

are increasing functions, convex because of 'diminishing returns', and close to linear, and that $c(t) \ll h(t)$ —the ratio $c(t)/h(t)$ represents an effective transfer efficiency. Now, consider a strategy of expending an effort t on feeding on herbivores and $1-t$ on feeding on carnivores. Here $0 \leq t \leq 1$. We seek to maximise the total energy gain $h(t) + c(1-t)$ subject to the constraint that the organism expend at least a small effort ϵ in competing with (and incidentally feeding on) potential carnivore prey. Many factors influence ϵ , including territorial behaviour, ability to flee and population density. As long as

$$\left. \frac{dh(\tau)}{d\tau} \right|_{\tau=1-\epsilon} > \left. \frac{dc(\tau)}{d\tau} \right|_{\tau=1-\epsilon}$$

or simply, $h'(t) > c'(1-t)$, for $0 \leq t \leq 1-\epsilon$, this maximum will occur at $t = 1-\epsilon$ (Fig. 1). Therefore, from the above assumptions, if relatively little energy ϵ need be expended for competition, such an organism should adopt the ESS of concentrating (spending effort $1-\epsilon$) on herbivores.

The option of switching to a lower trophic level is not available to first-level carnivores because of nutritional differences between plants and herbivores; herbivores clearly face far stricter constraints. Furthermore, these nutritional requirements arise from synthetic and degradative specialisations which are selectively advantageous. However, a parasite may be subject to different dynamics, and not always select the most numerous host because its host constitutes its entire thermodynamic and spatial environment, and is not a potential competitor under alternative trophic strategies. Thus, on the spatial scale of an individual parasite^{6,7}, a herbivore host might offer no advantages over a carnivore. It is also conceivable, but energetically unlikely, that diminishing returns could make $h'(t_*) = c'(1-t_*)$ for some $t_* < 1-\epsilon$. This yields a mixed strategy^{6,7}, with effort t_* expended on herbivores and $1-t_*$ on carnivores. Finally, the case of concave $h(t)$ or $c(t)$ is also energetically unlikely.

We have shown that in the absence of non-nutritive constraints, grazing food chains should evolve towards the evolutionarily stable length of three. Parasitism and opportunistic feeding allow for some chain lengthening. Longer chains may also exist transiently, possibly being relatively long-lived, or may persist due to special constraints such as size and habitat compatibility of predator and prey. Differences in nutritional value of predators and prey are unlikely to be as significant for protista as for metazoans, but size constraints may be more important. These factors are independent of primary productivity. Further, our argument that optimal foraging subject to biochemical and physiological constraints is an ESS applies to all trophic levels and strategies, independently of the detailed structure of the food web. We therefore predict that the length of food chains will be relatively constant over wide ranges in primary productivity. This agrees well with field data^{4,5}.

We thank Drs John Glasser, Gary Harrison, Robert May and Bernard Patten for helpful conversations. We acknowledge partial support from NSF grant MCS77-01628 (H.M.H) and a visiting appointment in the Department of Mathematics and Institute of Ecology at the University of Georgia (H.M.H.) during which this research was done.

Received 31 May; accepted 24 October 1979.

- Hutchinson, G. E. *Am. Nat.* **93**, 145-159 (1959).
- Odum, H. T. & Odum, E. P. in *Fundamentals of Ecology* (ed. Odum, E. P.) 2nd edn 43-87, 3rd edn, 37-85 (Saunders, Philadelphia, 1959).
- Slobodkin, L. *Growth and Regulation of Animal Populations*, 159 (Holt, Reinhart and Winston, New York, 1961).
- Cohen, J. E. *Food Webs and Niche Space* (Princeton University Press, 1978).
- May, R. M. in *Population Dynamics* (eds Anderson, R. M., Turner, B. D. & Taylor, L. R.) (Blackwell, Oxford, 1979).
- Maynard-Smith, J. & Price, G. R. *Nature* **246**, 15-18 (1973).
- Maynard-Smith, J. *Am. Scient.* **64**, 41-45 (1976).
- Pimm, S. L. & Lawton, J. H. *Nature* **268**, 329-331 (1977).
- Saunders, P. T. *Nature* **272**, 189-190 (1978).
- MacArthur, R. H. & Pianka, E. R. *Am. Nat.* **100**, 603-609 (1966).

