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## Spontaneous emergence of leaders and followers in foraging pairs

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Animals that forage socially<sup>1</sup> often stand to gain from coordination of their behaviour<sup>2–5</sup>. Yet it is not known how group members reach a consensus on the timing of foraging bouts. Here we demonstrate a simple process by which this may occur. We develop a state-dependent, dynamic game model<sup>6</sup> of foraging by a pair of animals, in which each individual chooses between resting or foraging during a series of consecutive periods, so as to maximize its own individual chances of survival<sup>6,7</sup>. We find that, if there is an advantage to foraging together<sup>1,2,8</sup>, the equilibrium behaviour of both individuals becomes highly synchronized. As a result of this synchronization, differences in the energetic reserves of the two players spontaneously develop, leading them to adopt different behavioural roles. The individual with lower reserves emerges as the 'pace-maker' who determines when the pair should forage, providing a straightforward resolution to the problem of group coordination. Moreover, the strategy that gives rise to this behaviour can be implemented by a simple 'rule of thumb'<sup>9</sup> that requires no detailed knowledge of the state of other individuals.

When animals forage, they have to make many decisions<sup>7,10</sup>: when to rest or to forage, when to leave a patch, and which food items to seek. Their behaviour is likely to reflect a trade-off between the risks of starvation and predation<sup>11,12</sup>, changing over the short-term in response to both their energy reserves and the environment<sup>6</sup>. For animals living in social groups, foraging is further complicated by the actions of other individuals<sup>1</sup>: it will usually be safer to forage at the same time as other members of the group<sup>2,8</sup> (although this may also entail competition for food<sup>2</sup>), favouring some coordination of activity<sup>3–5,13</sup>. How can group members reach a consensus on the timing of foraging bouts? Models of self-organization in biological systems<sup>9</sup> have shown how coordinated patterns of activity can emerge spontaneously in groups of individuals following simple, predetermined behavioural rules. Here we describe a dynamic, game-theoretical model of foraging in a pair (see Supplementary Information for details), in which the evolutionarily stable rule governing the timing of individual foraging bouts leads in this way to a simple resolution of the problem of group coordination.

Our model considers decisions of the pair of animals over a large number of discrete time periods. During a given period, each individual can choose to forage or to rest. Foraging increases energy reserves, and hence decreases the forager's starvation risk. However,

