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Life-history trade-offs favour the evolution of animal personalities

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In recent years evidence has been accumulating that personalities are not only found in humans[1] but also in a wide range of other animal species[2–8]. Individuals differ consistently in their behavioural tendencies and the behaviour in one context is correlated with the behaviour in multiple other contexts. From an adaptive perspective, the evolution of animal personalities is still a mystery, because a more flexible structure of behaviour should provide a selective advantage[9–11]. Accordingly, many researchers view personalities as resulting from constraints imposed by the architecture of behaviour[7] (but see ref. 12). In contrast, we show here that animal personalities can be given an adaptive explanation. Our argument is based on the insight that the trade-off between current and future reproduction[13] often results in polymorphic populations[14] in which some individuals put more emphasis on future fitness returns than others. Life-history theory predicts that such differences in fitness expectations should result in systematic differences in risk-taking behaviour[15]. Individuals with high future expectations (who have much to lose) should be more risk-averse than individuals with low expectations. This applies to all kinds of risky situations, so individuals should consistently differ in their behaviour. By means of an evolutionary model we demonstrate that this basic principle results in the evolution of animal personalities. It simultaneously explains the coexistence of behavioural types, the consistency of behaviour through time and the structure of behavioural correlations across contexts. Moreover, it explains the common finding that explorative behaviour and risk-related traits like boldness and aggressiveness are common characteristics of animal personalities[2–8].

The phenomenon of animal personalities is one of the most intriguing challenges to the adaptationist programme in behavioural research. Empirical findings in more than 60 species, ranging from primates to ants, suggest that animal behaviour is much less flexible than previously thought[2–8]. Individuals consistently differ in whole suites of correlated behaviours and these differences are often heritable[16–19]. At present, the existence of such personalities (also termed behavioural syndromes[20], coping styles[5] or temperaments[21]) is puzzling in several respects. First, why do different personality types stably coexist? Second, why is behaviour not more flexible but correlated across contexts and through time? And third, why are the same types of traits correlated in very different taxa[5–7]? Here we develop an evolutionary model that provides answers to all of these questions.

We start with the observation that some of the most prominent personality traits described in the literature can be categorized in terms of risk-taking behaviour. A good example is the correlation between aggressiveness towards conspecifics and boldness towards predators: individuals that risk more in intraspecific fights also risk more when confronted with a predator. This aggression–boldness syndrome has been described for many species[7], including fish[22,23], birds[8] and rodents[5]. From life-history theory it is known that individuals should adjust their risk-taking behaviour to their residual reproductive value[13,15], that is, their expected future fitness. Individuals with relatively high expectations should be relatively risk-averse, because they have to survive to realize those expectations. By the same reasoning, individuals with relatively low expectations should be relatively risk-prone because they have little to lose. Consequently, whenever individuals differ in their fitness expectations, we should expect stable individual differences and correlated behavioural traits: some individuals are consistently risk-prone whereas others are consistently risk-averse.

By means of a simple model we now show that these intuitive arguments do indeed provide an evolutionary explanation for animal personalities. We proceed in three steps. First, we show that the trade-off between current and future reproduction can easily give rise to polymorphic populations in which some individuals put more emphasis on future reproduction than others. Second, we demonstrate that this variation in life-history strategies selects for systematic differences in risk-aversion. Third, we show that these differences in risk-taking behaviour extend to various risky situations and are stable over time, thereby giving rise to animal personalities.

Consider the following stylized life history (Fig. 1a). Individuals live for two years and reproduce at the end of each year. The foraging habitat is heterogeneous with both high- and low-quality resources. Individuals face a trade-off between reproduction in year 1 and reproduction in year 2 that is mediated by exploration behaviour. We characterize the exploration behaviour by the strategic variable x, which ranges from superficial ($x=0$) to thorough ($x=1$). Individuals that explore their environment thoroughly have a high probability of obtaining a high-quality resource in year 2. For simplicity, we let this probability correspond to x. Yet, the probability of reproducing in year 1, $g(x)$, decreases with the intensity of exploration. Here we take $g(x)=(1-x)^{\beta}$, where $\beta>1$.

