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

Max Wolf, G. Sander van Doorn, Olof Leimar & Franz J. Weissing

The conclusions in the main text are based on general arguments that are supported by individual-based simulations. We show here that the corresponding simulation results are robust and apply to a broad range of parameter regimes. Throughout we assume that individuals follow the basic life cycle that is illustrated by Figure 1a in the main text. In our model, a prerequisite for the evolution of animal personalities is a stable polymorphism of the exploration trait x. We therefore start by demonstrating that the coexistence of superficial and thorough explorers is a stable evolutionary outcome whenever the trade-off between current and future reproduction is convex (Section 1). In Sections 2 and 3, we study the consequences of this dimorphism in exploration traits on the evolution of behavioural strategies in a single anti-predator game and a single hawk-dove game. Here, as in the subsequent sections, we allow individuals to condition their behaviour in these games on their explorative behaviour. For both games the result is that in evolutionary equilibrium superficial explorers will always be at least as risk-prone as thorough explorers and strictly more risk-prone for a broad range of parameter combinations. In Sections 4 and 5, we study the evolution of behavioural correlations across games (i.e., one anti-predator and one hawk-dove game) and stable individual differences within games (i.e., two hawk-dove games). We demonstrate that personalities are stable evolutionary outcomes for a broad range of parameter settings.

1. Coexistence of exploration strategies

As in the main text, we first focus on the situation where individuals play no games. In the simulations, we observed the emergence of a dimorphism in exploration strategies: the investment in exploration is high (even maximal) for part of the population (thorough explorers; $x_h = 1$) while it is low (even minimal) for the rest (superficial explorers; $x_l = 0$). We here show that this is a robust outcome.

Result 1. The dimorphism $\left(x_h = 1, x_l = 0\right)$ is a stable evolutionary equilibrium whenever $\beta > 1$ and $2f_l > f_h > 1$, i.e. whenever the trade-off between current and future reproduction is convex and the intrinsic benefit f_h of obtaining a high-quality resource is high enough to prevent extinction of the population but not high enough to make thorough exploration the dominant strategy.

Proof. Let n_h and n_l denote the density of age 1 individuals with exploration trait $x_h = 1$ and $x_l = 0$, respectively. Let F_h and F_l be the number of offspring produced by individuals feeding on a high- and a low-quality resource, respectively. The population dynamics of the dimorphic population $\left(x_h, x_l\right)$ is then governed by the equations

$$\begin{aligned} n_h(t+1) &= n_h(t-1)F_h(t) \\ n_l(t+1) &= n_l(t)F_l(t) + n_l(t-1)F_l(t) \end{aligned} \tag{1}$$

with $F_h(t) = \dfrac{f_h}{1+\alpha n_h(t-1)}$ and $F_l(t) = \dfrac{f_l}{1+\alpha\left(n_l(t)+n_h(t)+n_l(t-1)\right)}$. It is obvious from (1) that in any population dynamical equilibrium $\hat{F}_h = 1$ and $\hat{F}_l = \frac{1}{2}$. The unique population dynamical equilibrium with positive densities for both exploration types is therefore given by

$$\hat{n}_h = \frac{f_h - 1}{\alpha}, \quad \hat{n}_l = \frac{2f_l - f_h}{2\alpha}. \tag{2}$$

For $2f_l > f_h > 1$ a positive equilibrium exists, which is always asymptotically stable.

Let us therefore assume that the dimorphic population (x_h, x_l) has settled on its population dynamical equilibrium (2). We now show that this dimorphism is globally invasion stable, as long as $\beta > 1$. In other words, no rare mutant with an exploration intensity $0 < x < 1$ can grow in the population. The population dynamics of a rare mutant with strategy x is given by

$$n(t+1) = n(t)(1-x)^{\beta}\,\hat{F}_l + n(t-1)\big((1-x)\,\hat{F}_l + x\hat{F}_h\big). \tag{3}$$

