and because this work demonstrates quenching of metastable neutral atoms by optical pumping in selected regions of space (Fig. 4), what we describe here is, in principle, an "all-optical" method of forming nanometer-scale patterns.

REFERENCES AND NOTES

1. R. G. Nuzzo, F. A. Fusco, D. L. Allara, *J. Am. Chem. Soc.* **114**, 1990 (1987).
2. C. D. Bain, J. Evall, G. M. Whitesides, *ibid.*, p. 7155.
3. G. M. Whitesides and C. B. Gorman, *Handbook of Surface Imaging and Visualization*, in press.
4. C. S. Adams, M. Sigel, J. Mlynek, *Phys. Rep.* **240**, 143 (1994).
5. A. Kumar, H. A. Biebuyck, G. M. Whitesides, *Langmuir* **10**, 1498 (1994).
6. N. L. Abbott, J. P. Folkers, G. M. Whitesides, *Science* **257**, 1380 (1992); R. C. Tiberio *et al.*, *Appl. Phys. Lett.* **62**, 476 (1993); J. L. Wilbur, A. Kumar, E. Kim, G. M. Whitesides, *Adv. Mater.* **7-8**, 600 (1994); G. P. Lopez, H. A. Biebuyck, R. Harter, A. Kumar, G. M. Whitesides, *J. Am. Chem. Soc.* **115**, 10774 (1993); C. S. Dulcey *et al.*, *Science* **252**, 551 (1991); J. M. Calvert *et al.*, *Thin Solid Films* **211**, 359 (1992); J. Huang, D. A. Dahlgren, J. C. Hemminger, *Langmuir* **10**, 626 (1994).
7. H. Conrad, G. Ertl, J. Kuppers, S. W. Wang, *Phys. Rev. Lett.* **42**, 1082 (1979).
8. D. W. Fahey, W. F. Parks, L. D. Schearer, *J. Phys. E* **13**, 381 (1980).
9. For recent improvements in metastable atom sources, see, for example, J. A. Brand, J. E. Furst, T. J. Gay, L. D. Shearer, *Rev. Sci. Instrum.* **63**, 163, (1992).
10. E. Kim, A. Kumar, G. M. Whitesides, *J. Electrochem. Soc.* **142**, 628 (1995).
11. G. Timp *et al.*, *Phys. Rev. Lett.* **69**, 1636 (1992); J. J. McClelland, R. E. Scholten, E. C. Palm, R. J. Celotta, *Science* **262**, 877 (1993); K. K. Berggren, M. Prentiss, G. Timp, R. E. Behringer, *J. Opt. Soc. Am. B* **11**, 1166 (1994); J. J. McClelland, *ibid.*, in press.
12. Gold films were formed by electron-beam evaporation of ~1.5 nm of Ti (adhesion promoter) and ~20 nm of gold (99.999%) onto a silicon wafer.
13. Several mechanisms for deexcitation of Ar* by the surface are possible. We do not know which mechanism results in damage to the SAM. See F. Bozco, J. T. Yates Jr., J. Arias, H. Metiu, R. M. Martin, *J. Chem. Phys.* **78**, 4256 (1983).
14. We used an aqueous ferricyanide etch [0.001 M $K_4Fe(CN)_6$, 0.01 M $K_3Fe(CN)_6$, 0.1 M $K_2S_2O_3$, and 1 M KOH]; Y. Xia; M. Zhao, G. M. Whitesides, unpublished results.
15. H. W. Webb *Phys. Rev.* **24**, 113 (1924).
16. These detectors typically operate with efficiencies of between 4 and 22% for Ar*. See F. B. Dunning and A. C. H. Smith, *J. Phys.* **B4**, 1696 (1971). If we assume a detector efficiency of 13%, we can estimated the flux of metastable atoms to be 2.6×10^{12} atoms per second per square centimeter. We refer to the dose of metastables in "atoms per DDT molecule" (or just "monolayers") which corresponds to 4.6×10^{14} atoms per square centimeter.
17. J. L. Wilbur, E. Kim, Y. Xia, G. M. Whitesides, *Adv. Mater.*, in press. We used 1% NH_4F (~1 min) to remove the native SiO_2 and an alcoholic solution of potassium hydroxide (4 M KOH, 15% isopropyl alcohol, 60°C, 15 min) to etch silicon. See (*10*) for details.
18. The source produced electrons and positive ions that were deflected away from the sample by a stainless steel rod maintained at ~1700 V. Higher voltages did not further reduce the detector current. It also generated photons (visible to vacuum ultraviolet) and neutrals with high kinetic energies.
19. The light intersected the atomic beam just before the beam left the discharge area (before the collimating aperture). See Fig. 2.
20. This observation also confirmed that metastable atoms were the major component of the signal on the detector (or sample).
21. We have used a standing wave of 764-nm light as an optical mask to fabricate arrays of lines with micrometer-scale features. J. L. Wilbur, K. K. Berggren, A. Bard, S. L. Rolston, J. D. Gillaspy, M. Prentiss, G. M. Whitesides, unpublished results.
22. The transition from a pattern that was marginally visible by eye to a pattern that was distinctly visible occurred in <5 min. The estimated error in t_{etch} is therefore ± 2.5 min.