The payoff from feeding on high- or low-quality resources declines with the density of individuals (N_{high} or N_{low}, respectively) competing for such resources. It is given by:

$$F_i=\frac{f_i}{1+\alpha N_i} \qquad (1)$$

for $i=$high or low, where $\alpha>0$ represents the strength of competition and f_{high} and f_{low} (where $f_{\mathrm{high}}>f_{\mathrm{low}}$) denote the intrinsic benefits of obtaining a high- and a low-quality resource, respectively. At the end of each year, individuals produce a number of offspring that is proportional to the payoff they obtained in that year. To summarize, an individual with exploration intensity x produces $g(x)F_{\mathrm{low}}$ offspring at the end of its first year; at the end of its second year it produces F_{high} offspring with probability x and F_{low} offspring with probability $1-x$.

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For this basic life cycle, natural selection gives rise to the stable coexistence of two extreme exploration strategies (Fig. 1b): some individuals explore the environment thoroughly, thereby investing in future reproductive success, whereas others explore superficially, putting more emphasis on current reproduction. This dimorphism is a stable evolutionary outcome whenever $2f_{\text{low}} > f_{\text{high}} > 1$ (see Supplementary Information).

We now extend the above life history by assuming that each individual is confronted with a number of risky contexts[20] throughout its lifetime (see Methods). Between year 1 and year 2, each individual may face one or more foraging decisions under predation risk (anti-predator games) and one or more aggressive encounters with randomly chosen conspecifics. In each of the anti-predator games an individual can either behave in a bold or a shy manner. Only bold individuals receive a payoff (in terms of higher fecundity) but they also incur some risk of dying. Aggressive encounters are modelled as hawk–dove games[24], in which hawks receive a higher payoff than doves but do not always survive hawk–hawk interactions.

Let us first consider the two most basic cases, where all individuals either play one anti-predator game or one hawk–dove game. Our individual-based simulations (Fig. 2) confirm the general principle[15] that individuals with higher future expectations (in our case, thorough explorers) should behave in a more cautious way. Superficial explorers evolve to behave boldly (aggressively), whereas thorough explorers evolve low levels of boldness (aggressiveness). This outcome is consistent across replicate simulations and holds for a broad range of parameter conditions (see Supplementary Information).

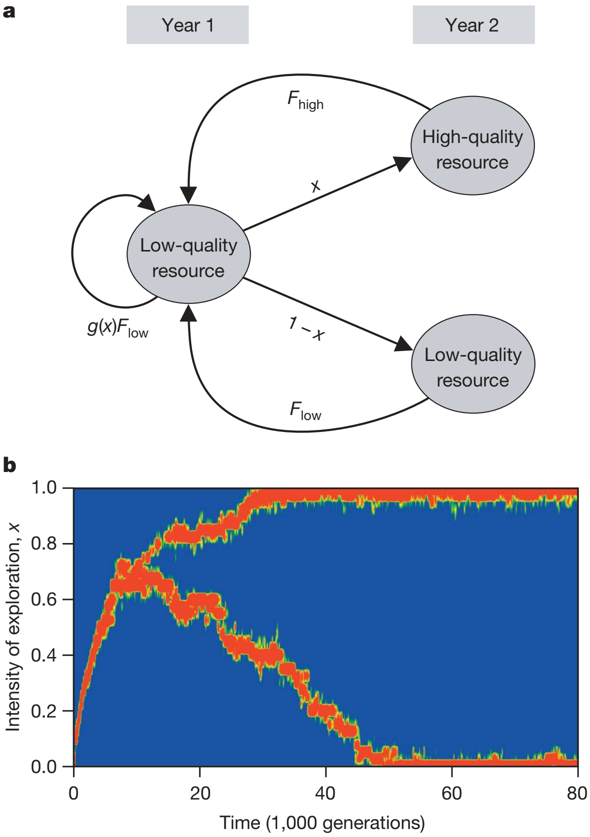

Figure 1 | Stable coexistence of exploration strategies owing to a life-history trade-off. **a**, Structure of the life-history model illustrating the trade-off between current and future reproduction. Natural selection acts on the exploration intensity x that corresponds to the probability of finding a high-quality resource in the future. Although having a positive effect on reproduction in year 2 (future fitness), a high value of x decreases the probability $g(x)$ of obtaining reproductive resources in year 1. F_{low} and F_{high} denote the reproductive output in the case of a low- and high-quality resource, respectively. **b**, The trade-off in **a** induces disruptive selection on exploration intensity and gives rise to the stable coexistence of superficial ($x = 0$) and thorough ($x = 1$) explorers.

