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Maynard Smith J & Parker G A. The logic of asymmetric contests. *Anim. Behav.* 24:159-75, 1976.

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If two animals are competing for some resource (e.g., a territory), and if there is some discernible asymmetry (e.g., between an "owner" and a later animal), then it is evolutionarily stable for the asymmetry to settle the contest conventionally, without fighting. [The *SCI*® indicates that this paper has been cited in over 330 publications.]

Do Animals Respect Ownership?

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In 1973 George R. Price and I published a paper¹ arguing that the theory of games, originally conceived by Von Neumann and Morgenstern as a method of analysing human conflicts, could usefully be applied to animals. At first sight this was unexpected, because the central assumption of classical game theory was that people behave rationally, whereas we made no such assumption about animals: in our theory, natural selection replaces reason. One prediction of that theory was that one would expect to find animals adopting "mixed strategies," doing sometimes one thing and sometimes another. After the paper appeared, I learnt that Geoff Parker had already shown that the dung flies he had studied for his PhD were behaving in precisely the way predicted by our theory. This led me to contact Parker and to our joint paper on asymmetric contests.

We were both convinced that, if one is to understand what animals do, one must take into account not only what they want to do (technically, their motivations), but also what they are capable of doing (technically, the set

of possible "strategies"). This may seem so obvious as not to need saying, but in those days it did. For ethologists, everything must be explained by differences in motivation. I was once driven to point out that, if a cheetah chases and kills an antelope, it would be silly to say that the antelope did not escape because it did not want to.

The result that interested us most at that time, and that has interested students of behaviour ever since, was our apparently paradoxical finding that asymmetries in size, age, sex, or ownership can be used as conventional cues to settle conflicts, without escalated fighting. This is true even if the asymmetry does not alter the value of the resource or the likelihood of winning an escalated fight. It is almost as if animals could toss a coin to decide who is the winner. I think that one reason our paper has been cited so often is that field workers would like to show that we were wrong. There seems little doubt that "ownership"—that is, prior occupancy of a territory or of some other resource—does settle contests without escalation. Great efforts have been made to show that, in such cases, the value of the resource is greater to the owner. Sometimes this is true, and sometimes it isn't, but in any case it is usually irrelevant, because ownership would settle the contest even if there was no difference in value.

There is also extensive data to show that asymmetries of size often settle contests conventionally and that displays have evolved that reveal to the contestants any difference in size. For example, funnel-web spiders fight over webs. Early in a fight they vibrate the web, and this reveals any difference in mass that may exist: the smaller spider then retreats. A potential loser can be converted into a winner by gluing a small lead weight to its back. In birds, contests are sometimes settled by differences in plumage brightness, and it is at least possible that these differences have evolved because they provide a conventional cue and so reduce the likelihood of escalated fights.^{2,3}

1. Maynard Smith J & Price G R. The logic of animal conflicts. *Nature* 246:15-8, 1973. (Cited 365 times.)
2. Maynard Smith J. *Evolution and the theory of games*. Cambridge, England: Cambridge University Press, 1982. 224 p. (Cited 390 times.)
3. Maynard Smith J & Harper D G C. The evolution of aggression: can selection generate variability? *Phil. Trans. Roy. Soc. London B* 319:557-70, 1988.

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