The growth rate $\lambda(x)$ of this mutant is given by the dominant solution of the corresponding characteristic equation, which in view of $\hat{F}_h = 1$ and $\hat{F}_l = \frac{1}{2}$ is given by

$$\lambda^2 - (1-x)^{\beta}\,\hat{F}_l\,\lambda - \big((1-x)\,\hat{F}_l + x\hat{F}_h\big) = \lambda^2 - \tfrac{1}{2}(1-x)^{\beta}\,\lambda - \tfrac{1}{2}(1+x) = 0\,. \tag{4}$$

The resident equilibrium is immune against invasion by x if $\lambda(x)$ is smaller than one, the growth rate of the two resident strategies. It is well known (e.g., Edelstein-Keshet 2005) that the dominant solution of the quadratic equation $\lambda^2 + a_1\lambda + a_0 = 0$ is smaller than one in absolute value whenever $|a_1| < 1 + a_0 < 2$. When applied to equation (4), this yields $\frac{1}{2}(1-x)^{\beta} < \frac{1}{2}(1-x) < 2$ or, equivalently, $\beta > 1$. Hence no mutant strategy $0 < x < 1$ can invade the resident dimorphism if $\beta > 1$. This establishes Result 1.

2. Risk-aversion in a single anti-predator game

In view of Result 1, from now on we make the simplifying assumption that the population is dimorphic with respect to exploration intensity, with $x_h = 1$ and $x_l = 0$. In this section we study a situation were each individual plays one anti-predator game between year 1 and year 2. In this game, individuals can either be bold or shy. A bold individual receives a payoff b but dies with probability γ whereas a shy individual receives no payoff and always survives. Since the anti-predator game is embedded in a life-history context we imagine b to be relatively small when compared to the life-history payoff (i.e., $b < \hat{F}_l = \tfrac{1}{2}$).

Individuals can condition their behaviour on their exploration intensity x. The strategy of an individual is therefore a pair $y = (y_h, y_l)$, where y_h (resp. y_l) is the probability of behaving boldly given that the individual has explored its environment with intensity x_h (resp. x_l). We now derive

Result 2. The unique invasion proof equilibrium strategy $y^* = (y_h^*, y_l^*)$ has the following properties:

(a) Superficially exploring individuals are at least as risk-prone as thoroughly exploring individuals, i.e. $y_l^* \geq y_h^*$.

(b) For $\tfrac{1}{2}\Gamma < b < \Gamma$ superficial explorers are always bold whereas thorough explorers are always shy:

$$\tfrac{1}{2}\Gamma < b < \Gamma \quad \Leftrightarrow \quad (y_h^*, y_l^*) = \left(0,1\right) \tag{5}$$

where $\Gamma = \dfrac{\gamma}{1-\gamma}$ is a measure for the mortality-risk in the anti-predator game.

Proof. Consider a resident population playing $\hat{y} = (\hat{y}_h, \hat{y}_l)$ at its population dynamical equilibrium, with corresponding payoffs $(\hat{F}_h, \hat{F}_l)$. Let us first consider a mutant with $y = (y_h, \hat{y}_l)$, i.e. a mutant only differing from the resident in its probability of being bold after having explored the environment thoroughly. Since the mutation has no effect in case of superficial exploration we can, without loss of generality, focus on mutants that are thorough explorers. The population dynamics of such a mutant is characterised by

$$n(t+1) = n(t-1)\Big(\left(1 - y_h\right)\hat{F}_h + y_h\left(1-\gamma\right)\left(\hat{F}_h + b\right)\Big). \tag{6}$$

The growth rate $\lambda(y,\hat{y})$ of this mutant is therefore

$$\lambda(y,\hat{y}) = \sqrt{\,y_h\left((1-\gamma)b-\gamma\hat{F}_h\right)+\hat{F}_h\,}\,. \tag{7}$$