To show that this principle gives rise to personalities, we next consider scenarios where individuals play several risky games between year 1 and year 2. We stress that, in principle, fully flexible behaviour could evolve in all our simulations. For example, an individual that behaves aggressively in a first hawk–dove game could behave shyly in an anti-predator game and show any level of aggression in a subsequent hawk–dove game. Yet, we find that selection gives rise to stable individual differences within the same game and correlated behavioural traits across different games (Fig. 3). Figure 3a considers the scenario where individuals play two hawk–dove games sequentially. Here superficial explorers evolve high levels of aggression in both games, whereas thorough explorers evolve to be consistently non-aggressive. Figure 3b depicts the scenario where individuals face one anti-predator and one hawk–dove game sequentially. Here evolution gives rise to the coexistence of superficial explorers that are both bold and aggressive and thorough explorers that are shy and non-aggressive. These results are consistent across replicate simulations (Fig. 3c, d), they hold for a broad range of parameter conditions (see Supplementary Information) and they extend to more complex situations where individuals play more than two games (not shown). In other words, we robustly observe the well-known behavioural syndrome linking explorative behaviour, aggression and boldness, which has been reported for numerous species in a diversity of taxa[5,7,8].

Up to now we have assumed, for simplicity, that individuals reproduce asexually. We obtain qualitatively the same results for scenarios that allow for recombination and diploid genetics, as long as individual alleles have a large phenotypic effect. Under this condition disruptive selection gives rise to a small number of discrete phenotypes[25,26], each corresponding to a distinct personality type. A more realistic approach, however, would be to consider quantitative traits, which are often thought to be influenced by many loci with small effects. We now incorporate such quantitative genetics into our model (see Methods).

Consider a scenario where individuals face one anti-predator and one hawk–dove game sequentially. As shown in Fig. 4a, disruptive selection does not now result in two extreme exploration strategies but in the stable coexistence of a broad range of explorative behaviours. Similarly, with respect to both boldness and aggressiveness,

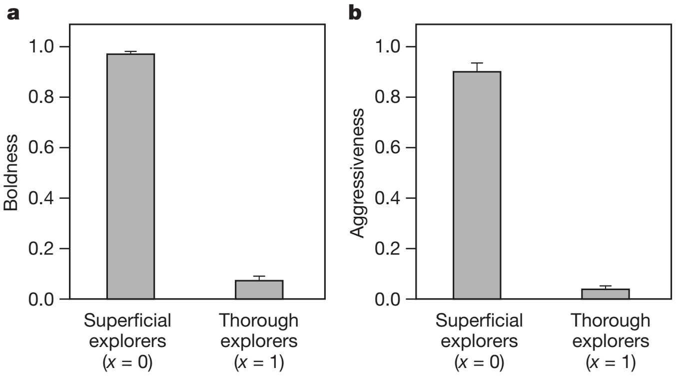

Figure 2 | Evolution of variation in risk-taking behaviour. The outcome of evolution after 3×10^5 generations of selection where individuals following the life cycle depicted in Fig. 1 play a single risky game between year 1 and year 2. **a**, In the case of an anti-predator game superficial explorers evolve high levels of boldness, whereas thorough explorers show low levels of boldness. **b**, In the case of a hawk–dove game superficial explorers are aggressive, whereas thorough explorers are non-aggressive. The bars correspond to mean trait values averaged over ten replicate simulations (error bars indicate standard errors).