Male lions in large coalitions gain reproductive advantages

J. David Bygott*, Brian C. R. Bertram† & Jeannette P. Hanby*

* Sub-Department of Animal Behaviour, Madingley, Cambridge, UK
 † Research Centre, King's College, Cambridge, UK

Cooperation between two or more individuals has been shown to yield short-term benefits in several vertebrate species¹⁻⁴, and various hypotheses have been developed to explain the evolution of cooperative behaviour⁵⁻⁷. However, until now there has been no evidence to show that such cooperation actually does confer lifetime's reproductive advantages on more than one member of the coalitions concerned^{8,9}. Long-term studies of wild lions (*Panthera leo* L.) have now provided such evidence. We show that, compared with singletons and pairs, male lions in groups of three or more can more reliably gain tenure of female prides, retain tenure for longer, mate with more different females, and produce more surviving offspring; thus each individual has higher fitness through cooperation.

Lions were observed in the Serengeti National Park and in the adjacent Ngorongoro Conservation Area, Tanzania, in 1966-69 by G. B. Schaller²; in 1969-73 by B.C.R.B.^{10,11}; and in 1974-78 by J.D.B. and J.P.H.¹². Observations on the same prides in comparable habitats were spread over periods of 3-12 years. All members of these prides were known individually by natural markings¹³.

A lion pride is a matrilineal group of 2-18 (mean 6)^{2,12,14} genetically related females, plus their cubs. Young male lions usually leave their natal pride as a group of relatives shortly before sexual maturity. Then, as a coalition, they gain and retain sole possession of a pride for a variable period, excluding rival male groups. The male group's tenure, and therefore its effective reproductive life¹⁰, typically ends when they are displaced from their pride and their area by a new group of males. Here we compare aspects of the reproductive success of the male groups of different sizes.

Table 1 The frequency of male lion groups of different sizes, and the probability that they will have tenure of a pride of lionesses

No. of males in group	No. of male groups		Probability of having tenure	Significance of difference
	Total	No. which had tenure		
1	23	4	17.4%	} <0.01
2	39	23	59.0%	
3	12	11	91.7%	
4	4	4	100.0%	
5	1	1	100.0%	
6	3	3	100.0%	
7	1	1	100.0%	

Total 183 adult males (that is, ≥ 4 yrs old), observed in the Serengeti region over more than 2 yrs during 1969-78.

Table 1 shows that single males in the Serengeti region were rarely successful in gaining tenure of a pride (4/23), whereas pairs quite often were (23/39 pairs); large groups (3 or more males) were almost always in possession of a pride (20/21 groups).

Having gained tenure, large male groups were also more successful in retaining it. Data henceforth refer to 25 male

groups. Figure 1a shows that compared with pairs (mean tenure 18 months), groups of 3 males stayed at least 2.3 times as long, and groups of six males stayed over 3.8 times as long with their prides. Note that the tenure periods of all the large groups (but of only some of the small groups) are underestimated because they extended beyond the beginning or end of the observation periods; thus the differences shown are conservative.

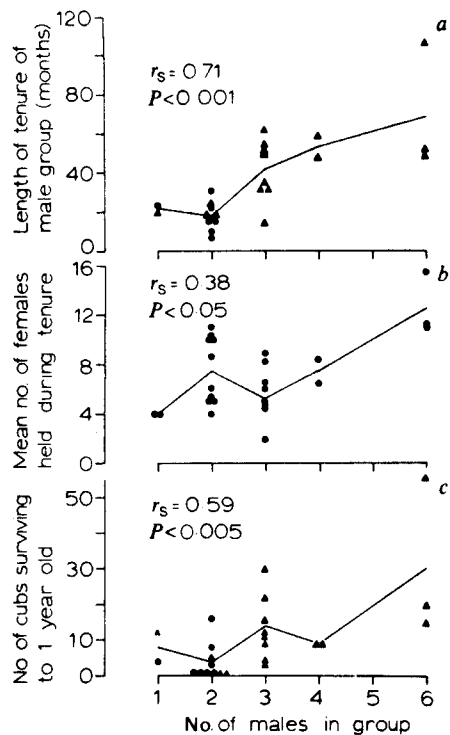


Fig. 1 Aspects of the reproductive success of male lion groups of different sizes. *a*, The numbers of months that each group retained tenure of a pride or prides in the study area. *b*, The mean numbers of females concurrently in the possession of the male groups, averaged over their observed period of tenure. *c*, The total numbers of cubs fathered during the male groups' tenure which survived to 1 yr old (by which age 77% of cub mortality has occurred¹⁰). \blacktriangle , Points which are minimum figures because the male groups' periods of tenure extended beyond the beginning or end of the study period; \bullet , points which are not underestimates.

