0.51$, $p = 0.767$; and $p > 0.167$ for all polynomial contrasts). This suggests that the results presented here are neither confounded by any effect of time of season, nor by any carry-over effects of the experimental treatments upon sentinel behaviour during subsequent days. Within the same mixed-model ANOVA, a significant effect by type of group member on sentinel behaviour occurred (figure 1; $F_{2,21} = 15.96$, $p < 0.001$), with alpha males acting as sentinels significantly more than beta males (contrast $t_{21} = 2.26$, $p = 0.035$) and both classes of males acting as sentinels more frequently than the rest of the group (contrast $t_{21} = 5.18$, $p < 0.001$). However, no significant interaction occurred between type of group member and the amount of sentinel behaviour on the six control days (figure 1; $F_{10,105} = 0.10$, $p = 0.444$). In addition, these results hold if control days are reclassified to represent pre- and post-alpha/beta male supplementations, confirming that no detectable carry-over effects occurred specific to any of the experimental treatments upon sentinel behaviour recorded on subsequent control days.

Figure 1 displays the effect of the food supplementations, namely an increase in sentinel effort by the supplementally fed male and a decrease in effort by the remaining non-supplementally fed birds in the group. On days when the alpha male was supplementally fed, sentinel effort changed relative to the average for all control days combined, and this change was significantly different between the different types of group member (figure 2; $F_{2,21} = 38.25$, $p < 0.001$). This was caused by a significant relative increase in alpha male sentinel effort when supplementally fed, compared with a relative decrease in the effort of the non-supplementally fed beta males and the rest of the group (contrast $t_{21} = 8.56$, $p < 0.001$). No significant difference occurred in the
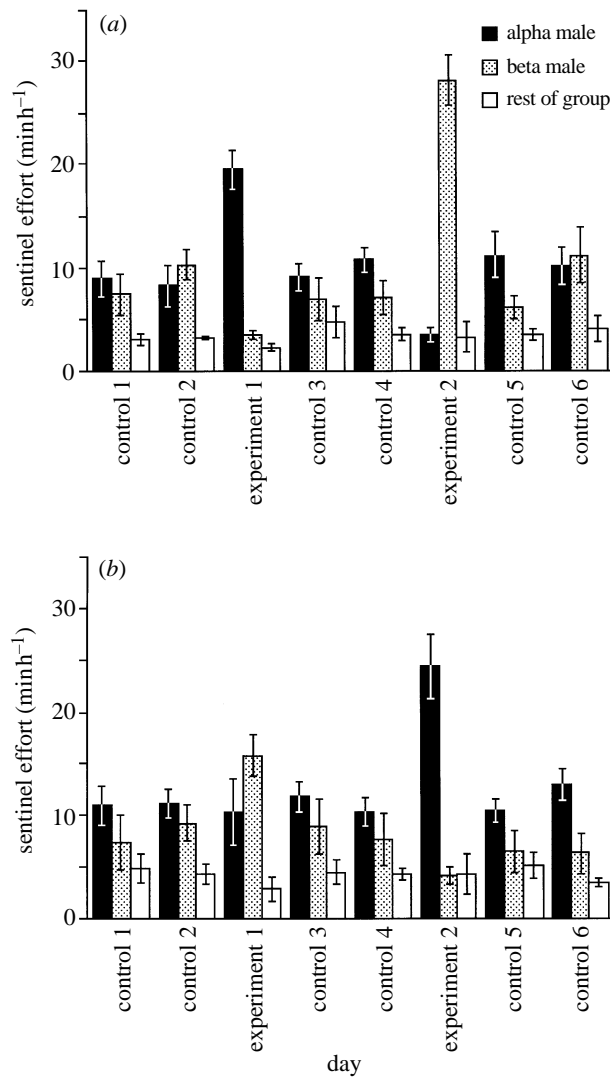
Figure 1. Sentinel effort per hour (mean ± s.e.) for each day of the experiment (see §§ 2 and 3) for alpha males and beta males, and the rest of the group combined, for (*a*) the four groups where the alpha male was fed on the first experimental day and then the beta male on the second experimental day; and (*b*) the four groups where the beta male was fed on the first experimental day and the alpha male on the second.