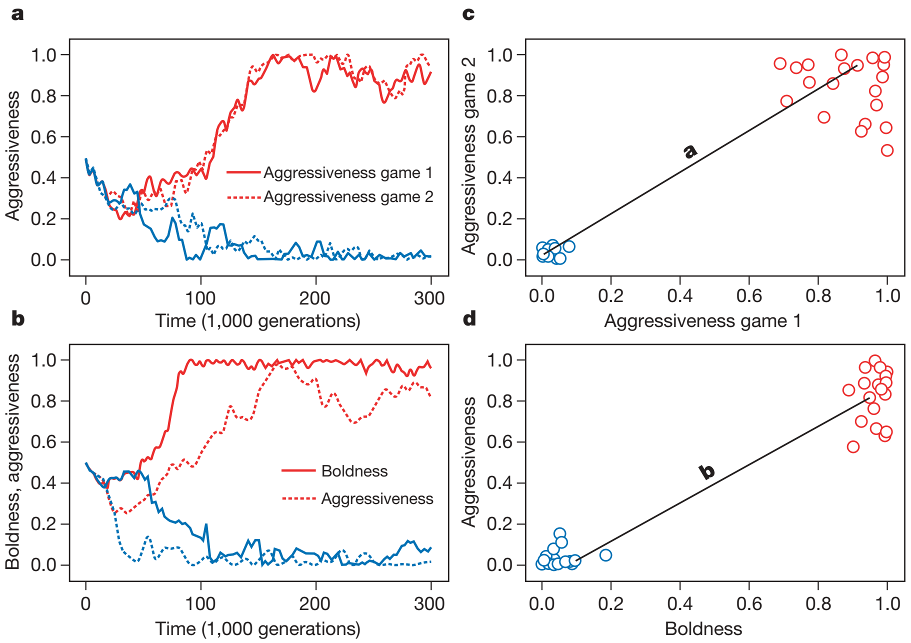

Figure 3 | Evolution of personalities. Simulations illustrating the evolution of consistent individual differences between superficial explorers (red) and thorough explorers (blue). **a**, When individuals face two hawk–dove games superficial explorers evolve high levels of aggressiveness in both games, whereas thorough explorers are consistently non-aggressive. **b**, Confronted with both an anti-predator and a hawk–dove game a behavioural syndrome evolves: superficial explorers are bold and aggressive, whereas thorough explorers are shy and non-aggressive. These outcomes are robust across replicate simulations. **c** and **d** summarize the outcome of 20 replicate simulations for the scenarios in **a** and **b**, respectively. Each simulation is represented by two circles corresponding to the evolved trait combinations of superficial and thorough explorers. Black lines indicate the trait combinations for the simulations depicted in **a** and **b**.

we find a gradation of behavioural traits ranging from low to high levels (Fig. 4b, c). A clear pattern emerges: the more superficially an individual explores its environment (Fig. 4a), the more boldly it behaves in the anti-predator game (Fig. 4b) and the more aggressive it is in the hawk–dove game (Fig. 4c). In other words, in the case of quantitative genetic variation we find a whole spectrum of personality types, which is in line with many empirical studies[12,27] (but see ref. 5).

To sum up, our model offers a plausible explanation for individual differences within a population, the evolution of behavioural correlations within and across contexts and the fact that particular traits such as explorative behaviour, boldness and aggressiveness tend to be associated. Our theory is well testable by predicting (1) under what circumstances behavioural correlations should occur, (2) what particular traits should be correlated and (3) what sign the correlations should take. Behavioural correlations are to be expected whenever individual differences in residual reproductive value (that is, expected future fitness) occur. One might think of the difference between high- and low-ranking individuals in a dominance hierarchy, between dispersers and philopatric individuals in a metapopulation or between residents and floaters in a territorial system. In any such situation, we would expect correlations between those behavioural traits that involve risks that might prevent individuals from reaping the returns from reproductive investments. In addition to intraspecific aggression and boldness, one might also think of behaviours such as brood defence, nest guarding or conspicuous displays to attract mates. All other things being equal, we would expect such traits to be positively correlated.

