NEWS & VIEWS

Born leaders

In animals that live in groups, some individuals are leaders and others are followers. A modelling study shows that variation in leadership evolves spontaneously and need not be related to differences in knowledge or power.

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Social animals face a dilemma. To reap the benefits of group living, they have to stay together. However, individuals differ in their preferences as to where to go and what to do next. If all individuals follow their own preferences, group coherence is undermined, resulting in an outcome that is unfavourable for everyone. Neglecting one's own preferences and following a leader is one way to resolve this coordination problem. But what attributes make an individual a 'leader'? A modelling study by Johnstone and Manica[1] illuminates this question.

Writing in *Proceedings of the National Academy of Sciences*, the authors consider a famous coordination problem known to game theorists as the Battle of the Sexes[2]. Imagine a married couple who want to spend the evening together. Husband and wife (the players) can either go to a football game or to the opera, but they cannot communicate with each other about where to meet. Neither wants to miss their partner by going to a different event from them. If that happens, both get a pay-off of zero. When they go to the same event, the wife would prefer the opera, whereas the husband would prefer the football game. When meeting at the same event, the players get the pay-offs 1 and $1-k$ (where $0 < k < 1$), depending on whether or not they realize their preferred option.

Johnstone and Manica model such an interaction (and generalize it to the case of more than two players). They assume that the same players interact repeatedly, and that each time they can either choose their preferred option or copy the previous action of the other player. Each player is characterized by a strategy, λ, corresponding to the player's probability of sticking to his or her preferred action. This strategy is viewed as a player's degree of leadership: players with a high value of λ are leaders, in that they ignore the actions of others and obey their own preferences; players with a low value of λ are followers, in that they tend to copy the choices of others.

Johnstone and Manica[1] investigate how natural selection shapes intrinsic leadership in a population in which individuals produce offspring in proportion to their pay-off in

Figure 1 | Out in front. An implication of Johnstone and Manica's model[1] is that leadership may simply reflect an intrinsic tendency to follow one's own preferences.

the coordination game. A population of only leaders ($\lambda = 1$) is not evolutionarily stable: if both players stick to their preferred option, they will never meet and will get a pay-off of zero. Likewise, a population of only followers ($\lambda = 0$) is not stable, because the players will again miss each other if both have a tendency to dither, continually switching to the previous action of the other. Instead, the population will first evolve to an intermediate value of λ (say, $\lambda = 0.5$). But, intriguingly, this is not the final outcome. From the intermediate strategy, the population will diversify and evolve to a state where two strategies coexist — a leader strategy (say, $\lambda = 0.9$) and a follower strategy (say, $\lambda = 0.1$).

This outcome makes intuitive sense, because a leader–follower pair of players is most efficient in solving the coordination problem: both will eventually choose the preferred option of the leader. The leaders seem to have the better part (a pay-off of 1 is higher than a pay-off of $1-k$), but this holds only when they are teamed up with a follower. On the population level,

leaders and followers have the same average pay-off. This is because leaders are more frequent than followers (because of their higher pay-off in leader–follower interactions) and therefore find themselves relatively often teamed up with another leader (giving a pay-off of zero).

These results[1] are interesting for several reasons. First, they provide an explanation for empirical observations in the lab and field. For example, experiments with sticklebacks[3] have revealed pronounced individual differences in the tendency to lead that resemble those in the model. Second, the results show that leadership and 'followership' can evolve in the absence of any other differences between individuals. In the behavioural sciences, there is much discussion about which traits make someone a leader[4]. According to Johnstone and Manica's model, leadership need not be associated with being better informed, being more dominant or having superior communication skills. Instead, leadership may simply reflect an intrinsic tendency to follow one's

own preferences and disregard the choices of others (Fig. 1).

The third interesting aspect is that the paper provides a link to the issue of animal 'personalities'[5], the phenomenon that animals differ systematically in their behaviour in a manner that is individually stable across a variety of contexts. In nature, leadership seems to be a personality trait that is correlated with general activity level, aggressiveness and boldness[3]. Johnstone and Manica provide a neat explanation for the emergence of individual differences in leadership, but it is an open question how such correlations between leadership and other personality traits have evolved.

The type of model presented by Johnstone and Manica sacrifices realism for conceptual clarity and analytical tractability. It remains to be seen whether the results are robust when more-realistic assumptions are incorporated or more-complex strategies are considered. For good reason, the authors have assumed that the players do not differ in features such as knowledge and power. In more realistic settings, asymmetries between the players will undoubtedly occur; such asymmetries can help to solve a coordination problem[6].

Moreover, even in symmetric settings, differences in leadership will not necessarily evolve if more-complex strategies are available. An example can be taken directly from the authors' experimental work[7]: sticklebacks that have diverging preferences take turns in leadership, rather than specializing in the roles of leader and follower. Perhaps most importantly, a group of individuals engaging in prolonged interactions can be expected to learn each others' characteristics (for example, their degree of leadership). It would be worthwhile investigating how the evolutionary outcome would change if individuals could signal their leadership tendencies — as humans clearly do.

This work[1] may be criticized for its restricted view of leadership. One could argue that the 'leaders' in the model do not really lead, but simply refrain from following others. Leaders are defined as being stubborn, refusing to react to their fellow group members. Accordingly, the evolution of differences in leadership in this model bears some resemblance to the evolution of individual variation in responsiveness[8] and social sensitivity[9] seen in other models. In reality, there are more dimensions to leadership, and it is not obvious that stubbornness and antisocial behaviour are characteristic features of leaders. In African elephants, for example, the most responsive and socially sensitive individuals have the highest propensity to become leaders of the herd[10].

Johnstone and Manica's concept of leadership seems to be most easily applicable to fish shoals and other anonymous societies. Still, even for highly structured social systems such as those of humans and elephants, their insights provide clues to how intrinsic differences in leadership could evolve as a fundamental means to resolve the tension between individual interests and the desire to live in a group. ∎

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