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Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems

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Ecologists have long been studying stability in ecosystems by looking at the structuring and the strengths of trophic interactions in community food webs. In a series of real food webs from native and agricultural soils, the strengths of the interactions were found to be patterned in a way that is important to ecosystem stability. The patterning consisted of the simultaneous occurrence of strong "top down" effects at lower trophic levels and strong "bottom up" effects at higher trophic levels. As the patterning resulted directly from the energetic organization of the food webs, the results show that energetics and community structure govern ecosystem stability by imposing stabilizing patterns of interaction strengths.

The stability of community food webs depends on properties of food web structure, such as the number of groups (*1*), the frequency of interactions (*1*, *2*), and the length of the food chains (*3*, *4*). The strength with which organisms influence each other's population dynamics is also considered an important factor in the stability of complex communities. However, little is known about the way this factor is manifested in real ecosystems, partly because of a shortage of empirically based estimates of the interaction strengths, but also because of a lack of congruence in the way interaction strength is defined and treated in theoretical models versus experimental studies. Theoreticians have defined interaction strength mathematically as the elements of the Jacobian "community" matrix (*1*) and used values based on general assumptions with respect to the nature of the organisms rather than on observations (*1–3*, *5*, *6*), whereas empiricists have derived interaction strength from the observed impacts of species manipulations on food web structure (*7–11*). Here, we link the two approaches by deriving values of the Jacobian matrices from field and laboratory observations for seven food webs from native and agricultural soils (*12*) and by evaluating their importance to ecosystem stability.

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We constructed material flow descriptions of the food webs; a description of one of the webs is given in Fig. 1. Feeding rates were calculated from the observed population sizes, death rates, and energy conversion efficiencies (*13*). As expected, the feeding rates were relatively large at the lower trophic levels and small at the higher trophic levels (Fig. 2A). From these food web energetics, we could estimate the strengths of the trophic interactions, following the principles of May (*1*) and using standard Lotka-Volterra equations (*14*). In Fig. 2B, the interaction strengths in one of the food webs are given as a representative example (*15*). A distinction was made between the per capita effects of predators (j) on their prey (i) (negative values of α_{ij}) and the per capita effects of prey on their predators (positive values of α_{ji}). Both types of per capita effects were patterned along trophic position: the absolute value of the negative α_{ij} decreased significantly ($P < 0.01$) with trophic position, and the positive α_{ji} increased significantly ($P < 0.05$) with trophic position.

This kind of interaction strength, however, does not necessarily refer to the impact of the interaction on the functioning of the community. Therefore, we separately established the impacts of the interactions on food web stability by constructing Jacobian community matrices (*1*), including the estimated patterns of interaction strengths, and analyzed the sensitivity of the stability of these matrices to variation in the values of one pair of elements, referring to the strength of one interaction (*16*). In this

way, the impact of an interaction on ecosystem stability was expressed in terms of the probability that the matrices became unstable because of the variation in the element values (Fig. 2C). These impacts on stability were found to be not equally large for all interactions. Moreover, impacts on stability were not correlated with feeding rates nor with interaction strength: changes in energetically unimportant links could lead to a substantial decrease in stability (Fig. 2, A and C), whereas changes in the strength of some energetically important links had no effect at all. We also found strong links with a weak impact and weak links with a strong impact (Fig. 2, B and C).

