# Evolution of animal personalities

**Arising from:** M. Wolf, G. S. van Doorn, O. Leimar & F. J. Weissing *Nature* **447,** 581–584 (2007).

Wolf *et al.*[1] propose a model to explain the existence of animal personalities, consistent with behavioural differences among individuals in various contexts[2–4]—their explanation is counter-intuitive and cogent. However, all models have their limits, and the particular life-history requirements of this one may be unclear. Here we analyse their model and clarify its organismal scope.

Under some conditions, Wolf *et al.*[1] find consistent behavioural differences between individuals that reproduce early in life and those that delay reproduction to explore their habitats instead to enhance future reproduction. Non-explorers that reproduce early in life later become bold and aggressive, whereas exploratory individuals with greater future reproductive potential are shy and unaggressive. These differences are caused by asset protection[5] where individuals with greater future fitness take fewer risks that would jeopardize that fitness.

Asset protection, however, is a negative feedback process that, given time, makes individuals more alike, not less. In Clark's original asset protection paper[5], many decisions are made over an animal's lifespan. Over time, individuals tend towards similar behaviour, despite any initial differences in assets, because those with assets take few risks and acquire little new fitness. Those without high assets take more risks and (unless they die trying) acquire new fitness assets that become worth protecting.

If, in the model of Wolf *et al.*, individuals experience many hawk–dove encounters, successful hawks would eventually accumulate enough fitness for playing dove to become their optimal behaviour. Given time to accrue new assets, behavioural types would converge. Two particular conditions that could prevent this convergence are: animals with very short lives might not have time to change their assets sufficiently to cause changes in behaviour; and early life-history choices can have such large fitness consequences that subsequent bold and aggressive behaviour has relatively little influence on assets. Notably, these conditions do not seem to fit the maintenance of stable personalities in long-lived organisms such as humans.

The model of Wolf *et al.* requires bold/aggressive contexts not to dominate one another in fitness consequences, otherwise the negative feedback of asset protection will apply at this smaller scale (Supplementary Fig. 2 of ref. 1: in the square in which behavioural correlations could evolve, there is a wedge-shaped region without correlation between the hawk–dove and predator games). We reproduced their model and found that, in this region, thorough explorers are less aggressive than non-explorers, but no one is bold. Without the hawk–dove game, explorers would be shy and non-explorers bold, but when the hawk–dove game has sufficiently higher fitness consequences than the boldness game, all individuals are shy to eliminate the risk of dying before the fitness windfall from the hawk–dove game. This is the asset-protection principle, working on the scale of the low-fitness behavioural contexts, producing behavioural inconsistency, unless the contexts do not dominate one another.

An alternative way of explaining behavioural consistency and correlations is through positive (not negative) feedback. For example, if thorough explorers gain assets (energy, size, knowledge) that improve their abilities to escape predators or to win fights, then we might find positive correlations between exploration, boldness and aggressiveness. Additional behaviour would positively feed back on state, maintaining differences in assets and behavioural types. What is needed next is a unified modelling framework in which both negative and positive state feedback, as well as other mechanisms, can be compared.

**Richard McElreath[1], Barney Luttbeg[2], Sean P. Fogarty[2], Tomas Brodin[2] & Andrew Sih[2]**
[1]Department of Anthropology, University of California, Davis, California 95616, USA.
[2]Department of Environmental Science and Policy, University of California, Davis, California 95616, USA.
e-mail: btluttbeg@ucdavis.edu

**Received 26 June; accepted 3 September 2007.**

1. Wolf, M., van Doorn, G. S., Leimar, O. & Weissing, F. J. Life-history trade-offs favour the evolution of animal personalities. *Nature* **447**, 581–584 (2007).
2. Gosling, S. D. From mice to men: what can we learn about personality from animal research? *Psychol. Bull.* **127**, 45–86 (2001).
3. Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* **79**, 241–277 (2004).
4. Sih, A., Bell, A. & Johnson, J. C. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378 (2004).
5. Clark, C. W. Antipredator behavior and the asset-protection principle. *Behav. Ecol.* **5**, 159–170 (1994).

**doi:**10.1038/nature06326

---

# *Wolf* et al. *reply*

**Replying to:** R. McElreath, B. Luttbeg, S. P. Fogarty, T. Brodin & A. Sih *Nature* **450,** doi: 10.1038/nature06326 (2007).