Note that λ is a strictly monotonic function in the mutant trait y_h. Using $\hat{F}_h = \dfrac{1-\hat{y}_h(1-\gamma)b}{1-\gamma\hat{y}_h}$ it is easy to see that the coefficient of y_h in (7) is positive for $b>\Gamma$ and negative for $b<\Gamma$, where $\Gamma = \dfrac{\gamma}{1-\gamma}$. Hence $y_h = 1$ is the best response to $\hat{y}$ for $b>\Gamma$ (i.e., the strategy y maximising $\lambda(y,\hat{y})$), while $y_h = 0$ is the best response to $\hat{y}$ for $b<\Gamma$. As a consequence, $y_h^* = 1$ is the unique invasion proof behaviour for $b>\Gamma$ whereas $y_h^* = 0$ is the unique invasion proof behaviour for $b<\Gamma$.

Let us now consider a mutant of the form $y = (\hat{y}_h, y_l)$. In this case we can assume, without loss of generality, that the mutant is a superficial explorer. The population dynamics of such a rare mutant is now governed by

$$n(t+1) = n(t)\hat{F}_l + n(t-1)\Big((1-y_l)\hat{F}_l + y_l(1-\gamma)\big(\hat{F}_l + b\big)\Big). \tag{8}$$

Using $\hat{F}_l = \dfrac{1-\hat{y}_l(1-\gamma)b}{2-\gamma\hat{y}_l}$, analogous considerations as above show that $y_l^* = 1$ is the unique invasion proof behaviour for $b > \frac{1}{2}\Gamma$ whereas $y_l^* = 0$ is the unique invasion proof behaviour for $b < \frac{1}{2}\Gamma$. Taken together, these considerations establish Result 2.

3. Risk-aversion in a single hawk-dove game

In this section we study a situation where each individual plays one hawk-dove game with a randomly chosen partner between year 1 and year 2. If two doves are matched, both get a payoff $V/2$. If a hawk meets a dove, the hawk gets V while the opponent gets 0. If two hawks are matched, one gets V while the opponent gets 0 and moreover dies with probability δ. Now we imagine V to be relatively small compared to the life-history payoffs (i.e., $V < \hat{F}_l = \frac{1}{2}$).

As in the case of an anti-predator game, the strategy of an individual is a pair $z = (z_h, z_l)$, where z_h and z_l are the conditional probabilities with which an individual plays hawk. We now show

Result 3. Any invasion proof equilibrium strategy $z^* = (z_h^*, z_l^*)$ has the following properties:

(a) Superficial explorers are at least as risk-prone as thorough explorers, i.e. $z_l^* \geq z_h^*$.

(b) If the payoff V is sufficiently small, superficial explorers will play hawk with a strictly higher probability than thorough explorers:

$$V < \delta \quad \Rightarrow \quad z_l^* > z_h^*. \tag{9}$$

Proof. Consider a resident population playing $\hat{z} = (\hat{z}_h, \hat{z}_l)$ at its population dynamical equilibrium $(\hat{F}_h, \hat{F}_l, \hat{\pi})$, where $\hat{\pi}$ is the frequency of hawks in the resident population. Again we consider two types of rare mutants in turn. First consider a mutant strategy of the form $z = (z_h, \hat{z}_l)$. As in the previous section we may assume that the mutant is a thorough explorer. This implies that the population dynamics of the rare mutant is given by

$$n(t+1) = n(t-1)\left(z_h \hat{E}_{hawk} + \left(1 - z_h\right) \hat{E}_{dove} \right) \tag{10}$$

where $\hat{E}_{hawk}$ and $\hat{E}_{dove}$ is the expected reproductive success of a thoroughly exploring individual given that it plays hawk or dove, respectively. These expectations are given by

$$\begin{aligned} \hat{E}_{hawk} &= (1 - \tfrac{1}{2}\delta\hat{\pi})\hat{F}_h + \left(1 - \hat{\pi}\right)V + \hat{\pi}\tfrac{1}{2}V = \hat{F}_h + V - \hat{\pi}\tfrac{1}{2}(V + \delta\hat{F}_h) \\ \hat{E}_{dove} &= \hat{F}_h + \left(1 - \hat{\pi}\right)\tfrac{1}{2}V. \end{aligned} \tag{11}$$