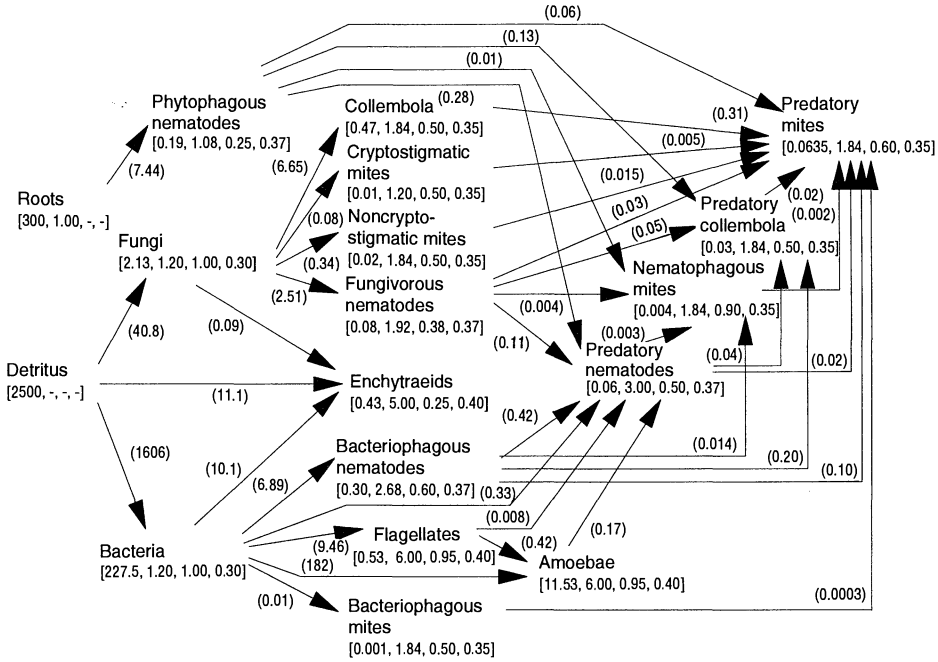

Fig. 1. Material flow diagram of the food web from the conventional practice of the Lovinkhoeve Experimental Farm (*12*). Species were aggregated into functional groups (*28*). For each group *i*, the data used to calculate the interaction strengths (*14*) are given in (square brackets) the sequence biomass (B_i, kg ha^{-1}), specific death rate (d_i, year^{-1}), assimilation efficiency (a_i), and production efficiency (p_i). Feeding rates of group *j* on group *i* (F_{ij}, kilograms per hectare per year) *13*) are given near their respective arrows (parentheses).

