Life decisions separate 'hawk' from 'dove'

ASK anyone who has regular contact with animals - from farmers to pet owners - and they will tell you that animals have personalities. Some are docile, some are tetchy. Animals are individuals, with a range of temperaments, from aggressive to shy. Explaining the evolution of personality has been difficult. Now it seems the decisions animals make about how to live their lives and when to reproduce may be what gives them their personalities.

To test the idea, Max Wolf of the theoretical biology group at the University of Groningen, the Netherlands, and colleagues built an evolutionary model based on trade-offs animals face during their lives. For example, young oystercatchers have to decide whether to move into a vacant territory with a poor food supply and start breeding, or wait for higher quality territory to become available. "We predict that the ones that delay reproduction will be more risk-averse, and more shy, and non-aggressive, than the ones that start reproducing immediately," says Wolf. This example is in birds, but all animals face similar decisions.

The model incorporates this dilemma over current or future reproduction, and looks at how behavioural traits evolve over many generations. Individuals in the model are confronted with a risky situation in which they might get injured but where there is also a chance of a high pay-off. This is similar to the famous "hawk-dove" game in which an individual who behaves aggressively has a higher chance of winning a fight over a resource than one who behaves meekly. Hawks, however, are more likely than doves to die in the attempt.

The team also examined how animals forage when there are predators around. Bolder individuals get more food because they don't waste time hiding - but they also run the risk of being eaten. In other words, individuals that live fast do risk dying young.

In the model, individuals can differ in their aggressiveness, boldness and intensity of exploratory behaviour. These behaviour traits are linked to the probability of obtaining resources and successfully reproducing (*Nature*, vol 447, p 581).

"We find that evolution results in personalities," says Wolf. "Individuals that have more to lose evolve to be more risk-averse in the different risk situations." Individuals that put more emphasis on future reproduction evolve to have low levels of aggression and behave shyly. In contrast, individuals that invest more in current reproduction evolve to be more aggressive risk-takers.



It is the first time that a formal mathematical model has been produced incorporating these different parameters to explain why individual animals have different personalities. The model also explains consistency in behaviour, says Wolf.

Judy Stamps of the University of California, Davis, has also suggested there is a link between life-history trade-offs and personality (*Ecology Letters*, vol 10, p 355). But she points out that the first set of models produce bimodal personalities: animals that are either bold or shy, but never in between. In real life, animals are not just one thing or the other. Wolf and colleagues address this in another model by invoking "genetic constraints", says Stamps, arguing that many genes with small effects govern the development and expression of personality traits.

"I have trouble accepting this result because there is plenty of evidence that genetic systems can produce highly bimodal behavioural trait distributions, when those distributions are adaptive," says Stamps. "The authors may need to think a bit more about the processes that generate continuous trait distributions."

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