LETTERS

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

Max Wolf[1], G. Sander van Doorn[1]†, Olof Leimar[2] & Franz J. Weissing[1]

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:

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

for $i =$ high or low, where $\alpha > 0$ represents the strength of competition and f_{high} and f_{low} (where $f_{high} > f_{low}$) 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 $g(x)F_{low}$ 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 $1 - x$.

[1]Theoretical Biology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Kerklaan 30, 9751 NN Haren, The Netherlands. [2]Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden. †Present address: Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA.

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 $2f_{low} > f_{high} > 1$ (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).

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,
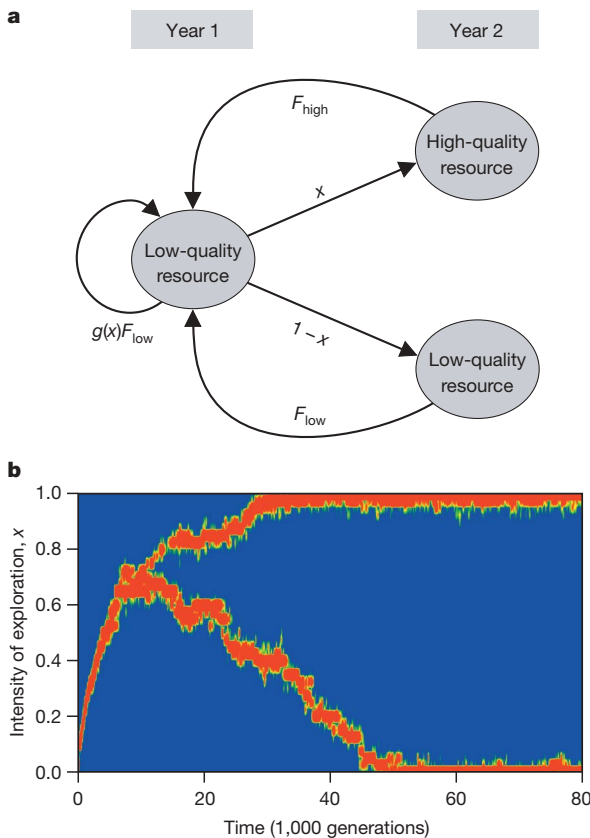

Figure 1 | Stable coexistence of exploration strategies owing to a life-history trade-off. a, Structure of the life-history model illustrating the trade-off between current and future reproduction. Natural selection acts on the exploration intensity x that corresponds to the probability of finding a 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.
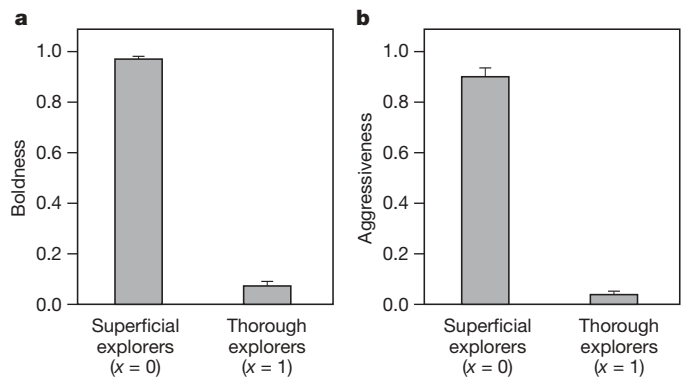