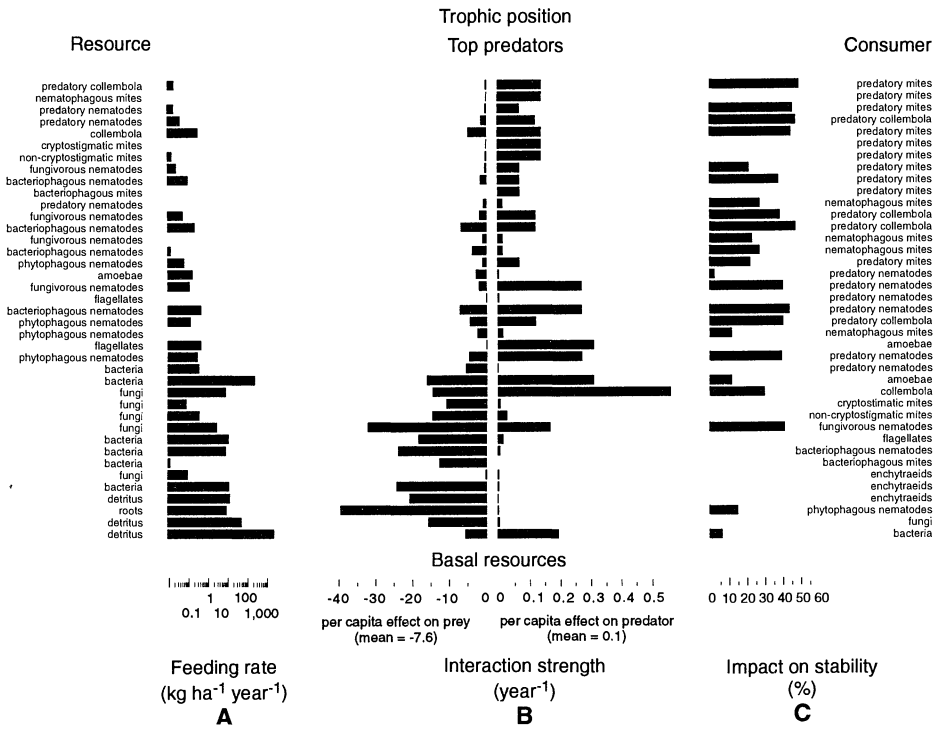

Fig. 2. Feeding rates (**A**), interaction strengths (**B**), and impacts of the interactions on food web stability (**C**) arranged according to trophic position in the food web of the conventional practice at the Lovinkhoeve Experimental Farm (*12*).

Even though there was no correlation between the strength of a particular interaction and its impact on food web stability, the observed patterning of the interaction strengths (Fig. 2B) was found to be an important factor in the stability of the webs. This was shown by a comparative analysis in which the stability of community matrix representations of the seven food webs, including the estimated patterns of interaction strengths (*14*, *17*) (lifelike matrices), was compared with that of matrices with similar structures but without the pattern. These matrices include (i) theoretical matrices, in which interaction strength was sampled from proposed theoretical intervals (*3*, *18*); (ii) disturbed matrices, in which the lifelike patterns of interaction strength were disturbed by random permutation of the nonzero pairs of elements (*19*); and (iii) test matrices, in which the values of the parameters (population sizes, specific death rates, and energy conversion efficiencies) used to calculate the feeding rates and interaction strengths were not based on observations but were randomly chosen (*20*). This comparison showed that the lifelike matrices were more likely to be stable than their theoretical, disturbed, or test counterparts (Fig. 3). The comparison with the theoretical and disturbed matrices showed that including the estimated values of interaction strength enhanced stability and that this enhancement could not be attributed to the occurrence of particular ranges of element values nor to the overall strength of the trophic interactions relative to the strength of intragroup interference (*19*). Hence, this enhancement resulted from the way in which the element values were arranged in a specific pattern. Furthermore, the comparison with the test matrices showed that the high likelihood of stability of the lifelike matrices was not an artifact of the (equilibrium) assumptions underlying the equations we used to calculate the feeding rates and interaction strengths. Rather, it was connected to the field and laboratory data that formed the empirical basis of the calculations.

These results demonstrate that the stability in ecosystems may depend strongly on the patterning of the interaction strengths and therefore reinforce the corollary of May

(*1*) and the assertions of Moore and Hunt (*21*) that interaction strengths within ecosystems are patterned in ways that are important to stability. Our results are from a limited set of soil food webs, but the structure of these webs in terms of diversity and connectance (frequency of interactions) corresponded to many other food webs from different kinds of ecosystems (*22*). The stabilizing patterning of the interaction strengths consisted of strong "top down" effects at the lower trophic positions and strong "bottom up" effects at the higher trophic positions, which supports the idea that top down and bottom up forces act on communities simultaneously (*23, 24*). It is not yet clear how precisely the patterning relates to stability. Possibly, the patterning reduces the effects of potentially destabilizing configurations in the structure of the webs. For example, the fact that short loops are concentrated at the lower trophic positions, and that the strongest negative effects are restricted to these loops, might suggest that the destabilizing properties of longer loops (*25*) are reduced this way. A correlation analysis between the interaction strengths (α_{ij} and α_{ji}) and some energetic parameters [obtained by combining the equations in (*13*) and (*14*)] indicated which energetic regularities in the food webs might have been important to the patterning of the interaction strengths. The decrease of the absolute value of the negative α_{ij} with trophic position went along with a decrease in the proportion of prey i in the diet of predator j and, to a lesser extent, with a decrease in the energy requirements of the predator $[d_i/(a_j\ p_j)]$ (*13*). This decrease of energy requirements with trophic position is in accordance with the observation that body size and maintenance cost are negatively correlated (*26*) as body size increased with trophic position. The increase in the positive α_{ji} with trophic position went along with an increase in the ratio of the population size of predator j to that of prey i.

