Do animal personalities emerge?

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The evolution of animal personalities is a topic of primary importance in behavioural ecology. An intriguing empirical fact is the consistency of animal responses to repeated stresses or threats. Wolf *et al.* propose an evolutionary model to explain the emergence of consistent personalities[1]. They show that a population dimorphism for an exploration trait implies the existence of behavioural syndromes, such as decreased aggressiveness and the boldness of 'thorough explorers'. This finding helps explain how animal responses can be consistent, despite the seeming advantages of flexible responses. However, we contend that the emergence of a dimorphism depends critically on the intensity of the trade-off between exploration investment and first-year fecundity.

Wolf *et al.*[1] introduced a model of temporal allocation to fecundity to answer questions related to animal personalities. Their model is based on four ingredients: individuals reproduce twice during their lives; two habitats are available (bad and good) and influence the fecundity of individuals (individuals in bad habitats produce fewer offspring); all individuals first reproduce in a bad habitat; individuals can trade off some of their fecundity during their first reproduction event to find a better habitat to reproduce in the second year. Thus, 'thorough explorers' bet on their second reproduction event, while 'superficial explorers' reproduce equally well at all opportunities. The authors prove that a population dimorphism of the exploration trait

influences the evolution of behavioural responses in hawk–dove and predator–prey games. Without introducing any constraints on responses to these games, they predict the emergence of two extreme syndromes, with superficial explorers being consistently bold and aggressive and thorough explorers, shy and non-aggressive. These results encompass the predictions of Bishop–Cannings' theorem[2], which states that strategies yielding stochastic responses cannot be evolutionarily stable. The authors take a step further by showing the consistency of responses across different games.

Despite its interesting conclusions, this model has a weak point. The conclusions of Wolf *et al.* are based on the existence of a population dimorphism of the exploration strategy. Although the authors do prove that a dimorphic population is protected from further invasions, they leave unaddressed the issue of its emergence. We looked at the fitness of a rare mutant in an initially monomorphic population, as is classically done in adaptive dynamics studies[3–9]. A pairwise invasibility plot[7–9] confirms that the parameter set investigated by the authors ($\alpha = 0.005$, $f_h = 3.5$, $f_l = 3.0$, $\beta = 1.25$) leads to a dimorphism through a branching point (Fig. 1a). However, this result depends critically on parameter β, which controls the trade-off between exploration investment and first-year fecundity: for higher β, pairwise invasibility plots display a branching point, an evolutionary repellor and an evolutionarily stable strategy ($\beta = 1.6$, Fig. 1b), two
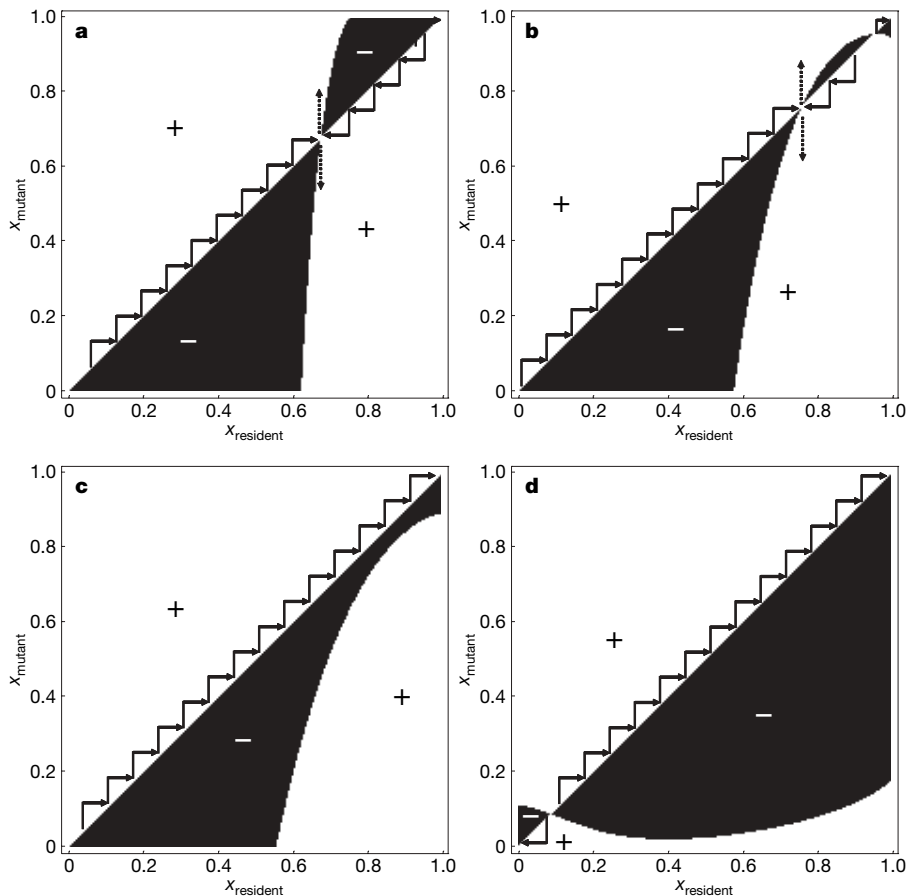
Figure 1 | Pairwise invasibility plots. These diagrams show which mutant strategies can invade in an initially monomorphic situation. The x axis represents the initial exploring strategy ($X_{resident}$), and the y axis, the mutant strategy (X_{mutant}). White regions indicate cases where the mutant can invade ($+$), while black regions ($-$) represent cases where an initially rare mutant

