

$$\alpha_{ij} = c_{ij}X_i^* = -\frac{F_{ij}}{B_j}$$

and the per capita effect of prey  $i$  on predator  $j$  as

$$\alpha_{ji} = c_{ji}X_j^* = -\frac{a_{ji}p_jF_{ij}}{B_j}$$

15. The results given for this particular food web are representative for the other food webs, as in all seven webs the negative  $\alpha_{ij}$  decreased significantly with trophic position at least at the  $P < 0.01$  level, whereas the positive  $\alpha_{ji}$  increased significantly with trophic level at the  $P < 0.05$  level, except for the webs from Horseshoe Bend (12) and Central Plains (12), for which  $\alpha_{ji}$  showed no correlation. The impacts as shown in Fig. 2C are also representative for the other food webs, in that for all webs impacts on stability were correlated neither with feeding rates nor with interaction strengths.
16. The values of one pair of the matrix elements, referring to one interaction, were varied within the range of  $[0, 2\alpha_{ij}]$ , where  $\alpha_{ij}$  is the estimated interaction strength (14), keeping all other elements fixed at their calculated values. The sensitivity analysis was done with matrices in which the mean values of the diagonal terms were close to (1% below) the critical value for stability and were based on 100 runs. We assessed the stability of the matrices by testing whether all eigenvalues of the community matrices had negative real parts (7).

17. The diagonal matrix elements referring to intragroup interferences could not be derived from the empirical data and therefore were set at various levels of magnitudes ( $s_i$ , with  $0 \leq s_i \leq 1$ ) proportional to the specific death rates ( $d_i$ ), with  $s_i = 1, 0.1$ , and  $0.01$  and hence  $\alpha_{ii} = -d_i, -0.1d_i$ , and  $-0.01d_i$  for all groups equally. Intragroup interference was modeled this way, as the values published by Hunt *et al.* (27) for the specific natural death rates ( $d_i$ ) include all nonpredatory losses that can be expected in populations with population size ( $B_i$ ) in their natural environment. In terms of the Lotka-Volterra equations, this way of modeling intragroup interference implied that  $b_i = (1 - s_i)d_i$  and  $c_{ii} = s_i d_i / B_i$ ; hence,

$$\alpha_{ii} = (\partial X_i / \partial X_i)^* = -s_i d_i$$

Elements referring to the feedbacks to detritus were derived in the same way as the trophic interactions with the modification of the Lotka-Volterra equation for detritus (4).

18. Diagonal terms and feedbacks to detritus in the theoretical matrices were chosen from ranges similar to those in the lifelike matrices relative to the strength of the trophic interactions.
19. This kind of disturbance preserved the placing of the positive, zero, and negative elements, the logical pairing of element values referring to the same trophic interaction, and the overall strength of the trophic interactions relative to the strength of intragroup interference (5).

20. Values were sampled from the interval  $[0, 1]$ , which is appropriate for the energy conversion efficiencies by definition and for the specific death rates and population sizes, which depend on the scale.
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## Complex Cooperative Strategies in Group-Territorial African Lions

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Female lions (*Panthera leo*) showed persistent individual differences in the extent to which they participated in group-territorial conflict. When intergroup encounters were simulated by playback of aggressive vocalizations, some individuals consistently led the approach to the recorded intruder, whereas others lagged behind and avoided the risks of fighting. The lead females recognized that certain companions were laggards but failed to punish them, which suggests that cooperation is not maintained by reciprocity. Modification of the “odds” in these encounters revealed that some females joined the group response when they were most needed, whereas others lagged even farther behind. The complexity of these responses emphasizes the great diversity of individual behavior in this species and the inadequacy of current theory to explain cooperation in large groups.

African lions engage in a wide variety of group-level activities, including group hunting, communal cub rearing, and group territoriality (1, 2). However, recent research has revealed lions to be less cooperative than previously supposed. Although lions will hunt cooperatively when their prey is difficult to capture (3–5), cooperation often breaks down when the prey is relatively easy to catch (3, 4). Female lions nurse each others' cubs, but nonoffspring nursing is secondary to the females' joint defense of young against infanticidal males (2, 6). Indeed, the threat of attack by conspecifics appears to be the driving force in lion sociality (2). Large prides dominate smaller ones, and solitary animals are fre-

quently killed or injured in attacks by like-sexed strangers (1, 2). Territorial incursions can be simulated by the playback of recorded roars, and these routinely elicit cooperative defense (7, 8). Groups of lions will readily approach a hidden loudspeaker and will even attack a taxidermically mounted lion concealed behind the speaker (8). These experimental studies indicate that lions can distinguish pride mates from strangers (9) and can assess the ratio of companions to intruders (the “odds”), approaching the speaker more readily when they outnumber their recorded opponents (7, 8). However, by performing a series of playbacks to the same groups of females over a 2-year period, we have discovered that certain individuals consistently lag behind their companions during the group response. We show here that these females are recognized as laggards by their companions and that many of these laggards vary their behavior according to the odds.