Figure 2 | Evolution of variation in risk-taking behaviour. The outcome of evolution after 3×10^5 generations of selection where individuals following the life cycle depicted in Fig. 1 play a single risky game between year 1 and year 2. **a,** In the case of an anti-predator game superficial explorers 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).
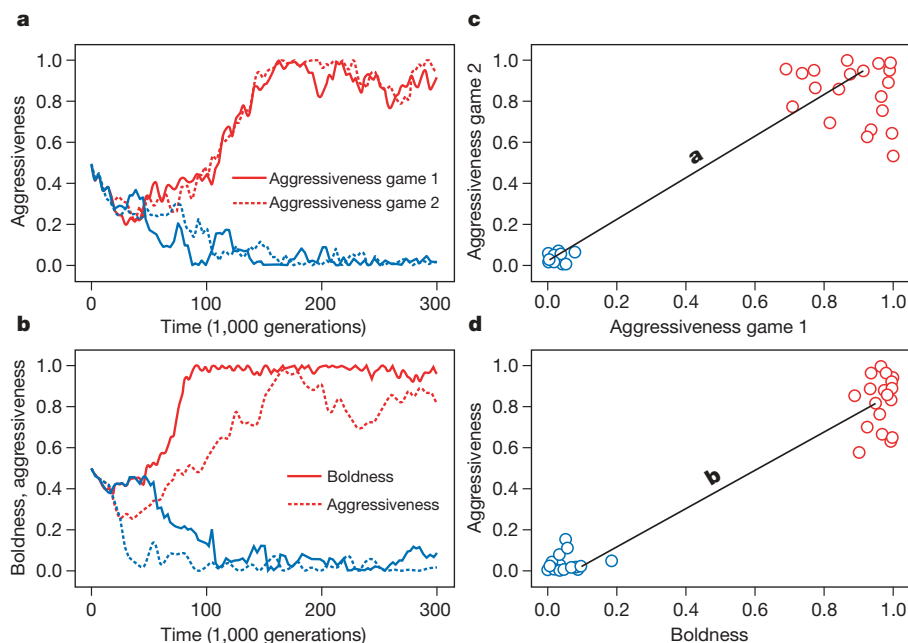
Figure 3 | Evolution of personalities. Simulations illustrating the evolution of consistent individual differences between superficial explorers (red) and thorough explorers (blue). **a**, When individuals face two hawk–dove games superficial explorers evolve high levels of aggressiveness in both games, 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 person-ality 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 corre-lations 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 correla-tions should take. Behavioural correlations are to be expected when-ever 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 hier-archy, between dispersers and philopatric individuals in a meta-population 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 person-alities (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.
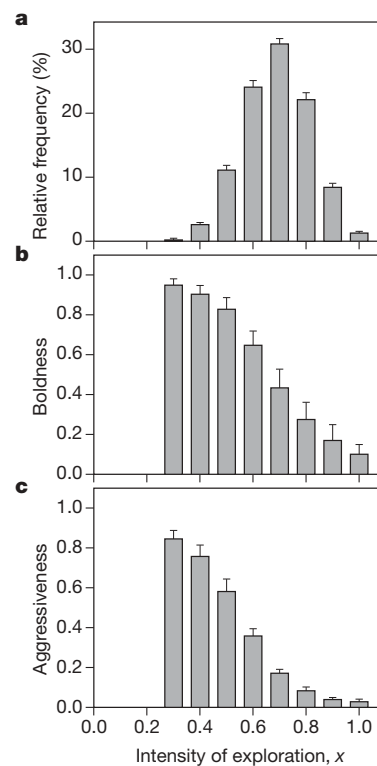

Figure 4 | Evolution of continuous variation in personalities. a, If all traits are encoded by multiple loci with small effects, disruptive selection on the exploration intensity x does not result in two discrete phenotype classes but in a broad distribution of exploration strategies. The graphs depict 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.