The evolution of animal personalities is still poorly understood. The emergence of consistent individual differences is relatively easy to envisage when initial differences in behaviour are reinforced by positive feedback mechanisms. Such reinforcement might act through learning or training, or through behaviour-induced changes in an individual's condition[1] or environment[2]. However, positive feedback is not required. We showed that, even without such feedback, differences in fitness expectations result in consistent differences in risk-taking behaviour[3]. This was illustrated by a model that, for simplicity, considers a short life history. McElreath *et al.*[4] argue that our results extend to long-lived organisms only under specific conditions. Although we agree that the full scope and limitations of our model still have to be mapped out, we believe that our arguments are also relevant to long-lived organisms.

Our theory is based on the principle of asset protection[5]: the more an individual stands to lose, the more cautiously it should behave. McElreath *et al.*[4] argue that asset protection entails a negative feedback that tends to erode individual differences. This may indeed be the case if large assets can be accumulated by risky behaviour: risk-proneness while accumulating assets would then be followed by risk-aversion while protecting the acquired assets. However, the analysis of McElreath *et al.* is incomplete for at least two reasons.

First, not all payoffs should be considered as assets. Payoffs can be either spent immediately in current reproduction or invested into future reproductive potential. Only the latter, resulting in an increase in future reproductive value[6], corresponds to assets. Consequently, when the payoffs of risky games only affect immediate reproduction, no asset accumulation takes place and there is no negative feedback eroding individual differences. There might even be positive feedbacks, enhancing individual differences, if risky payoffs tend to be immediate whereas non-risky payoffs tend to increase the future reproductive value.

Second, McElreath *et al.* extrapolate our model to long-lived organisms in a one-sided manner. They assume that differences in assets due to life-history decisions only occur once in an individual's lifetime whereas the number and importance of risky games increases with life expectancy. There are certainly examples where an individual's fate is governed by a single life-history switch. Yet, such 'career decisions'[7] are typically associated with long-lasting fitness consequences that are not eroded by everyday risky behaviour. More commonly, however, life-history decisions (such as thorough or superficial exploration) have to be taken repeatedly throughout an individual's life. As a consequence, assets are not only eroded but can also be built up.

In conclusion, the potential of negative feedback to erode individual differences is substantially smaller than McElreath *et al.* suggest. We therefore maintain that asset protection furthers the understanding of animal personalities in both short- and long-lived organisms. Yet, there are certainly situations in which negative feedbacks as described by McElreath *et al.* are important. In such situations, a switch might occur from a risk-prone to a risk-averse personality. Indeed, personalities are not always stable from the cradle to the grave. Take our own species, where young individuals with a risky lifestyle become more cautious later in life (when assets are at stake). Similarly, hover wasps switch from risk-prone to risk-averse behaviour once they are close enough to the breeding position[8]. Our theory accounts for such switches associated with asset accumulation and it produces testable predictions for their occurrence. Hence, even in the presence of negative feedbacks, the principle of asset protection is crucial for understanding animal personalities.

**Max Wolf**[1], **G. Sander van Doorn**[2], **Olof Leimar**[3] **& Franz J. Weissing**[1]
[1]Theoretical Biology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Kerklaan 30, 9751 NN Haren, The Netherlands.
[2]Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA.
[3]Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden.
e-mail: f.j.weissing@rug.nl

1. Rands, S. A., Cowlishaw, G., Pettifor, R. A., Rowcliffe, J. M. & Johnstone, R. A. Spontaneous emergence of leaders and followers in foraging pairs. *Nature* **423,** 432–434 (2003).
2. Hemelrijk, C. K. & Wantia, J. Individual variation by self-organisation. *Neurosci. Biobehav. Rev.* **29,** 125–136 (2005).
3. Wolf, M., van Doorn, G. S., Leimar, O. & Weissing, F. J. Life-history trade-offs favour the evolution of animal personalities. *Nature* **447,** 581–584 (2007).
4. McElreath, R., Luttbeg, B., Fogarty, S. P., Brodin, T. & Sih, A. Evolution of animal personalities. *Nature* **450,** doi: 10.1038/nature06326 (2007).
5. Clark, C. W. Antipredator behavior and the asset-protection principle. *Behav. Ecol.* **5,** 159–170 (1994).
6. Williams, G. C. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100,** 687–690 (1966).
7. Ens, B. J., Weissing, F. J. & Drent, R. H. The despotic distribution and deferred maturity: two sides of the same coin. *Am. Nat.* **146,** 625–650 (1995).
8. Field, J., Cronin, A. & Bridge, C. Future fitness and helping in social queues. *Nature* **441,** 214–217 (2006).

**doi:**10.1038/nature06327