Female lions live in fission-fusion social groups (prides) that typically contain 3 to 6 related adults (numbers can range from 1 to 18), their dependent offspring, and a coalition of immigrant males (10, 11). The males defend the pride against incursions by other males (8, 10), and the females defend their young against infanticidal males and their territory against incursions by other females. The territory is essential for successful breeding and can only be held by two or more females (2) that advertise ownership by roaring (1, 7). Here we consider the territorial responses of females to other females, presenting data collected on eight prides in the Serengeti National Park and Ngorongoro Crater, Tanzania. Each pride was composed of two to seven adult females of known age and kinship (10, 11). To simulate varying levels of territorial threat, we followed McComb *et al.* (7) in broadcasting the roars of either one or three females (12). Most individuals responded by looking toward the speaker and approaching directly at a walking pace. Females that led the response typically adopted a tense posture with head held low, and their approach was often punctuated by pauses and glances back at lagging companions [also see (8)]. Each animal's response was measured in four ways: its latency to the midpoint (100 m) between the pride's original position and the speaker, the difference between its own latency and that of the leader (“lag time”), the order within the group when each animal reached the midpoint, and the number of backward glances to lagging companions. The order in which individuals approached the speaker usually remained the same throughout the playback, and these ranks were standardized to a value between  $-1$  (last) and  $1$  (first) to control for group size.

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We used the females' standardized ranks to measure their average response to territorial intrusion. An analysis of variance within each pride shows significant individual differences in seven of eight prides (28 of 34 individuals,  $0.043 > P > 0.0001$ ). Of these 28, 12 had mean standardized ranks below 0 (that is, consistently remained at the rear of the group), and these were defined as laggards. Mean rank does not depend on age or body size (13), nor do female lions show any discernible dominance hierarchy (14), so differences between individuals do not obviously relate to fighting ability. A female's typical response does not appear to be maternally inherited (15); laggards are not any less closely related to the pride (16) nor are they any more or less likely to participate in group hunts (17). Although the biological basis of these individual differences is not yet clear, lagging behavior appears early in life and persists into adulthood (18).

Territorial fights often lead to severe injury or death (1, 2, 10), and females most frequently attempt to expel intruders if they outnumber them (7). Thus, a rapid response by every group member would reduce their companions' risk of injury or defeat. However, laggards followed 50 to 200 m behind the leader and typically reached the speaker 30 to 120 s later. In every real interpride encounter where lagging was observed and a female was attacked, the victim was always the lead female ( $n = 5$ ). Thus laggards are safer from any initial attack, and leaders appear to incur a risk proportional to their companions' lagging distance.

Because laggards may gain greater immediate rewards by letting their companions bear the full costs of territorial defense, we tested whether female lions behave in a manner predicted by theoretical models of the iterated prisoner's dilemma (19). In a single-encounter game, mutual cooperation results in a greater payoff than does mutual defection, but the greatest payoff is achieved by "cheating" on a cooperative partner, and the least payoff results from "cooperating" when the partner cheats. The two best strategies in an iterated game, tit-for-tat (19) and Pavlov (20), punish cheaters by withdrawing further cooperation. Tit-for-tat cannot be exploited as it reciprocates acts of both cooperation and cheating. Pavlov is similar but can also exploit an unconditional cooperator. Cooperation in larger groups is more complicated and may operate either through a system of pairwise interactions (21) or through  $n$ -person games in which many individuals cooperate simultaneously (22).

We examined each female's response to lagging in a two-person game by playing the roar from a single intruder to a leader (mean rank  $> 0$ ) matched first with another leader and then on a separate occasion with a lag-

gard. In each case, the pair was a subset of a larger pride but were temporarily separated from the remainder of their companions, and individuals were classed according to their behavior in previous experiments (23). In six matched pairs of playbacks, the leader approached the speaker less quickly and stopped more often to look behind at her companion when she was paired with a laggard (Table 1). Thus, females "mistrust" their lagging companions, which suggests that they have the cognitive ability to implement score-keeping (19, 24). However, leaders do not conform to models of reciprocity, as they fail to "punish" laggards by halting their own approach to the speaker. Although more cautious, leaders continue to bear the costs of either arriving alone or arriving 48 to 106 s before their lagging companion (Table 1). Their acceptance of laggards also rules out Pavlov (20), a strategy in which only mutual cooperation or mutual cheating can lead to further cooperation.