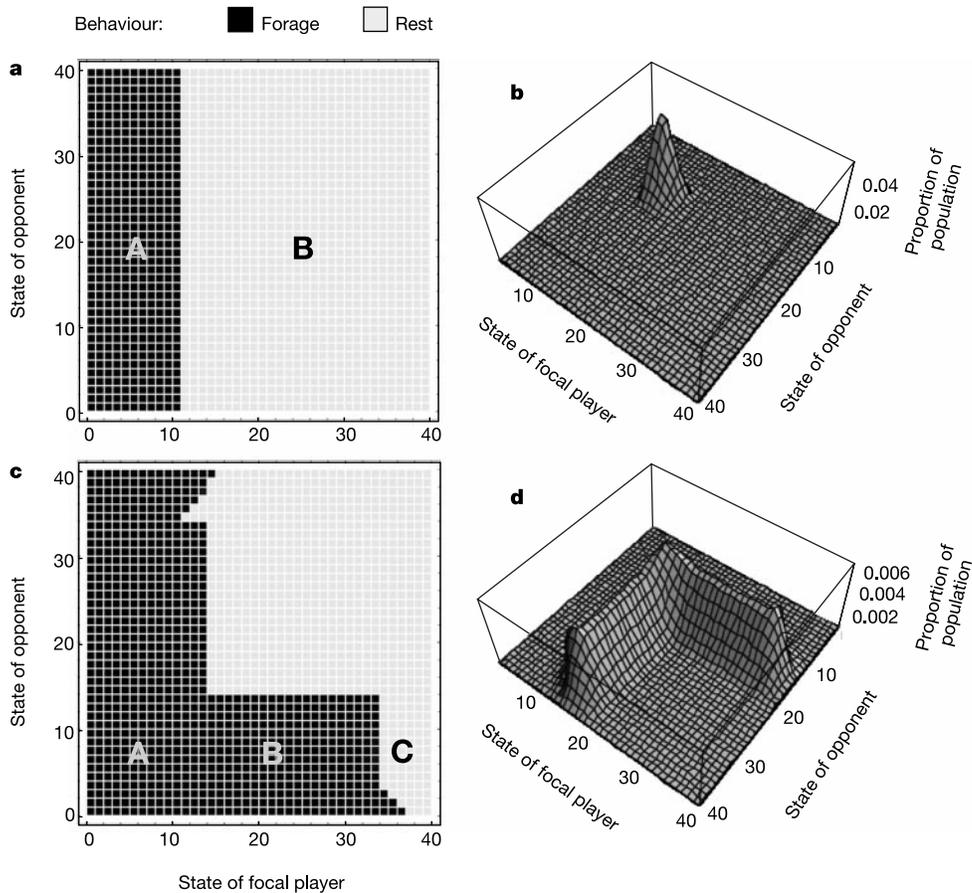
it may also entail an increased risk of predation<sup>11,12</sup>. Previously, dynamic programming<sup>6,14,15</sup> has been successfully used to examine the effects of trade-offs between starvation and predation risk on the short-term, minute-to-minute behaviour of individual foragers. Dynamic games use similar techniques<sup>6</sup>, but allow us to model the behaviour of groups. Although state-dependent models of group-foraging have been developed previously, looking at optimal group size<sup>16,17</sup>, diurnal routines<sup>18</sup>, foraging strategy<sup>1</sup>, sentinel behaviour<sup>19</sup> and social hierarchy effects<sup>20,21</sup>, we believe the model presented here to be the first that has explicitly considered the coordination of foraging among individuals within a group. In the form presented here, the model only considers a pair of players. The same approach could in principle be used to generate predictions about the behaviour of foragers in larger groups, but the computations involved have proved to be unfeasibly time-consuming.

The state of both players is represented by their level of energetic reserves, bounded by a maximum above which a player cannot gain further reserves and a minimum level at which the player is assumed to have starved. We assume that each player has exact knowledge of both its own and its partner's state (though, as we discuss later, this assumption ultimately proves unnecessary). At the beginning of a period, each player decides whether to rest or to forage. If a player rests, on average it incurs a net loss in reserves. If a player forages, on average it receives a net gain. Both energetic costs and the amount of food found during a period vary probabilistically with a known distribution. All behaviours have a risk of predation attached to them<sup>22,23</sup>—foraging alone is assumed to be more (or equally) risky than foraging in a pair, which itself is more (or equally) risky than resting. The results presented in the figures are based on the assumption that the average amount of energy gained by a foraging individual is independent of the number of others foraging at the same time, although we also explored the effects of relaxing this assumption.

We calculated the evolutionarily stable strategy (ESS) for players in this game, for a range of different parameter values. In particular, we focused on the effect of omitting or incorporating a benefit of foraging together—we obtained closely similar results when foraging together gave either a safety benefit (that is, reduced predation risk) or an energetic benefit (that is, higher mean individual net gain) compared to foraging alone. The ESS in any one case was found using an iterated, damped best-response procedure<sup>6,24</sup>, incorporating some likelihood of errors in decision making<sup>25</sup>. We were then able to predict the long-term stable state distribution, and the expected behaviour of a pair of individuals that adopt this strategy. In particular, we examined the expected level of behavioural coordination at equilibrium, quantified using the relative disequilibrium parameter<sup>26</sup>  $D'$  (where  $D' = 1$  implies that pair members always adopt the same behaviour,  $D' = 0$  implies that their actions are uncorrelated, and  $D' = -1$  implies that they always adopt different behaviours). We also examined the mean state of players, the mean difference in state between them, and the correlation between their states.

When there is no benefit to foraging in a pair, both players behave independently, that is, the action adopted by either is not affected by the other's state. The optimal policy under these conditions, as in optimization models of individual behaviour<sup>6</sup>, is to forage when an individual's own state drops below some threshold value, and otherwise to rest (Fig. 1a). As a result, the energetic reserves of both players settle at similar levels, fluctuating around the threshold value (because a player below the threshold will forage until its reserves rise above the cut-off point, after which it should rest until its reserves again fall below this value). This gives a single peak in the stable state distribution for the pair (Fig. 1b). In this simple case, there is no correlation between the behaviours of the players ( $D' = 0$ ).