never invades. The solid arrows suggest possible evolutionary trajectories under the assumption of small mutation effects. Dashed arrows indicate evolutionary branching after monomorphic evolution. Parameter values: in all panels $\alpha = 0.005$, $f_h = 3.5$ and $f_l = 3.0$; in **a** $\beta = 1.25$ (as in ref. 1); in **b** $\beta = 1.6$; in **c** $\beta = 1.8$; and in **d** $\beta = 10$.

evolutionarily stable strategies and an evolutionary repellor ($\beta = 10$, Fig. 1d) or only one evolutionarily stable strategy ($\beta = 1.8$, Fig. 1c). These situations do not generically lead to a stable dimorphism.

Proving that a dimorphic coalition is protected from invasions or that it emerges through evolutionary branching are different tasks[5,10,11]. Wolf and colleagues' proof deals only with the former. We have shown that the emergence of a dimorphism happens only under restricted conditions. The emergence of animal personalities might thus be limited by extrinsic constraints, for example, the difficulty of both rearing offspring and looking for a better habitat. Finally, branching points in haploid models cannot be literally translated as the emergence of dimorphism in diploid sexually reproducing organisms because recombination and the absence of assortment or dominance can prevent the evolution of genotypic bimodality[9].

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The more an individual stands to lose, the more cautious that individual should be. We have shown[1] that this basic principle gives rise to consistent individual differences in risk-related behaviour whenever individuals have different future fitness expectations. To illustrate this, we considered a model where differences in fitness expectations result from a trade-off between current and future reproduction. Massol and Crochet argue[2] that the emergence of such differences depends on the shape of this trade-off. Their claim is based on the technical argument that our model has a 'branching point' only for a limited range of the trade-off parameter β. In contrast, we show here that the emergence of individual differences is a robust phenomenon that does not depend on such details. Our analysis illustrates the important insight that a branching point is not needed for the emergence of polymorphism.

In our Supplementary Information[1], we prove that a dimorphic population consisting of the two extreme exploration strategies $x = 0$ and $x = 1$ is stable. This is reflected in the fact that in all pairwise invasibility plots for $\beta > 1$ (such as those shown by Massol and Crochet[2]) a mutant with strategy $x_m = 0$ can invade in an $x = 1$ resident population, and vice versa. Yet it is not self-evident that such a stable dimorphism is attainable from a monomorphic ancestral state. According to adaptive dynamics theory[3], a stable polymorphism will evolve in the presence of a branching point. Massol and Crochet correctly argue[2] that our model has a branching point only if the trade-off is moderate (for example, $\beta = 1.25$, Fig. 1a) but not if it is very strong (for example, $\beta = 2.0$, Fig. 1c). Nevertheless, our individual-based simulations[1] led us to conclude that a dimorphism emerges for all $\beta > 1$. In other words, a dimorphism can evolve in the presence (Fig. 1b, $\beta = 1.25$) but also in the absence of a branching point (Fig. 1d, $\beta = 2.0$).

To substantiate this result we ran more than 1,000 additional individual-based simulations with varying initial conditions and varying β values. To be specific, 100 β values were randomly drawn from the uniform distribution on the interval $1 < \beta < 10$. For each of these β values we ran 11 simulations with initial x values between 0.0 and 1.0 in steps of 0.1. The mutation rate was $\mu = 1 \times 10^{-5}$, and the

mutational effect sizes were drawn from a normal distribution with mean zero and standard deviation 0.3. The outcome was unambiguous: the stable dimorphism of the two extreme strategies $x = 0$ and $x = 1$ emerged in all these simulations, irrespective of the initial conditions and the value of β.

How can this seeming discrepancy with the adaptive dynamics approach be explained? Adaptive dynamics analysis often makes two important assumptions[3], which may be considered a worst-case scenario for the emergence of polymorphism. First, populations have a low level of diversity because the resident population is only rarely challenged by mutants. Second, mutations have small phenotypic effect. The scope of these assumptions has been debated[4–6] and neither of them is strictly satisfied in our individual-based simulations. First, several mutants are typically present simultaneously, because new mutations often occur before old ones are ousted from the population. Second, mutational effect sizes are drawn from a normal distribution, implying that mutations of large effect are rare but sometimes occur. The consequence of these differences in assumptions can be illustrated by the pairwise invasibility plot in Fig. 1c. When mutations are very rare and have small effects one would predict (as do Massol and Crochet[2]) that evolution gives rise to the monomorphic population $x = 1$, which can be considered an evolutionary trap. Yet, as can also be seen in Fig. 1c, a mutant with a sufficiently deviant phenotype ($x_m < 0.83$) can invade the population and trigger the evolution to the stable dimorphism.