Our model certainly does not explain all aspects of animal personalities (for example, cooperativeness[28]) and alternative evolutionary mechanisms may also have an important role (refs 10, 11, 29, 30). Yet, as argued above, we believe that our line of argument applies to a broad class of ecological situations. In all these situations the same basic principle will give rise to the evolution of animal personalities: the more an individual has to lose, the more risk-averse it should be, across contexts and through time.

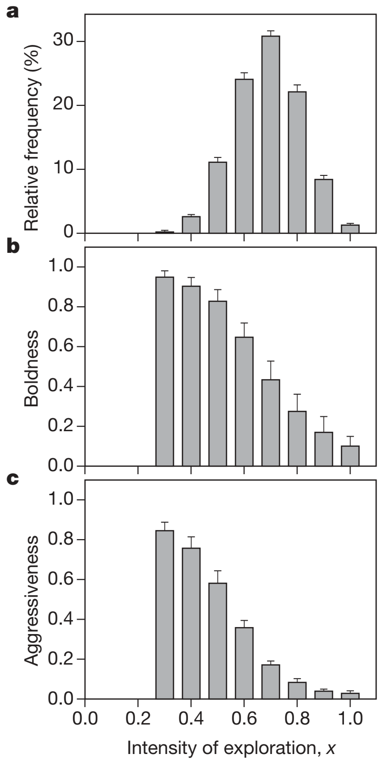

Figure 4 | Evolution of continuous variation in personalities. a, If all traits are encoded by multiple loci with small effects, disruptive selection on the exploration intensity x does not result in two discrete phenotype classes but in a broad distribution of exploration strategies. The graphs depict the average level of boldness (**b**) and aggressiveness (**c**) that evolved as a function of x within 2×10^5 generations (mean of ten replicate simulations; error bars indicate standard errors). The evolved levels of boldness and aggressiveness are strongly correlated, corresponding to a boldness–aggressiveness syndrome (correlation coefficients in the ten simulations ranged from 0.40 to 0.81, with a mean value of 0.65).

METHODS SUMMARY

Our conclusions are based on general arguments that are supported by individual-based simulations (main text) and analytical results based on evolutionary invasion considerations (Supplementary Information). We consider a population where individuals follow the basic life cycle illustrated by Fig. 1a. Moreover, between year 1 and year 2, each individual plays one or more anti-predator games and/or one or more hawk–dove games. Individuals are characterized by a suite of heritable traits corresponding to (1) their life-history strategy x, (2) for each anti-predator game the tendency to be bold, and (3) for each hawk–dove game the tendency to be aggressive. Individuals could in principle evolve fully flexible behaviour. For example, an individual that behaves aggressively in a first hawk–dove game could exhibit low levels of aggressions in a subsequent hawk–dove game.

The reproductive success of individuals is frequency- and density-dependent and reflects the fecundity associated with the life-history strategy, the mortality risks associated with bold and aggressive behaviour, and the payoff accumulated in the games. The resulting fitness function is analysed in the Supplementary Information by means of an invasion analysis. In the main text, the assumptions are implemented in individual-based simulations in which trait frequencies change over time under the influence of natural selection. The simulations were run until evolutionary equilibrium was reached. The resulting population was analysed focusing on three key questions. First, does evolution give rise to the coexistence of life-history strategies? Second, does evolution result in stable differences between individuals if the same game is played repeatedly? And third, does evolution lead to behavioural correlations between boldness and aggressiveness?

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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METHODS

Basic model. We first consider an asexual population of haploid individuals. Each individual is characterized by the allelic values at $k+1$ loci, where one locus determines the exploration behaviour and the other loci determine the behaviour in the k games played between year 1 and year 2. Allelic values range between 0 and 1 and correspond to the exploration intensity x or the strategy in a particular game (probability of being bold or aggressive).

In the first year, an individual with exploration intensity x produces $g(x)F_{\mathrm{low}}$ offspring, where $g(x) = (1-x)^{\beta}$. All figures are based on $\beta = 1.25$, but similar results are obtained for all $\beta > 1$. Between years 1 and 2, an individual accumulates payoffs in the games it participates in, but it also runs the risk of dying (see below). If an individual survives, its reproductive output in year 2 is increased by the payoff it accumulated in these games. All figures shown are based on $f_{\mathrm{high}} = 3.5$, $f_{\mathrm{low}} = 3.0$ and $\alpha = 0.005$, but similar results are obtained as long as $2f_{\mathrm{low}} > f_{\mathrm{high}} > 1$.