By contrast, when we introduce a benefit to foraging together, through a lower predation risk than that incurred when foraging alone (or through an increase in mean energetic gain, although this



**Figure 1** Evolutionarily stable policies (left column) and the probabilities that a pair of individuals following the policy exhibit any particular combination of states (right column), with differing benefits of foraging together. In **a** and **b**, there is no benefit to foraging together (following the standard parameter set given in Supplementary Information, but with  $m_{FT} = m_{FA} = 0.0005$ , where  $m_{FT}$  and  $m_{FA}$  are respectively the predation risks of foraging together and foraging alone). Policy **a** shows that if the state of the focal player falls below a threshold value, it should forage (zone A), whereas if its state rises above this threshold, it should rest (zone B). Both players follow the same policy, and so the states of both remain near the threshold (**b**). In **c** and **d**, foraging together yields a safety benefit (following the standard parameter set). Policy **c** has a similar focal state threshold to policy **a**, below which the focal player must forage to avoid starvation (zone A). However, there is

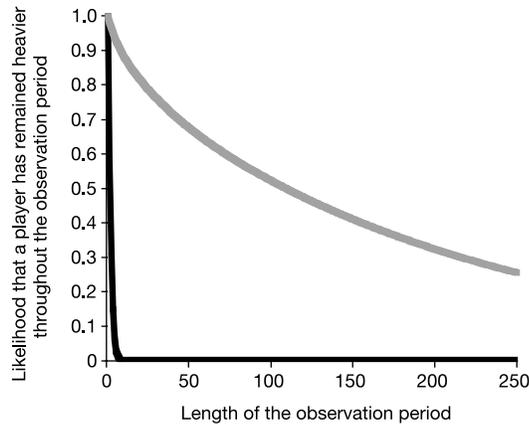
also a region above the threshold (B) in which it should forage—this occurs when the partner has a low state, and so is likely to forage. The focal player therefore also forages (despite having high reserves) because it incurs a lower predation risk if it does so, rather than waiting until its reserves have fallen to a critical level and then potentially having to forage alone (incurring a greater predation risk). This is true for all but the highest of the focal player's states (zone C)—here, the player should always rest, because the ceiling on the level of reserves the animal can store negates any extra benefits of foraging. The state distribution (**d**) for this policy demonstrates that if one player has reserves above the threshold, its colleague should be on the threshold. Hence, one player always has low reserves when there is some benefit to foraging together.

latter possibility is not illustrated), the equilibrium behaviour of each individual becomes highly dependent upon the reserves of its partner, as well as its own state. Figure 1c describes a typical policy when there is a safety benefit of foraging together. Each individual forages when either its own state or that of the other player drops below some threshold value (unless the individual making the decision is approaching maximum reserve levels, in which case nothing further can be gained by foraging). Sensitivity analyses show that this result is extremely robust, as systematic and thorough variation of the parameters defined (such as the mean energetic gains, costs or predation risk of the behavioural options) did not lead to any qualitative differences between the strategies that were calculated.

The above strategy is beneficial because an individual that forages when its partner's reserves are low is likely to gain the safety benefit of joint activity (as under these circumstances the partner will probably also choose to forage). The correlation between the behaviour of the players following the policy shown in Fig. 1c is  $D' = 0.9985$ , which indicates that their activities are very tightly synchronized indeed. Surprisingly, however, the equilibrium correlation between the states of the players is negative ( $\rho = -0.589$ ), implying that if one player has low reserves, its partner is likely to

have high reserves. This negative correlation in state is a consequence of behavioural synchronization. When foraging behaviour becomes tightly coupled, there is no opportunity for a player with lower reserves to forage while its partner rests, and so to reduce the difference in state between them. Consequently, the mean equilibrium difference in state between the two players builds up to  $13.08 \pm 7.91$  state units (Fig. 1d); this value is approximately ten times greater than the mean difference of  $1.77 \pm 1.42$  state units, which occurs when there is no benefit to foraging together and behaviour is unsynchronized (Fig. 1b).