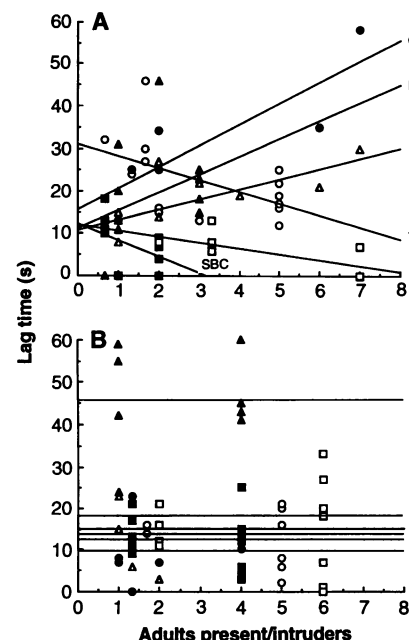
These arguments only consider short-term consequences of territorial defense, but individuals should also be sensitive to the long-term effects of their behavior. Although lions might be tempted to reduce their risk of injury from territorial defense, they must act to maintain both their long-term territory and sufficient numbers of companions to defend it (2, 7, 8, 10). In addition, female lions need companions to share in the protection of young (2, 6) and the capture of large prey (2, 4), and companions are recruited only through births within the

**Table 1.** Latency (in seconds) to the midpoint (100 m) by pairs of females and the number of glances given by the leader to her companion. The same leader is matched either with another leader or with a laggard (23), and in all cases the pair were separated from the rest of their pride by at least 2 km. All playbacks were of the recorded roar of a single "intruder." The leader's latency and her number of glances are both greater when the companion is a laggard (Wilcoxon signed-rank test, two-tailed,  $P = 0.031$ ). Asterisk indicates that laggard reached the midpoint but stopped before reaching the speaker.

Pair	Latency (s)	Glances (n)
<i>Leader-leader</i>		
CS55-CS63	128, 129	2
CSN-CS46	185, 186	0
L75-L78	55, 80	0
MSF-MKM	134, 143	3
MKU-MKT	91, 97	1
Nymph-Nell	65, 85	0
<i>Leader-laggard</i>		
CS55-CS60	224, 310	7
CSN-CS27	304, 362*	4
L75-L72	191, 271	2
MSF-MKS	174, 280*	5
MKU-MKO	126, 174	4
Nymph-NW15	134, 190*	4

pride (10, 25). Thus, endangering a companion would eventually have long-term costs outweighing the short-term temptation to cheat (8, 26), especially when companions are close kin. Consequently, females might be expected to cooperate unconditionally (3, 26, 27) during territorial defense or to cooperate whenever their participation would shift the odds in their favor.

We therefore tested to see how lagging behavior was influenced by the odds and discovered that the 12 laggards could be classified according to three different strategies (Fig. 1). The lag time of six individuals was independent of the ratio of companions to intruders, three laggards joined the leaders when most needed (significantly positive slopes), and the remaining three laggards held back even farther (significantly negative slopes). Thus, in the context of group territoriality, we suggest that female lions may be classified according to four discrete strategies: "unconditional cooperators" who always lead the response, "unconditional laggards" who always lag behind, "conditional cooperators" who lag least



**Fig. 1.** Lag times of the 12 laggards plotted against the number of adults present at the playback divided by the number of "intruders." Inclusion of both individual intercepts ( $F_{11,107} = 3.39$ ,  $P = 0.0006$ ) and slopes ( $F_{11,96} = 2.27$ ,  $P = 0.016$ ) significantly improved the overall model. Two other factors were tested but found not to be significant: the total number of adults in the pride (but not necessarily present) and the number of subadults present. (A) All laggards with nonzero slopes ( $P < 0.05$ ). Open circles, Trifle; solid circles, CS38; open triangles, CS27; solid triangles, LK23; open squares, LKG; and solid squares, SBC. (B) All laggards with constant lagging times. Open circles, Trim; solid circles, MG17; open triangles, MGQ; solid triangles, Laika; open squares, NW15; and solid squares, NW06.