During reproduction, mutations occur with a small probability $\mu = 2 \times 10^{-3}$. Mutations have a small effect: they change the allelic value by a value that is drawn from a normal distribution with mean zero and standard deviation 0.02, with the constraint that allelic values remain in the interval from 0 to 1. All results are independent of the specific parameter values for the mutational process and the initial conditions.

Anti-predator games and aggressive encounters. In each of the anti-predator (hawk–dove) games, an individual behaves boldly (aggressively) with a probability determined by its genotype. In an anti-predator game, a bold individual obtains a payoff b but dies with probability γ, whereas a shy individual obtains no payoff and always survives. Aggressive encounters are modified hawk–dove games where individuals fight for a resource of value V. In such an encounter, individuals are paired at random. Payoffs are obtained as in the standard hawk–dove game[24] with one exception: if two aggressive ('hawk') individuals meet, one gets V while the opponent gets 0 and moreover dies with probability δ. All figures are based on $b = 0.1$ and $\gamma = 0.1$ for each of the anti-predator games and $V = 0.1$ and $\delta = 0.5$ for each of the hawk–dove games.

Quantitative genetics. In the model underlying Fig. 4, we consider a sexual population of diploid individuals in which each behaviour is governed by multiple loci with small effects. We consider a scenario with one anti-predator and one hawk–dove game. In total there are five different traits (see below), each of which is governed by a set of five unlinked diallelic loci. There is additive interaction within and across loci, implying that there are in total 11 equidistant phenotypic values for each trait. The first trait corresponds to the exploration strategy, where the different genotypes correspond to 11 exploration tendencies ranging from 0 to 1 in steps of 0.1. The strategy in the anti-predator (hawk–dove) game is modelled as a norm of reaction[13]. The shape of the reaction norm is characterized by two genetically determined parameters a and b such that an individual with exploration intensity x behaves boldly (aggressively) with a probability given by the logistic function $1/\{1 + \exp[-b(x-a)]\}$. The value of a corresponds to the exploration intensity at which both behavioural options (bold–shy and hawk–dove, respectively) are chosen with equal probability, whereas b determines the slope of the reaction norm at $x = a$. As described above, a and b are each encoded by a set of five loci with range restrictions $0 \leq a \leq 1$ and $-25 \leq b \leq 25$.

Payoffs are obtained as described above, individuals mate at random, and the number of offspring produced per individual at the end of each year is proportional to the total payoff obtained in that year. With a small probability ($\mu = 2 \times 10^{-5}$) a mutation occurs at a randomly chosen locus. When this happens, the affected allele changes into the alternative allele.

Do animal personalities emerge?