Figure 2. Responses to food supplementation expressed as a change in sentinel effort relative to control days (mean ± s.e.), by alpha males, beta males and the rest of the group combined, for experimental days when either the alpha male or the beta male had been supplementally fed.

relative decrease in effort between the non-supplementally fed beta males and the rest of the group ($t_{21} = 0.178$, $p = 0.089$). When the beta male was supplementally fed, the change in sentinel effort relative to control days was also significantly different between the types of group member (figure 2; $F_{2,21} = 20.17$, $p < 0.001$). Again, this was caused by a significant increase in sentinel effort by the supplemented beta male, which compared with a decrease in effort by the non-supplementally fed alpha male and the rest of the group (contrast $t_{21} = 6.29$, $p < 0.001$), with no significant difference in relative decrease between the non-supplementally fed alpha male and the rest of the group ($t_{21} = 0.89$, $p = 0.385$).

The scale of the response by alpha and beta males to the supplementations did not differ significantly in both the increased sentinel effort following feeding and
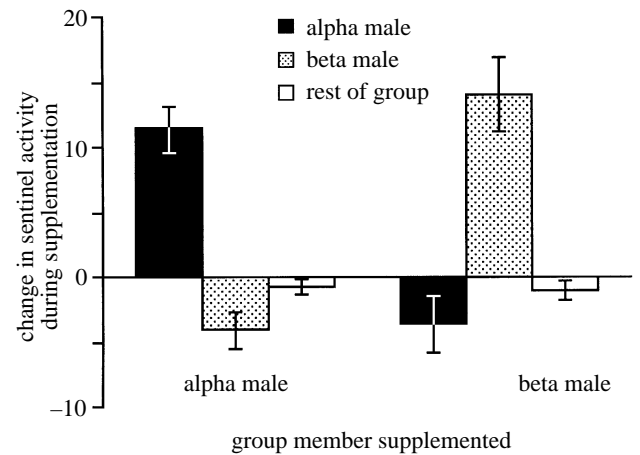
the decreased effort when the other male was fed (figure 2; $F_{1,12} = 0.27$, $p = 0.612$). The overall effect of food supplementations was to significantly elevate total group sentinel effort on experimental days relative to control days, in both alpha male supplementations ($t_7 = 2.84$, $p = 0.025$) and beta male supplementations ($t_7 = 3.63$, $p = 0.008$). Curiously, the second supplementation within each group produced a significantly greater effect (figure 1; $F_{1,12} = 5.86$, $p = 0.032$), but with no significant interaction between this order effect and the dominance rank of the two males ($F_{1,12} = 0.06$, $p = 0.808$). However, this phenomenon had no influence upon any of the experimental effects.

On control days, significant differences were evident in mean body mass between the three types of group member (figure 3; $F_{2,15} = 4.42$, $p = 0.031$). This was not the result of any significant difference between alpha and beta males (contrast $t_{15} = 0.86$, $p = 0.402$), but rather due to the greater body mass of both classes of high-ranking male compared with the rest of the group (contrast $t_{15} = 2.84$, $p = 0.012$). Virtually identical results were obtained when using only those body mass measurements taken in the early morning or only those taken in the early afternoon.

Relative to average body mass measurements for all control days combined, the change in mass on days when alpha males were supplementally fed differed significantly between the different types of group member (figure 4; $F_{2,13} = 6.48$, $p = 0.011$). This was caused by a significant increase in alpha male mass over that of beta males (contrast $t_{13} = 2.78$, $p = 0.015$), with no significant difference in the relative change in mass between non-supplementally fed beta males and the rest of the group ($t_{13} = 0.79$, $p = 0.443$). Relative to control days, the change in mass when beta males were supplementally fed did not differ significantly between the types of group members (figure 4; $F_{2,11} = 1.12$, $p = 0.353$), although all of the trends in the data appear similar to those seen when alpha males were supplementally fed. Therefore, alongside increases in sentinel effort,
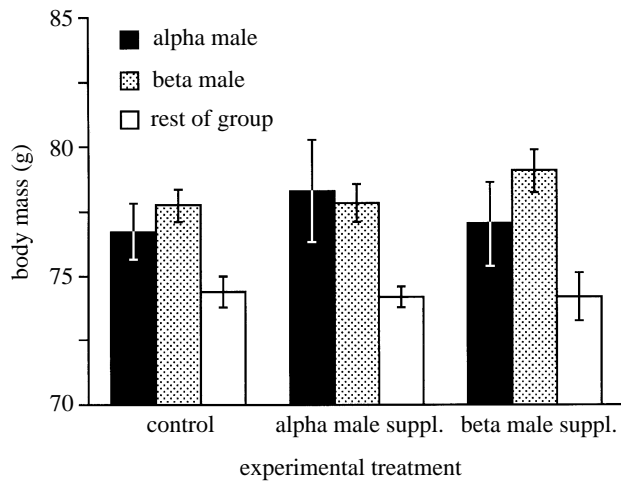
Figure 3. Body mass (mean ± s.e.) at the end of each observation session for alpha males, beta males, and the rest of the group combined, for control days and experimental days when either the alpha male or the beta male had been supplementally fed.

