Serengeti Lions

largest component of variation in seed size occurs between species. Is the adaptive problem of seed size (for individuals of a particular species) dominated by competition with conspecifics or with other species? And does the answer affect the level of variation expected within species? We now have reasons to believe that variation in seed size need not be maladaptive. But does the observed distribution of sizes within species distinguish adaptive from nonadaptive variation? A good model need not provide all the answers if it succeeds in reframing the questions.

David Haig

Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA

References

1 Westoby, M., Jurado, E. and Leishman, M. (1992) **Comparative evolutionary ecology of seed size,** *Trends Ecol. Evol.* 7, 368–372

2 Michaels, H.J. *et al.* (1988) **Seed size variation: magnitude, distribution, and ecological correlates,** *Evol. Ecol.* 2, 157–166

3 Smith, C.C. and Fretwell, S.D. (1974) **The optimal balance between size and number of offspring,** *Am. Nat.* 108, 499–506

4 Geritz, S.A.H. (1995) **Evolutionarily stable seed polymorphism and small-scale spatial variation in seedling density,** *Am. Nat.* 146, 685–707

5 Tilman, D. (1994) **Competition and biodiversity in spatially structured habitats,** *Ecology* 75, 2–16

Cooperative lions escape the Prisoner's Dilemma

Lions (*Panthera leo*) are an emblem of cooperation for many people: males united in protecting their pride, females defending their cubs and their territory in exemplary solidarity. This image persists despite empirical work over the past 15 years demonstrating that lion cooperation is more complex, subtle and context-dependent than the distorted representations of the 'Lion King'. The most recent work to emerge from the Serengeti lion population in Tanzania, East Africa, reveals the most disturbing truth yet: lionesses 'cheat' on their pridemates when defending the pride territory against intruding females[1]. This is the latest finding in a productive series of studies using playbacks of recorded lion roars to simulate different levels and types of territorial intrusions[1–3]. Two new papers examine the mechanisms of cooperation in group-territorial lionesses[1] and in coalitions of male lions[2]. They illustrate the difficulty of matching empirical work to existing theoretical models for cooperation.

The evolutionary basis for cooperation has received much theoretical attention since the theories of kin selection and reciprocal altruism emerged in the 1960s and 1970s. Cooperation between non-relatives remains the greater puzzle, and the most popular metaphor for the problem has been the two-person Prisoner's Dilemma game[4]. A strong temptation to exploit a cooperative protagonist together with a low (sucker's) payoff for being exploited oneself makes defection the best solution to any round of the game. However, if a pair of individuals play each other repeatedly (Iterated Prisoner's Dilemma – IPD) cooperative strategies can evolve under certain conditions. Participants must interact a large but unknown number of times, no information can be exchanged during encounters, and participants must be able to 'score-keep' and 'punish' defectors. Consequently, they base their decision for each round of the game on the history of past encounters[4].

The best known strategy, tit-for-tat (TFT), came to prominence in a computer tournament. Tit-for-tat strategists begin by cooperating, but retaliate against cheating by withholding further cooperation[4]. However, TFT players are not invulnerable: participants may be locked into a series of mutual defections by mistakes. Also, a population of TFT players can be invaded passively by individuals who always cooperate, and this population in turn can be invaded by unconditional defectors[5]. Pavlov is a more robust strategy: pavlovians cooperate if the previous round was either mutual defection or mutual cooperation, but they will continue to defect if their partner cooperates persistently. Therefore, Pavlov strategists accommodate occasional mistakes and are able to exploit unconditional cooperators[5].

Considerable work has gone into refining and extending models dealing with the IPD, possibly at the expense of other approaches to cooperation[6]. For example, theoreticians have questioned whether any strategy can be a pure evolutionary stable strategy (ESS)[7], tested the performances of new strategies in the game[5], and investigated the effects of different degrees of mobility by participants and nonrandom interactions on game outcomes[8]. Empirical work has lagged behind. Evidence for reciprocity has come from a variety of taxa but the data have been received with some scepticism. The most contested example, predator inspection by fish, is claimed to be a case of the IPD where participants in the game play TFT[9]. Critics have suggested that selfish grouping effects[10,11] or predator deterrence[12] are more plausible explanations.