Large male groups, especially after staying with one pride for about 2 years, may gain access to one or more neighbouring prides as well. Their concurrent tenure of several prides gives them access to more oestrous females. Figure 1b shows that in general only the very largest male groups (>4) held appreciably more females concurrently. They did so not by holding larger prides but by holding two or more at the same time.

When a lioness comes into oestrus (lasting 2–5 d), any male in the group consorts alone with her, mating repeatedly. Having companions should subdivide a male's share of consortships; however, the available data show no significant negative correlation between the number of males in a group and their consortship scores ($n = 50$, $r_s = +0.14$, $P > 0.2$). Consortship scores were calculated as a percentage of total sightings, excluding males sighted fewer than 10 times. For 50 males, $\bar{x} = 19.6\%$, $s.d. = 8.6$).

There is no detectable hierarchy within male groups^{2,14}, all partners sharing their mating duties with remarkable equity. For example, no male was seen consorting more than 2.7 times as often as his partner(s), and in the most often observed group of 6 males ($\bar{x} = 81$ sightings of each male) no male was involved in >22% or <9% of all consortships seen. Overall, the difference

between consortship scores was smaller and far less variable between members of the same coalition ($\bar{x} = 7.6$, $s.d. = 5.6$, $n = 62$) than between members of different coalitions ($\bar{x} = 11.0$, $s.d. = 26$, $n = 1,138$; F test $P < 0.001$).

A female may sometimes change consorts during her oestrous period, and thus mate with more than one male. There are no indications that particular males are likely to be in consort with her at particular times during her oestrus. Copulation may occur as frequently as every 15 min, so only a minute proportion of copulations (<1%) leads to the birth of cubs^{2,10}. Hence, unlike some species^{15,16}, for lions the number of copulations would not provide a reliable indicator even of short-term reproductive success. Nor would the number of litters born, because cub mortality is high and because high mortality of lion cubs raises the birth rate¹⁰.

The best measure of lifetime reproductive success is the number of surviving offspring produced. Figure 1c shows that the total number of cubs surviving to 1 year old is correlated with their fathers' group size ($r_s = 0.59$, $P < 0.005$). The effect is achieved mainly by staying for longer and so fathering more cubs, rather than by improving their probability of survival. Nonetheless, some cub mortality is associated with male takeovers^{10,14}, caused by the new males killing or excluding some of their predecessors' offspring. Long tenure defers and so reduces this mortality.

We have shown above that larger groups as a whole do better. Figure 2 shows that, assuming equally shared paternity, each individual male in a large group achieves greater expected lifetime's reproductive success (that is, has greater fitness) than he would have achieved in a small group. Comparing the fitness

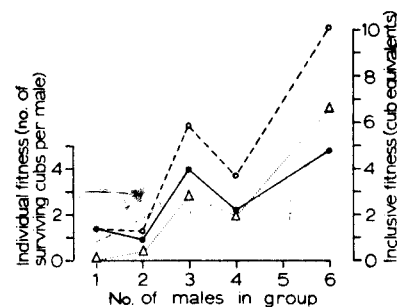


Fig. 2 Individual fitness and inclusive fitness of individual male lions in groups of different sizes. The line for mean individual fitness (\bullet) is derived from Fig. 1c assuming equally shared paternity of the cubs born during the males' tenure, and multiplying by the different probabilities of achieving tenure at all (from Table 1). The line for a male's mean inclusive fitness (\circ) is the sum of first, the number of cubs he has fathered (that is, his mean individual fitness) and second, the number of cubs fathered by his companions multiplied by 0.22 (that is, devalued by their coefficient of relatedness to him). The lowest line (\triangle) shows the inclusive fitness of a male who fathers no cubs of his own.

of males in large groups of 3 or more ($n_1 = 13$ groups) with that of males on their own or in pairs ($n_2 = 12$), the 3.8-fold difference is highly significant ($P = 0.001$, Mann-Whitney U -tests). The advantage does not continue to increase: thus the males in the few (5) very large groups (≥ 4 males) do not have higher fitness than the males in groups of 3.