Figure 4. Changes in body mass during supplementation days relative to control days (mean ± s.e.), for alpha males, beta males, and the rest of the group combined, for experimental days when either the alpha male or the beta male had been supplementally fed.

supplementally fed individuals appeared to increase their body mass, but no significant change occurred in the mass of non-supplemented males nor the rest of the group, despite reductions in their sentinel effort.

4. DISCUSSION

The clear and immediate effect of experimental food supplementation was to increase sentinel behaviour in individual babblers. If we assume that the food provided to supplementally fed birds, and their subsequent increase in body mass, caused an increase in individual state in terms of individual energy reserves, then these data provide strong support for state-dependent sentinel behaviour in Arabian babblers. This confirms the primary prediction of models of state-dependent sentinel behaviour (Bednekoff 1997), and concurs with similar experimental evidence from meerkats (Clutton-Brock *et al.* 1999). The apparent absence of cheating in this cooperative vigilance system can therefore be explained. Individual Arabian babblers always perform their share of sentinel duty, because whenever they are in a high enough energetic state it is the best activity for ensuring their own personal safety (see also Wright *et al.* 2001a).

In addition, as one babbler increased its time spent acting as a sentinel, all the other members of the group performed less sentinel behaviour. The compensatory decrease was incomplete, in that total group sentinel effort increased during the experimental supplementations. This mirrors other compensatory changes in individual sentinel effort that result from differences in group size in this species (Wright *et al.* 2001a). Incomplete compensation can be predicted by extending the logic of the Bednekoff (1997) model in which only one individual acts as a sentinel at any one time. This condition has been confirmed in Arabian babblers, in which only one individual is sentinel on 90% of occasions (Wright *et al.* 2001a). Interestingly, similar compensation reactions have also been predicted and experimentally demonstrated for cooperative nestling provisioning, in both biparental (e.g.
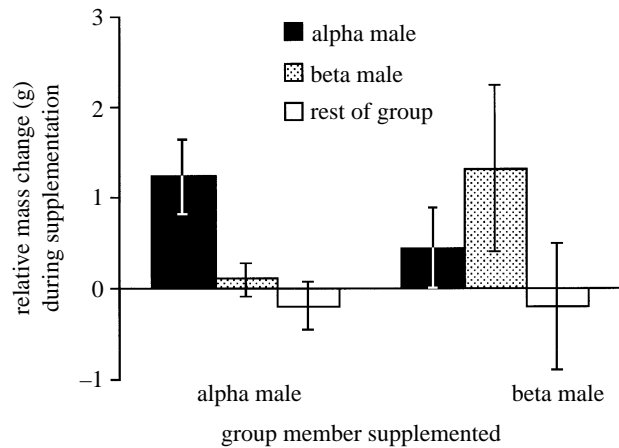
Wright & Cuthill 1989) and cooperative systems (Wright & Dingemanse 1999). This suggests that, as with cooperative provisioning behaviour, cooperative sentinel behaviour operates on the basis of simple individual-based decision rules, without the need for complex social interactions or signalling. Although we cannot exclude explanations based on kin selection, reciprocity or social prestige, all our data on sentinel behaviour in the Arabian babbler appear entirely consistent with Bednekoff's (1997) model of selfish state-dependent sentinel behaviour (Wright *et al.* 2001a,b).