Evidence from a long-term study of the Serengeti lions by Craig Packer and his colleagues indicates that, contrary to popular belief, lions do not live in groups because of the benefits of communal hunting[13]. Female-grouping patterns are best explained as facilitating cooperative defence of cubs against infanticidal males and defence of territory against other females[13]. Males form coalitions (with relatives or non-relatives) and cooperate to take over and maintain residence in a pride[2]. However, while animals may be in social groups for other reasons, they could still hunt in groups if there are mutualistic advantages in doing so[14]. For example, lions are more likely to participate in hunts of large or hard-to-catch prey[14,15], when the involvement of an additional hunter markedly improves the probability of capture. A lion will only join in a hunt for short-term benefits; reciprocity is not involved[15].

Lions advertise territory ownership by roaring[2,3]; territorial intrusions can be simulated by playing the recorded roars of strangers to the residents. Females respond to female intruders in a risk-sensitive manner: they are less likely to approach when the odds (ratio of challengers to defenders) are unfavourable[3]. Lionesses approach in single-file, and individuals at the front of the response expose themselves to a greater risk of attack and injury than those at the back, although all members of the group benefit from successfully repelling the intruders[1]. This situation resembles an IPD: defecting (lagging behind) while your partner cooperates (goes forward) results in the highest payoff, but mutual defection is less rewarding than mutual cooperation. Being at the front of the response while your partner lags behind incurs the sucker's payoff[1].

In repeated playbacks to the same prides over two years, Heinsohn and Packer[1] found that individuals consistently led or lagged in the playback response. The position of a lioness did not depend on age, body size, relatedness to pridemates or dominance (there is no discernible dominance hierarchy in lions). The authors exploited the fission–fusion nature of lion prides, and conducted playbacks on pairs of lionesses to test whether cooperation was maintained by reciprocity in a two-person game. They played recorded roars to pairs where known leaders were matched first with another leader and then with a laggard. The leading lioness approached the speaker more slowly and looked back to check on her companion more often if her companion was a laggard, suggesting that the leader recognized that her partner was a cheat from previous territorial conflicts. However, the leader continued to go forward to meet the enemy (and incur the sucker's payoff) instead of 'punishing' her defecting partner by refusing to cooperate. Therefore, she used neither of the two best strategies in an IPD, neither TFT nor Pavlov, since both punish cheaters by withholding cooperation. These experiments indicated that group-territoriality in lionesses is not maintained by reciprocity, despite their ability to recognize whether the other animal is a cheater or not.

The IPD assumes that payoffs to the participants in each round of the game do not depend (and have no effect) on the payoff to the other participant[4,16]. However, players may need each other in future rounds of the game[16]. Lionesses need companions to maintain their long-term territory, to collaborate in the communal rear-ing and defence of cubs, and to hunt large prey[1,13]. Laggards should not place their leading companions at too much risk, since loss of pridemates will rebound as a long-term cost to the laggard. In another sequence of playbacks, Heinsohn and Packer[1] manipulated the odds of the contest by playing the roars of one or three unfamiliar lionesses to residents. They predicted that laggards should lag less when the odds are unfavourable and the danger to the leading individuals increases. In fact they found diverse and unexpected behavioural strategies: a quarter of the laggards upheld the prediction, a quarter lagged more when the risk to companions increased, and half did not vary their lagging behaviour according to the odds.

Complementary work on male coalitions revealed that males are also sensitive to the odds but are more likely to approach intruders than females are, even when the odds are unfavourable[2]. Males leave their natal pride at independence, often in cohorts with close relatives. Singletons and pairs may team up with an unrelated male before gaining residence (and mating opportunities) in another pride. Acquiring and maintaining residence in a pride is the only way for males to father young[2]. When playbacks were opportunistically conducted to a single male temporarily separated from his coalition, he still went forward despite the opportunity to avoid the risk of conflict and defect without discovery by his partner(s). Grinnell *et al.*[2] argued that the best strategy for a resident male is to go forward regardless of the response (or presence) of his companions, since losing residency may jeopardize his entire lifetime reproductive success (LRS). Larger coalitions are more successful at acquiring and maintaining residency and a single male has no chance at all. Therefore the survival of each male in the coalition has an impact on every other male. Once again, the payoffs to individuals are influenced by the payoffs to their game partners[16].