This separation of the players into 'fat' (high reserves) and 'lean' (low reserves) roles persists for a much longer period of time than if there is no advantage to foraging together (Fig. 2). The players occasionally switch roles when, through a run of bad luck, the reserves of the 'fat' player drop below those of the 'lean' player, but this occurs only rarely: the median time for which one individual retains the 'fat' role is 109.07 periods (approximately 50 times longer than the equivalent median time of 2.28 when there is no advantage to foraging together). In other words, the model predicts that a temporarily stable asymmetry in state will emerge between two otherwise identical players that are both following an identical set of rules.



**Figure 2** Likelihood that ‘fat’ and ‘lean’ roles persist over time. Given that one individual has higher energy reserves than its partner at a known point in time, this graph shows the probability that it will still have higher energy reserves (that is, that no switch in roles will have occurred) after any given length of time, assuming that both players follow the equilibrium strategy. The black line shows the results of the model when foraging together yields no benefit (and behaviour is unsynchronized); the grey line shows results when foraging together yields a safety advantage—see Fig. 1 for parameters.

The difference in state between the two players leads to a simple resolution of the coordination problem. The reserves of the ‘lean’ player (as illustrated in Fig. 1d) settle around the lower critical state threshold, at which its behaviour is dictated solely by its own energy reserves, regardless of the state of its partner. By contrast, the reserves of the ‘fat’ player rise above this threshold, and it will therefore respond to the state (and probable behaviour) of the ‘lean’ player. As a result, the activities of both members of the pair are dictated by the player with the lower reserves, which becomes the ‘pace-maker’ for the group. Both players will forage when the pace-maker’s reserves drop below the lower critical threshold; both will rest when the pace-maker’s reserves rise above this threshold.

We have also examined the case in which foraging together is disadvantageous (owing, for instance, to greater predation risk than when foraging alone). This generates policies that lead to anti-synchronous behaviour, with a correlation approaching  $D' = 1$ . However, this finding is unlikely to prove biologically relevant. If social foraging has detrimental effects on the fitness of an individual, then foraging groups are unlikely to form in the first place, and the problem of behavioural coordination does not arise.

To sum up, our results indicate that the problem of group coordination may be easily resolved through the spontaneous emergence of temporary ‘leaders’ and ‘followers’, owing to the build-up of differences in energetic state (even if group members experience identical chances of foraging success and predation). In support of this prediction, studies of foraging in groups of fish have shown that leadership decisions may often be made by individuals with lower reserves<sup>27–30</sup>. Furthermore, we have shown that such coordination is possible even when individuals follow an evolutionarily stable strategy that maximizes their own chances of survival irrespective of the risks to other group members (in the same way that coordinated patterns of sentinel behaviour may emerge within groups of ‘selfish’ individuals<sup>19</sup>). This outcome is not the result of a communal group decision<sup>5</sup>, but emerges from the interaction between individuals who each make their own choices about when to forage or rest; as in other models of self-organization, the pattern of group activity is the product of individual decisions<sup>9</sup>.

We emphasize that although the focal player’s decisions in the model are based on an exact knowledge of the energetic reserves of both itself and its partner, this information is not necessary for implementation of the ESS policy that we have derived. Instead, the ESS policy can be closely approximated by a much simpler rule of

thumb: ‘I should forage if either my reserves have fallen below a certain threshold value, or my partner chooses to forage’. This tactic requires only the ability to observe and react (quickly) to a change in the partner’s behaviour, rather than detailed knowledge of its state. Nevertheless, it yields identical behaviour to the calculated ESS policy, because the focal individual’s partner will forage whenever its reserves drop below the threshold value. The simplicity of such a rule of thumb suggests that it may easily evolve, and implies that the solution we propose to the problem of coordination does not require any exceptional cognitive abilities. It also shows that very simple individual rules can be sufficient to generate seemingly complex patterns of social behaviour<sup>9</sup>.

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**Supplementary Information** accompanies the paper on [www.nature.com/nature](http://www.nature.com/nature).

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