The most striking feature of sentinel behaviour in this species is how orderly and apparently equitable it appears. Change-overs are usually quiet and efficient, involving one bird coming down before the next bird goes up to sentinel, and very rarely involve forced change-overs, physical contact or social interaction (Wright *et al.* 2001b). Little evidence existed in the present study to suggest that this behaviour was being used as a signal to 'show-off' and gain social prestige within groups (*sensu* Zahavi & Zahavi 1997). Babblers were almost never observed actively competing for sentinel positions, even during periods of experimentally induced changes in sentinel effort. In fact, dominance interactions appear no more common in the context of sentinel behaviour than in any other facet of babbler life. Contrary to the suggestion of Blumstein (1999), the Bednekoff (1997) model neither predicts nor explains potential observations of competitive sentinel behaviour. The present study clearly demonstrates that the two highest-ranking males, at least, will allow one other group-mate to perform a greater share of sentinel effort if possible. Therefore, any short-term increase in individual sentinel effort appears beneficial for everyone in the group, even when some of the individuals concerned are adjacent in dominance rank and likely to compete for future reproductive access to females.

Closer examination of the data on individual effort during control days revealed that the dominant alpha male and the beta male almost always performed the greatest share of group sentinel effort. This contrasts with approximately equitable effort within groups of closely

related jungle babblers (*Turdoides striatus*; Gaston 1977), although unequal contributions appear common in other sentinel systems (e.g. meerkats; Clutton-Brock *et al.* 1999). The extra sentinel effort by dominant male babblers corresponded with greater body mass in these high-ranking male individuals compared with the rest of the group. More extensive data from the same population has confirmed these patterns, demonstrating that heavier dominant males act as sentinels more frequently than lighter subordinate and/or female group members (Wright *et al.* 2001a). From the present study, it appears that this is not simply an effect of dominance *per se*, but that sentinel effort reflects short-term changes in individual energy reserves. Indeed, the correlation shown between body mass and sentinel effort both within and between individuals (see Wright *et al.* 2001a) suggests a fundamental link between individual energy reserves and cooperative sentinel behaviour.

The correspondence between dominance rank, body mass and subsequent sentinel effort does suggest, however, that more is going on in babbler groups than simple state-dependent cooperative sentinel behaviour amongst equals. Dominance appears to require that males are either inherently heavier, or that they maintain a greater body mass than other group members. The present study confirms that, even when relieved of their sentinel duties and given the opportunity for greater foraging time, subordinate group members do not increase their body mass (see also Wright & Dingemanse 1999). This consistency of individual body mass probably reflects a balance between the advantages of possessing greater energy reserves and the mass-dependent costs of carrying those fat reserves around (see Witter & Cuthill 1993; Cuthill & Houston 1997). Dominant males may require greater personal energy (fat) reserves or muscle mass in order for them to maintain their high-ranking position within the group. It is therefore possible that only high-quality individuals with superior foraging efficiency and predator avoidance skills can become dominant. Dominant group members may also benefit from priority of access to food resources in order to maintain their greater body mass. But this seems unlikely to be a major effect in this system, because Arabian babblers mostly feed on small, dispersed and cryptic prey, and foraging competition is rarely observed.

The question is whether dominant males maintain greater body mass specifically for the purposes of performing more sentinel behaviour, which might confer additional benefits on these particular males, in terms of them being better able to keep an eye on their rivals or protecting their kin and potential mates. Alternatively, additional body mass might be needed by dominant males for some other reason, for example conferring an advantage in extensive and energetically expensive aggressive encounters that occur between (but also occasionally within) groups. If this is the case, then greater mean sentinel effort is merely a by-product of these patterns in individual body mass and time budgets. The first possibility suggests that sentinel behaviour lies at the centre of babbler dominance, which seems unlikely given that it is performed to a large extent by all group members and is clearly characteristic of an anti-predation behaviour rather than serving any obvious social or

signalling function (see also Wright *et al.* 2001a,b). The second and more plausible suggestion is that the contrasting management of energy reserves required by individuals of different dominance rank has consequences in terms of the optimum level of sentinel behaviour they undertake.

In conclusion, sentinel behaviour in Arabian babblers is a conspicuous and characteristic behaviour carried out by all group members. Although correlated with individual body mass and therefore dominance rank, sentinel effort can be experimentally enhanced in individual males via supplementation with extra food. The immediate and sustained additional sentinel effort performed by supplementally fed group members did not persist beyond the day of extra feeding. Only one bird acted as a sentinel at any one time, with the consequence that an experimentally induced increase in effort by one individual resulted in a decrease in the contributions of all other birds, whilst total sentinel effort for the group as a whole increased. These results are consistent with recent theoretical and empirical studies, suggesting that sentinel behaviour in Arabian babblers is an individually selfish state-dependent behaviour, which is therefore not open to cheating, and results in the cooperative protection of groups from predation.

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