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when they are most needed, and “conditional laggards” who lag farthest when they are most needed (28).

Our analysis has revealed unexpected diversity in lion behavior. Some females cooperate unconditionally and others only cooperate when most needed. Both strategies ensure the long-term rewards of protecting essential companions and a stable territory. However, other females opt for additional short-term benefits by lagging behind pride mates during territorial disputes, and some females lag farthest when their help is most needed. Although leaders recognize laggards and behave more cautiously in their presence, they continue to lead the response. In a broader interpretation of cooperative behavior, leaders and laggards may be analogous to “producers” and “scroungers” in foraging groups (29) or “bold” and “shy” individuals in other contexts (30). As laggards avoid the costs of fighting (“producing”), their rewards are clearly frequency-dependent, and they exploit their pride’s corporate territoriality if enough of their companions cooperate (22). Under these conditions, laggards may coexist with leaders in a mixed evolutionarily stable strategy (31). This study suggests that cooperative groups can include a great variety of behavioral strategies. Most theory on the evolution of cooperation has focused on two-person games and has revealed extraordinary levels of complexity (32). Individual behavior in contests between larger groups may prove to be even more complex.

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- Between 6 and 15 of these playbacks were conducted to each pride over a 24-month period and only in the absence of adult males; all responses were videotaped. Roars from extra-pride females were played from 200 m with a Panasonic SV-250 digital audio tape recorder, an ADS p120 amplifier, and a Klipsch Hersey speaker hidden in long grass or bushes. All playbacks were conducted between 0.5 and 1.0 hours before dusk; recordings were between 20 and 55 s in duration and were played at 116 dB at 1 m. Females clearly distinguish between the roars of one and three intruders when played from a single loudspeaker (7). Use of particular recordings was randomized with respect to the identity and composition of each experimental group, and

individual responses were independent of the number of times an individual had heard a recording (7, 8).

- All females were between 3 and 14 years old. Each individual’s mean rank did not depend on age [degrees of freedom ( $F_{1,32}$ ) = 1.31] or body size (estimated from chest girths,  $n = 14$ ,  $F_{1,12} = 0.83$ ). To ensure that lagging was not caused by poor health, playbacks excluded all animals that were either emaciated or injured.
- In 14 cases of known maternity, the daughter’s mean rank was not significantly correlated with her mother’s ( $r = 0.19$ ,  $t = 0.66$ ).
- Five of 12 laggards had at least one sister that consistently approached the speaker in the front half of the group.
- Although we lack direct observations of the hunting behavior of most of these females, one laggard consistently failed to participate in group hunts, whereas another was an active hunter.
- Juvenile females (6 to 42 months) also differ in their preferred position relative to other juveniles ( $n = 38$ ,  $0.001 > P > 0.0001$ ), and juvenile behavior predicts adult behavior (10 of 10 juvenile laggards continued to lag as adults). Juveniles are not considered here because they all tended to stay behind the adults when approaching the speaker.
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## Endoreduplication in Maize Endosperm: Involvement of M Phase–Promoting Factor Inhibition and Induction of S Phase–Related Kinases

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Endoreduplication is an endonuclear chromosome duplication that occurs in the absence of mitosis and in *Zea mays* (L.) is required for endosperm development. Induction of DNA synthesis during early stages of endosperm development is maintained by increasing the amount and activity of S phase–related protein kinases, which was demonstrated here by their ability to interact with human E2F or with the adenovirus E1A proteins. In addition it was shown that endoreduplicated endosperm cells contain an inhibitor that suppresses the activity of the M phase–promoting factor (MPF). These results demonstrate that in maize endosperm, endoreduplication proceeds as a result of two events, inhibition of MPF and induction of S phase–related protein kinases.

A common method by which polyploidy occurs is through chromosome endoreduplication. This is an endonuclear duplication of the genome occurring in the absence of mitosis, and it leads to the production of chromosomes with  $2^n$  chromatids (1). This process is common in tissues with high metabolic activity, such as the silk glands of dipterans and the developing endosperm of

seeds, but it can also occur in tumor tissues (1). Endoreduplication appears to be an essential process for the development of *Zea mays* (L.) endosperm (2). One would predict that endoreduplication proceeds from two events: inhibition of mitosis and the constitutive induction of DNA synthesis. As the mechanism controlling endoreduplication is unknown, we have begun to characterize the factors regulating this process in maize endosperm.

We established the temporal expression of endoreduplication in maize endosperm

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