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Decision Making: Solving the Battle of the Fishes

A key question about animal group decision making is which conditions promote shared or unshared decisions. A recent experiment on sticklebacks demonstrates a compromise solution: turn-taking.

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Imagine a situation where a woman and a man would like to go out together rather than each going out alone because they disagree over where to go: to the ballet or to a football match. This classic scenario of the 'battle of the sexes' game [1] has hitherto received little attention when it comes to exploring the evolution of cooperation. In this issue of *Current Biology*, Harcourt and colleagues [2] describe an ingenious experiment on three-spined sticklebacks in which pairs are confronted repeatedly with a battle-of-the-sexes problem. Sticklebacks solve the conflict of interest by taking turns in leading the partner to the respective preferred sites, much like humans do [3].

Theoreticians typically explore cooperation using the iterated prisoner's dilemma game [4]. In this two-player game, partners can either cooperate or defect. Mutual cooperation yields a higher payoff than mutual defection but defecting yields higher payoffs than cooperating in each single round, independently of the partner's behaviour. This payoff structure causes maximal conflict of interest between potential partners. However, conflicts may be reduced in many potentially cooperative interactions where joint actions are invariably superior to mutual defection. The prime example are species living in groups where individuals are selected to stay together even though individuals may disagree over activity and movement patterns. Such disagreements naturally emerge as a consequence of different dietary needs and different optima for the trade-off between foraging efficiency and the risk of predation, depending on age or sex [5]. The battle-of-the-sexes game captures the key problem of such situations.

Recently, the question of how group decisions are made has received immense interest, providing both major conceptual advances and new empirical evidence [6]. Nevertheless, some classic studies are worth mentioning as they are easily overlooked. For example, a long-term field study on hamadryas baboons demonstrated both individual leadership and majority-voting [7,8]: males coerce their harem females into following [7], while male harem owners voted at which waterhole they would meet later in the day before splitting up when leaving the common sleeping places [8]. A study on bar-headed geese demonstrated that an individual's competence may also be important (parents lead when the goslings are still very young), while under certain circumstances an individual's need for food (females prior to the reproductive period, and older nestlings in their important growth phase) may make it a leader in the group [9,10].

Based on the geese data, Lamprecht [11] developed the first conceptual ideas about the emergence of leadership by combining the battle-of-the-sexes game with the 'war-of-attrition' game [12]. In this latter game, individuals compete over a resource by investing time in order to obtain it, and an individual emerges as the winner if it is willing to persist longer (i.e. to incur greater costs) than its opponent does. The combination of the two games resolves a major limitation of the original battle-of-the-sexes game, which is that partners cannot communicate. In the framework, an individual emerges as leader if it can accept larger separation distances than the partner, because it values the proximity of a partner less or values the access to another resource more than its partner does. The idea that variation in needs may lead to persistent leadership was also supported in much more formal mathematical terms [13].

The key question in recent years has been under which circumstances group decisions are shared or unshared [6,13–17]. Empiricists working on large anonymous aggregations predominantly found evidence for shared decision making [15], while evidence on small structured groups like hamadryas baboon harems or geese families suggests scope for unshared decisions. Clearly, what is needed at this stage are controlled experiments to identify key parameters that may favour either shared or unshared decision making. The studies on stickleback pairs by Harcourt and colleagues [2] provide a prime example of what can be learned from such experiments. In a recent study, they found that bolder stickleback individuals tend to make unshared decisions about foraging excursions when a pair faces the trade-off between foraging and safety and hence have to decide when to go foraging [18]. In the current study [2], they additionally created a conflict of interest over where to go, effectively creating a battle-of-the-sexes problem. Under these circumstances, variation in boldness became unimportant. Instead, turn-taking emerged as the solution under these new conditions.

First, fish were individually trained to locate food at one of two possible positions. Then individuals that had learned opposing locations were paired. During the experiments, no food was present and individuals could monitor each other's movements. Under these conditions, each individual initiated excursions to the food site it had been trained to visit. The probability that the partner followed was highest if the fishes alternated visits between the two food sites. Thus, turn taking in leadership was crucial to achieve high levels of coordination. The emergence of turn-taking is particularly surprising as the level of conflict over where to go was actually rather low: each fish would inspect both sites regularly even in the absence of the partner, with less than overall 60% of excursions to the baited site.

In conclusion, the key merit of the study by Harcourt *et al.* [2] lies in the ingenious general design of an experimental setup that allows the variation of potential key variables and to test how this variation affects group decision making. Until now, the setup has been used to test coordination between two individuals that can communicate through monitoring each others' movements. However, with some imagination one could vary the experimental setup by reducing the ability to communicate and, even more interestingly, by increasing group size and then test how decisions are made depending on the nature of conflict. Also, the setup seems to be adaptable to other taxa. No doubt that further exciting new evidence will come soon.

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