Comparison of our results with those obtained in manipulation experiments (*7–11*) shows how the different approaches in analyzing interaction strength may relate to each other. In our study, interaction strength was used in the way May defined it mathematically (*1*), whereas in experiments interaction strength was defined as the impact of species manipulations on food web structure and function. However, when the results of the manipulation experiments are compared with our theoretically constructed estimates of impacts on stability, we see two similarities. First, the occurrence of interactions with negligible impact on stability agrees with experimental findings that only a fraction of the species manipulations had strong effects on food web structure (*7, 8*). Second, the absence of a correlation between the impacts on stability and the feeding rates agrees with the experimental findings that interactions representing a relatively small rate of material flow can have a large impact on stability and interactions representing a large rate of material flow can have a small impact (*8, 11*). This absence of a correlation between energy flow and impact on stability, however, does not negate the importance of energetics to food web stability, as our results demonstrate that energetics determine the patterns in interaction strengths within communities, which form the basis of ecosystem stability.

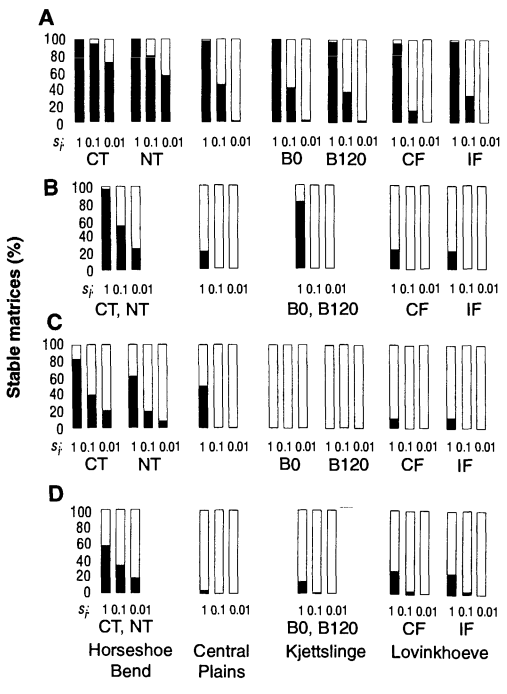

Fig. 3. Probability of the local stability of seven food webs from native and agricultural soils (*12*). Abbreviations are as in (*12*). The black fraction in the bars denotes the percentage of stable matrices based on 1000 runs. In the lifelike matrices (**A**), element values were sampled randomly from the uniform distribution with intervals [0, $2\alpha_{ij}$], in which α_{ij} is the value as derived from the observations (*14*). The diagonal matrix elements referring to intragroup interferences were set at three levels of magnitude (s_i = 1, 0.1, and 0.01) (*17*). In the theoretical matrices (**B**), interaction strengths were sampled from proposed theoretical ranges—that is, [−10, 0] for the per capita effect of a predator on its prey and [0, 0.1] for the per capita effect of a prey on a predator (*3, 18*). In the disturbed matrices (**C**), the lifelike patterns were disturbed by random permutation of the non-zero pairs of elements (*19*). In the test matrices (**D**), values of the parameters used to calculate the feeding rates and interaction strengths were not based on observations but were randomly chosen from the theoretical interval [0, 1] (*20*).

REFERENCES AND NOTES

1. R. M. May, *Nature* **238**, 413 (1972).
2. P. Yodzis, *ibid.* **284**, 544 (1980).
3. S. L. Pimm and J. H. Lawton, *ibid.* **268**, 329 (1977).
4. J. C. Moore, P. C. de Ruiter, H. W. Hunt, *Science* **261**, 906 (1993).
5. P. Yodzis, *Nature* **289**, 674 (1981).
6. S. L. Pimm and J. H. Lawton, *ibid.* **275**, 542 (1978).
7. R. T. Paine, *Ecology* **69**, 1648 (1988).
8. ———, *J. Anim. Ecol.* **49**, 667 (1980).
9. ———, *Nature* **355**, 73 (1992).
10. J. T. Wootton, *Ecology* **75**, 151 (1994).
11. G. A. Polis, *Aust. J. Ecol.* **19**, 121 (1994).
12. Webs are from the Horseshoe Bend Research Site (Athens, GA, USA) with a conventional tillage practice (CT) and a no tillage practice (NT) [P. F. Hendrix *et al.*, *INTECOL Bull.* **15**, 59 (1987)], the shortgrass prairie at the Central Plains Experimental Range (Nunn, CO, USA) (*27*), the Kjettslinge Experimental Field (Örbyhus, Sweden) from a barley practice with no nitrogen fertilizer (B0) and with fertilizer (B120) [O. Andrén *et al.*, *Ecol. Bull.* **40**, 85 (1990)], and the Lovinkhoeve Experimental Farm (Marknesse, Netherlands) from a conventional farming practice (CF) and an integrated farming practice (IF) [P. C. de Ruiter *et al.*, *Plant Soil* **157**, 262 (1993)]. Abbreviations refer to those used in Fig. 3.
13. We calculated the annual feeding rates among organisms by assuming that the annual average production of the organisms balances the rate of loss through natural death and predation, following Hunt *et al.* (*27*):