The male lions in a coalition are generally relatives: it has been calculated¹⁴ that a male's average degree of relatedness to his companions is 0.22, and that this is almost independent of group size. Cubs fathered by other males in the group also contribute to his inclusive fitness^{5,17}. We ignore for present purposes the common increment to inclusive fitness produced by the reproduction of all other relatives everywhere, and consider only the contribution by other members of the male group. It can

generally be assumed that a male forms a coalition with similar-age relatives if he has them. (This was true of 19 out of 21 coalitions whose origins were known; the other two cases were a pair of strangers and a trio of two brothers and a stranger.) The inclusive fitness of each male can thus be calculated, and is illustrated in Fig. 2. There is a marked increase in the inclusive fitness of a male the more related companions he has, such that the inclusive fitness of a male in a large group is 5.7 times that of a lone male or of one of a pair. The initial individual advantage gained through cooperation is amplified through kin selection^{5,14,17}.

We have assumed in our calculations that paternity (like consortships) is shared equally by all members of a coalition; naturally this is not certain, nor can it be tested in wild populations. However, it can be shown that even if paternity were unequally shared, the inclusive fitness of every member of a large kin-related coalition would still exceed that of a lone male or one of a pair. In the most extreme and improbable case, although a male might sire no cubs of his own, his support of the coalition would enhance the survival of his relatives' cubs. Other things being equal, this would therefore be a better genetic strategy for him than leaving the coalition (Fig. 2).

If members of large groups generally enjoy higher reproductive success, why do not all male lions form large coalitions? It is apparently difficult to form a successful coalition, probably because the bonds necessary have to be developed early in life. Although single unrelated males can sometimes form stable pairs eventually, they seem unable to form or join larger groups, which are intolerant towards strangers. Thus the size of male groups is determined by lion prides' ability to produce and rear male offspring. The small litter size (mean 2.5 cubs¹⁰), overall even sex ratio², and high (~75%) cub mortality^{2,10,12} mean that a large male peer group can reliably result only if a considerable number of lionesses in a large pride give birth synchronously. There are indications that prides in fact manage to produce large groups of young males more often than expected (J.D.B. and J.P.H., unpublished data), and how they do so is being investigated. Why they do so is now clear: females who manage to produce large groups of male cubs produce through their disproportionately many grandcubs. Previous cooperation by their mothers (in synchronising births¹⁰ and in rearing cubs cooperatively^{2,10}) is a prerequisite for the high lifetime's reproductive success of male lions cooperating in large coalitions.

We thank the Government of Tanzania and the Serengeti Research Institute for permissions and facilities; the NERC, Royal Society and African Wildlife Leadership Foundation (B.C.R.B.), and the SRC and New York Zoological Society (J.D.B. and J.P.H.) for financial support; Dr G. B. Schaller for some early records; and Drs P. P. G. Bateson, R. I. M. Dunbar, G. A. Parker, D. I. Rubenstein and R. W. Wrangham for comments.

Received 25 June; accepted 23 October 1979.

1. Packer, C. *Nature* **265**, 441-443 (1977).
2. Schaller, G. B. *The Serengeti Lion* (Chicago University Press, 1972).
3. Kruuk, H. *The Spotted Hyena* (Chicago University Press, 1972).
4. Emlen, S. T. in *Behavioural Ecology: An Evolutionary Approach* (eds Krebs, J. R. & Davies, N. B.) (Blackwell, Oxford, 1978).
5. Hamilton, W. D. *J. theor. Biol.* **7**, 1-52 (1964).
6. Maynard Smith, J. & Ridpath, M. G. *Am. Nat.* **106**, 447-452 (1972).
7. Trivers, R. L. *Q. Rev. Biol.* **46**, 35-57 (1971).
8. Hrdy, S. B. *The Langurs of Abu* (Harvard University Press, 1978).
9. Watts, C. R. & Stokes, A. W. *Scient. Am.* **224**, 112-118 (1971).
10. Bertram, B. C. R. *J. Zool., Lond.* **177**, 463-482 (1975).
11. Bertram, B. C. R. *E. Afr. Wildl. J.* **11**, 215-225 (1973).
12. Hanby, J. P. & Bygott, J. D. in *Serengeti: The Dynamics of an Ecosystem* (eds Sinclair, A. R. E. & Norton-Griffiths, M.) (Chicago University Press, in the press).
13. Pennycook, C. J. & Rudnai, J. *J. Zool., Lond.* **160**, 497-508 (1970).
14. Bertram, B. C. R. in *Growing Points in Ethology* (eds Bateson, P. P. G. & Hinde, R. A.) (Cambridge University Press, 1976).
15. LeBoeuf, B. J. *Behaviour* **41**, 1-26 (1972).
16. Gibson, R. M. & Guinness, F. E. *J. Anim. Ecol.* (in the press).
17. Wilson, E. O. *Sociobiology* (Belknap, Harvard, 1975).