1. Pervin, L. A. & John, O. P. (eds) *Handbook of Personality: Theory and Research* (The Guilford Press, New York, 1999).
2. Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446 (1994).
3. Boissy, A. Fear and fearfulness in animals. *Q. Rev. Biol.* **70**, 165–191 (1995).
4. Gosling, S. D. & John, O. P. Personality dimensions in nonhuman animals: a cross-species review. *Curr. Dir. Psychol. Sci.* **8**, 69–75 (1999).
5. Koolhaas, J. M. *et al.* Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* **23**, 925–935 (1999).
6. Gosling, S. D. From mice to men: What can we learn about personality from animal research? *Psychol. Bull.* **127**, 45–86 (2001).
7. Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* **79**, 241–277 (2004).
8. Groothuis, T. G. G. & Carere, C. Avian personalities: characterization and epigenesis. *Neurosci. Biobehav. Rev.* **29**, 137–150 (2005).
9. Coleman, K. & Wilson, D. S. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim. Behav.* **56**, 927–936 (1998).
10. Wilson, D. S. Adaptive individual differences within single populations. *Phil. Trans. R. Soc. Lond. B* **353**, 199–205 (1998).
11. Dall, S. R. X., Houston, A. I. & McNamara, J. M. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**, 734–739 (2004).
12. Bell, A. M. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *J. Evol. Biol.* **18**, 464–473 (2005).
13. Roff, D. A. *Life History Evolution* (Sinauer, Sunderland, 2002).
14. Rueffler, C., Van Dooren, T. J. M. & Metz, J. A. J. Adaptive walks on changing landscapes: Levins' approach extended. *Theor. Popul. Biol.* **65**, 165–178 (2004).
15. Clark, C. W. Antipredator behavior and the asset-protection principle. *Behav. Ecol.* **5**, 159–170 (1994).
16. Drent, P. J., Van Oers, K. & Van Noordwijk, A. J. Realized heritability of personalities in the great tit (*Parus major*). *Proc. R. Soc. Lond. B* **270**, 45–51 (2003).
17. Dingemanse, N. J., Both, C., Drent, P. J., Van Oers, K. & Van Noordwijk, A. J. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.* **64**, 929–938 (2002).
18. Bakker, T. C. M. Aggressiveness in sticklebacks (*Gasterosteus aculeatus*)—a behavior–genetic study. *Behaviour* **98**, 1–144 (1986).
19. Sinn, D. L., Apiolaza, L. A. & Moltschaniwskyj, N. A. Heritability and fitness-related consequences of squid personality traits. *J. Evol. Biol.* **19**, 1437–1447 (2006).
20. Sih, A., Bell, A. & Johnson, J. C. Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378 (2004).
21. Reale, D., Gallant, B. Y., Leblanc, M. & Festa-Bianchet, M. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim. Behav.* **60**, 589–597 (2000).
22. Huntingford, F. A. Relationship between anti-predator behavior and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus. Anim. Behav.* **24**, 245–260 (1976).
23. Bell, A. M. & Stamps, J. A. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus. Anim. Behav.* **68**, 1339–1348 (2004).
24. Maynard Smith, J. *Evolution and the Theory of Games* (Cambridge Univ. Press, Cambridge, 1982).
25. Rueffler, C., Van Dooren, T. J. M., Leimar, O. & Abrams, P. A. Disruptive selection and then what? *Trends Ecol. Evol.* **21**, 238–245 (2006).
26. Van Doorn, G. S. & Dieckmann, U. The long-term evolution of multi-locus traits under frequency-dependent disruptive selection. *Evolution* **60**, 2226–2238 (2006).
27. Dingemanse, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. Fitness consequences of avian personalities in a fluctuating environment. *Proc. R. Soc. Lond. B* **271**, 847–852 (2004).
28. McNamara, J. M., Barta, Z. & Houston, A. I. Variation in behaviour promotes cooperation in the prisoner's dilemma game. *Nature* **428**, 745–748 (2004).
29. 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).
30. Hedrick, A. V. Crickets with extravagant mating songs compensate for predation risk with extra caution. *Proc. R. Soc. Lond. B* **267**, 671–675 (2000).

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 $g(x)F_{low}$ 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 $f_{high} = 3.5$, $f_{low} = 3.0$ and $\alpha = 0.005$, but similar results are obtained as long as $2f_{low} > f_{high} > 1$.

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.