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

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

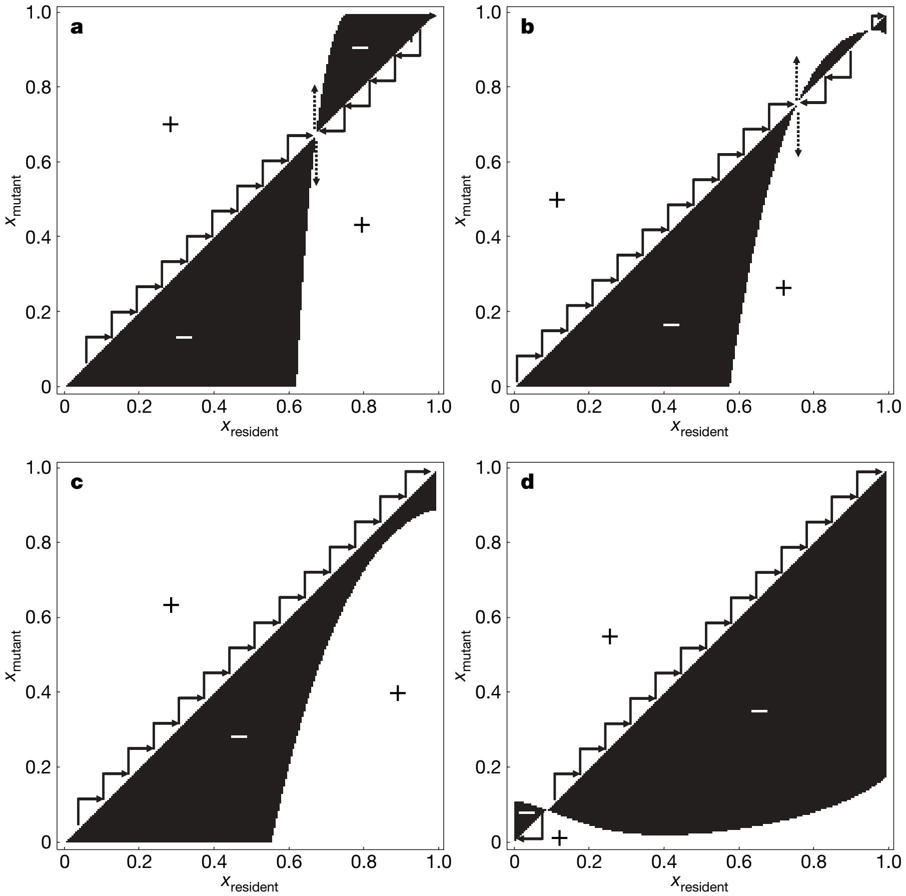

Figure 1 | Pairwise invasibility plots. These diagrams show which mutant strategies can invade in an initially monomorphic situation. The *x* axis represents the initial exploring strategy (X_{resident}), and the *y* axis, the mutant strategy (X_{mutant}). White regions indicate cases where the mutant 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

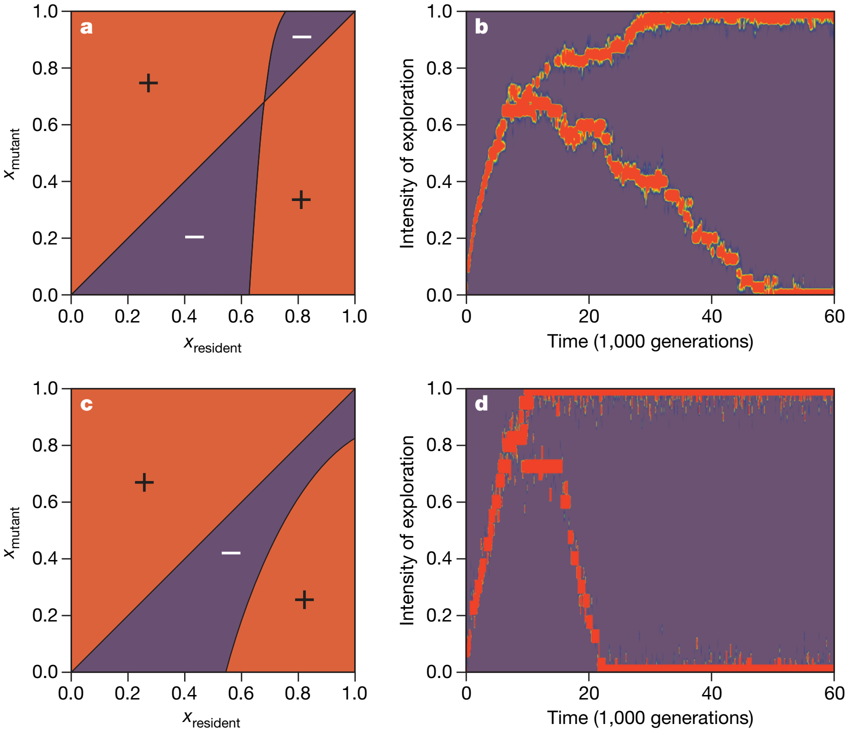

Figure 1 | Emergence of a polymorphism in the presence and in the absence of a branching point. Pairwise invasibility plots are shown together with corresponding individual-based simulation results for two values of the trade-off parameter β. In **a** and **b**, $\beta = 1.25$, the standard parameter 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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