Inhibition of mixed lymphocyte response by monoclonal antibody specific for a rat T lymphocyte subset

Michael Webb, Donald W. Mason & Alan F. Williams

MRC Cellular Immunology Unit, Sir William Dunn School of Pathology, University of Oxford, Oxford, UK

Cell-surface differentiation antigens which are associated with particular lymphocyte subsets are likely to be molecules which mediate specific functions of the cells which display them. One way to investigate this hypothesis is to see whether antibodies directed against such antigens will inhibit functional systems. This approach can be attempted with confidence if monoclonal antibodies are used, as these react with one antigenic determinant only and can be used in purified form. In this report we show that a monoclonal antibody which is specific for a subset of rat T lymphocytes inhibits the mixed lymphocyte response (MLR). The antibody acts on the responder cells without killing them.

The W3/25 mouse monoclonal antibody is specific for thymocytes and a subset of T lymphocytes in the rat and the cells in thoracic duct lymph that express the target antigen mediate helper and graft-versus-host functions^{1,2}. The W3/25 antigen is relatively sparsely represented on the cell membrane as only about 15,000 molecules of W3/25 antibody are bound at saturation to thymocytes or T cells, yet more than 5×10^5 anti-Thy-1.1 antibodies bind per rat thymocyte¹.

The effect of W3/25 IgG on the MLR is shown in Fig. 1. In these experiments 2×10^5 lymph node cells from PVG/c (RT1^c) rats were used as responders to 5×10^5 irradiated spleen cells from the congenic strain HO.B2 (RT1^u) in 0.2 ml cultures as described by Antczak *et al.*³. The W3/25 antibody was added to the cells at the start of the culture period and 0.5 μ Ci of tritiated thymidine (³H-TdR) were added after 72, 96 or 120 h in culture. After a further 18 h the cells were assayed for incorporated label. All assays were carried out in triplicate. Concentrations of W3/25 IgG up to 2.5 ng ml⁻¹ in 0.2 ml gave no inhibition but at a concentration of 25 ng ml⁻¹ the antibody reduced incorporations of ³H-TdR to a plateau level which was not affected by further increases in antibody concentration. We have observed this inhibition without exception in nine experiments where W3/25 antibody was added to MLRs. In 21 independent observations spread throughout these experiments the mean incorporation of fully inhibited cultures compared with control MLRs was 18.2%, standard deviation 7.3%. Within any one experiment the inhibition became greater, relative to a control MLR, with time up to 120 h. The inhibition was not confined to MLRs with PVG/c versus HO.B2 cells but was also seen in the reverse combination (see also Table 2) and in two other strain combinations which were tested (AO versus DA and PVG/c versus DA).

Other monoclonal antibodies were tested, including W3/13 antibody, which labels all T cells but not B cells¹; MRC OX 1 antibody, which labels all leukocytes⁴ and a monoclonal mouse IgG anti-Thy-1.1 antibody called MRC OX 7 (W. R. McMaster, unpublished) which labels thymocytes but only a small proportion of peripheral T cells in the rat⁵. These antibodies all bind at levels per labelled cell which are at least 2.5 times greater than W3/25 antibody, yet none inhibited the MLR, and W3/13 antibody gave a consistent stimulation of ³H-TdR incorporation (data for W3/25 and W3/13 in Fig. 1; that for MRC OX 1 and MRC OX 7 not shown). For W3/25 and W3/13 antibodies, the extent of binding was checked at 37 °C and greater than 90% saturation was achieved with the same assay conditions used for the MLR at 25 ng ml⁻¹ for W3/25 and 5 μ g ml⁻¹ for W3/13 antibody (D. W. M., unpublished). Furthermore, W3/13 antibody failed to have an inhibitory effect even at a concentration