We think that the assumptions used in our individual-based simulations are realistic. It is well known that natural populations tend to contain considerable amounts of standing genetic variation, and widely accepted approaches like quantitative genetics[7] are based on this fact. At present, the distribution of mutational effect sizes is only known for a small number of empirical examples[8,9]. The limited evidence available indicates that such distributions seem to have 'fat tails,' suggesting that mutations with larger effect sometimes occur. In fact, this is not implausible. The evo-devo revolution[10] has provided plenty of examples where single mutations (such as in a regulatory pathway) have a huge phenotypic effect. Traditionally it is assumed that such
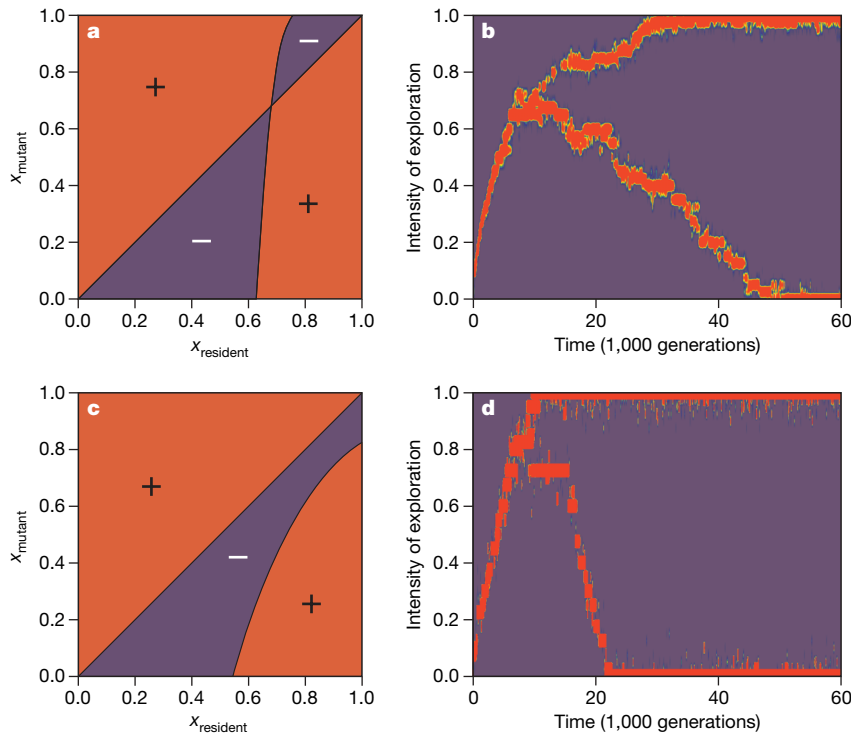
Figure 1 | Emergence of a polymorphism in the presence and in the absence of a branching point. Pairwise invasibility plots are shown together with corresponding individual-based simulation results for two values of the trade-off parameter β. In **a** and **b**, $\beta = 1.25$, the standard parameter setting used in ref. 1; and in **c** and **d**, $\beta = 2$. The orange regions ($+$) in the pairwise invasibility plots correspond to mutant strategies that can invade a given resident population, while purple regions ($-$) indicate mutants that cannot invade. According to adaptive dynamics theory[3], configuration **a** is a branching point leading to the emergence of a polymorphism. In **c**, there is a single evolutionary attractor at $x = 1$, and a branching point does not exist. Despite these differences, a dimorphism evolves in the individual-based simulations for both scenarios. In scenarios without a branching point (such as **c**) this happens whenever mutational effect sizes are not too small. Here the mutation rate was $\mu = 3 \times 10^{-4}$ and mutational effect sizes were drawn from a normal distribution with mean zero and standard deviation of 0.05.

mutations can be neglected because they generally result in disintegrated phenotypes with low fitness[11]. But this is not necessarily the case. Consider, for example, a switching device that switches between two well-integrated phenotypes (in our model: superficial and thorough exploration). It is easily conceivable that a mutation that has a large effect on the position of the switch (such as one that knocks out one of the two phenotypes, thereby leading to the unconditional expression of the alternative phenotype) gives rise to a high-fitness individual.

The issues raised by Massol and Crochet[2] are important, but they should be put into the proper perspective. Their critique does not touch upon the main thrust of our theory[1], which is that individual differences in future reproductive value give rise to consistent individual differences in risk-related behaviour. We worked out[1] one (potentially important) model for the emergence of differences in future reproductive value, but we stressed that there are more mechanisms and processes leading to such differences. In all these cases, our theory predicts the emergence of personalities.

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