Aside from kin selection, cooperation has been categorized into three non-exclusive types: group-selected behaviour, reciprocity and mutualism[6]. Yet theoretical attention has focused disproportionately on reciprocity, especially within the bounds of the IPD, even though other paradigms such as 'coalition games'[11] have been proposed. Although the IPD is a useful metaphor for thinking about cooperation, it has major limitations, particularly when considering cooperation in social groups. The game insists that no information is exchanged during each round, when in fact individuals probably monitor each other constantly during cooperative interactions. For example, lionesses continue to check the behaviour of group members during the response to a territorial intrusion[1-3]. Second, cooperation within groups is often not a simple two-person game. Third, for group-living animals the payoffs to participants depend partly on the payoffs allowed to the other participant(s) in the game[16], as exemplified by male lions[2]. Because of these limitations, empirical evidence for reciprocity invariably attracts scepticism[10-12] since efforts to explain data in the context of models like TFT are likely to be unsatisfying. The recent papers on cooperation (and the lack of it) in lions[1,2] show clearly that the IPD and its solutions are not necessarily the appropriate paradigm for cooperation. Perhaps lions are finally escaping the Prisoner's Dilemma?

Acknowledgements

Thanks to Rob Heinsohn and Craig Packer for making their manuscript available to me before publication, and Andrew Cockburn and Janet Gardner for helpful comments.

Sarah Legge

Evolutionary Ecology Group, Division of Botany and Zoology, Australian National University, Canberra, ACT, 0200, Australia

References

1 Heinsohn, R.G. and Packer, C. (1995) **Complex cooperative strategies in group-territorial African lions,** *Science* 269, 1260–1262

2 Grinnell, J., Packer, C. and Pusey, A.E (1995) **Cooperation in male lions: kinship, reciprocity or mutualism?** *Anim. Behav.* 49, 95–105

3 McComb, K., Packer, C. and Pusey, A. (1994) **Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*,** *Anim. Behav.* 47, 379–387

4 Axelrod, R. and Hamilton, W.D. (1981) **The evolution of cooperation,** *Science* 211, 1390–1396

5 Nowak, M. and Sigmund, K. (1993) **A strategy of win–stay, lose–shift that outperforms tit-for-tat in the Prisoner's Dilemma game,** *Nature* 364, 56–58

6 Dugatkin, L.A., Mesterton-Gibbons, M. and Houston, A.I. (1992) **Beyond the Prisoner's Dilemma: toward models to discriminate among mechanisms of cooperation in nature,** *Trends Ecol. Evol.* 7, 202–205

7 Boyd, R. and Lorberbaum, J.P. (1987) **No pure strategy is evolutionarily stable in the repeated Prisoner's Dilemma game,** *Nature* 327, 58–59

8 Ferriere, R. and Michod, R.E. (1995) **Invading wave of cooperation in a spatial iterated Prisoner's Dilemma,** *Proc. R. Soc. London Ser. B* 259, 77–83

9 Milinski, M. (1987) **TIT FOR TAT and the evolution of cooperation in sticklebacks,** *Nature* 325, 433–435

10 Lazarus, J. and Metcalfe, N. (1990) **TIT FOR TAT in sticklebacks: a critique of Milinski,** *Anim. Behav.* 39, 987–989

11 Noe, R. (1990) **A Veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation,** *Anim. Behav.* 39, 78–90

12 Godin, J-G.G. and Davis, S.A. (1995) **Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit,** *Proc. R. Soc. London Ser. B* 259, 193–200

13 Packer, C., Scheel, D. and Pusey, A.E. (1990) **Why lions form groups: food is not enough,** *Am. Nat.* 136, 1–19

14 Packer, C. and Ruttan, L. (1988) **The evolution of cooperative hunting,** *Am. Nat.* 132, 159–198

15 Scheel, D. and Packer, C. (1991) **Group hunting behaviour of lions: a search for cooperation,** *Anim. Behav.* 41, 697–709

16 Lima, S.L. (1989) **Iterated Prisoner's Dilemma: an approach to evolutionarily stable cooperation,** *Am. Nat.* 134, 828–834