$$F_j = \frac{d_j B_j + M_j}{a_j p_j}$$

where F_j is the feeding rate, d_j the specific death rate, B_j the average annual population size, M_j the death rate due to predation, a_j the assimilation efficiency, and p_j the production efficiency. For polyphagous predators, the feeding rate per prey type (F_{ij}) was based on the relative abundances of the prey types and on prey preference:

$$F_{ij} = \frac{w_{ij} B_i}{\sum_{k=1}^{n} w_{kj} B_k} F_j$$

where w_{ij} is the preference of predator j for prey i over its other prey types and k is the numerator of the summation over all (n) trophic groups. Calculations of feeding rates began with the top predators (which suffer only from natural death) and proceeded backward to the lowest trophic levels.
14. The dynamics of the trophic groups were described in terms of Lotka-Volterra–type equations, such that

$$\dot{X}_i = X_i[b_i + \sum_{j=1}^{n} c_{ij} X_j]$$

where X_i and X_j represent the population size of groups i and j respectively, b_i is the specific rate of increase or decrease of group i, and c_{ij} is the coefficient of interaction between group i and group j. The dot indicates a derivative by time. Detritus was modeled with a modification of the Lotka-Volterra equation (*4*). Interaction strengths (α_{ij}) were defined as the entries of the Jacobian community matrix (*1*) being the partial derivatives, $\alpha_{ij} = (\partial \dot{X}_i / \partial X_j)^*$, where the asterisk indicates that the partial derivatives are evaluated near equilibrium. Values for the interaction strengths were derived from the energetics (Fig. 1) by equating the death rate of group i due to predation by group j in equilibrium, $c_{ij} X_i^* X_j^*$, to the average annual feeding rate, $-F_{ij}$ (*13*), and equating the production rate of group j due to feeding on group i, $c_{ji} X_j^* X_i^*$, to $a_j p_j F_{ij}$ (*13*). With equilibrium population sizes (X_i^*, X_j^*) assumed to be equal to the observed annual average population sizes (B_i, B_j) (*13*), the per capita effect of predator j on prey i was calculated as

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

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

$$\alpha_{ji} = c_{ji}X_j^* = -\frac{a_j p_j F_{ij}}{B_i}$$

15. The results given for this particular food web are representative for the other food webs, as in all seven webs the negative α_{ij} decreased significantly with trophic position at least at the $P < 0.01$ level, whereas the positive α_{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 α_{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 α_{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 (*1*).
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 $0 \le s_i \le 1$) 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,

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

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.

21. J. C. Moore and H. W. Hunt, *Nature* **333**, 261 (1988).
22. F. Briand, *Ecology* **64(2)**, 253 (1983); J. C. Moore and P. C. de Ruiter, *Agric. Ecosyst. Environ.* **34**, 371 (1991); N. D. Martinez, *Science* **260**, 242 (1993).
23. M. D. Hunter and P. W. Price, *Ecology* **73**, 724 (1992).
24. D. L. DeAngelis, *Dynamics in Nutrient Cycling and Food Webs* (Chapman & Hall, New York, 1992), pp. 148–152.
25. R. Levins, in *Mathematics and the Life Sciences*, D. E. Matthews, Ed., vol. 18 of *Lecture Notes in Biomathematics* (Springer-Verlag, New York, 1977), pp. 153–199.
26. J. Phillipson, in *Physiological Ecology*, C. R. Townsend and P. Calow, Eds. (Blackwell, Oxford, 1981), pp. 20–45.
27. H. W. Hunt *et al.*, *Biol. Fertil. Soils* **3**, 57 (1987).
28. J. C. Moore, D. E. Walter, H. W. Hunt, *Annu. Rev. Entomol.* **33**, 419 (1988).

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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 other 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 frequently 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.

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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.