The growth rate of the mutant is of the form

$$\lambda(z,\hat{z}) = \sqrt{z_h \hat{E}_{hawk} + \left(1 - z_h\right) \hat{E}_{dove}} = \sqrt{\hat{E}_{dove} + z_h(\hat{E}_{hawk} - \hat{E}_{dove})}\,. \tag{12}$$

Note that λ is a strictly monotonic function in the mutant trait z_h, implying that $z_h = 1$ is the best response to $\hat{z}$ if $\hat{E}_{hawk} > \hat{E}_{dove}$, while $z_h = 0$ is the best response if $\hat{E}_{hawk} < \hat{E}_{dove}$. The difference $\hat{E}_{hawk} - \hat{E}_{dove}$ is proportional to $V - \hat{\pi}\delta\hat{F}_h$. Using the fact that in population dynamical equilibrium $\hat{F}_h = \left(1 - \frac{1}{2}V(1 + \hat{z}_h - \hat{\pi})\right) \big/ (1 - \frac{1}{2}\delta\hat{\pi}\hat{z}_h)$, a straightforward calculation yields that $\hat{E}_{hawk} > \hat{E}_{dove}$ whenever $\hat{\pi}^2 + 2C\hat{\pi} - \frac{2}{\delta} < 0$, where $C = \frac{1}{V} - \frac{1}{2}$. From this we can conclude:

$$\hat{E}_{hawk} - \hat{E}_{dove} > 0 \quad \Leftrightarrow \quad \hat{\pi} < T_h\left(V, \delta\right) = -C + \sqrt{C^2 + 2/\delta}\,. \tag{13}$$

Hence $z_h = 1$ is the best response to the resident strategy if $\hat{\pi}$, the frequency of hawks in the resident population is below the threshold value T_h, and $z_h = 0$ is the best response if $\hat{\pi}$ is above that value.

Next consider a rare mutant strategy of the form $z = (\hat{z}_h, z_l)$. In this case we may assume that the mutant is a superficial explorer. As a consequence, the population dynamics of the mutant is given by

$$n(t+1) = n(t)\hat{F}_l + n(t-1)\left(z_h \hat{E}_{hawk} + \left(1 - z_h\right)\hat{E}_{dove}\right) \tag{14}$$

with

$$\begin{aligned} \hat{E}_{hawk} &= \hat{F}_l + V - \hat{\pi}\tfrac{1}{2}(V + \delta\hat{F}_l) \\ \hat{E}_{dove} &= \hat{F}_l + \left(1 - \hat{\pi}\right)\tfrac{1}{2}V. \end{aligned} \tag{15}$$

Using the fact that $\hat{F}_l = \left(1 - \tfrac{1}{2}V(1+\hat{z}_l - \hat{\pi})\right) \Big/ (2 - \tfrac{1}{2}\delta\hat{\pi}\hat{z}_l)$, we now get $\hat{E}_{hawk} > \hat{E}_{dove}$ whenever $\hat{\pi}^2 + 2C\hat{\pi} - \frac{4}{\delta} < 0$, where again C is given by $C = \frac{1}{V} - \frac{1}{2}$. This yields:

$$\hat{E}_{hawk} - \hat{E}_{dove} > 0 \quad \Leftrightarrow \quad \hat{\pi} < T_l\left(V,\delta\right) = -C + \sqrt{C^2 + 4/\delta}\,. \tag{16}$$

Hence $z_l = 1$ is the best response to the resident strategy if $\hat{\pi}$ is below the threshold value T_l, and $z_l = 0$ is the best response if $\hat{\pi}$ is above that value.

Using (13) and (16) we can now characterise the equilibrium structure of the hawk-dove game. Note that $0 < T_h < T_l$ since $\delta > 0$. If $V > \delta$, both thresholds are larger than one and (13) and (16) imply that hawk is the dominant strategy, irrespective of the exploration behaviour. Hence $(z_h^*, z_l^*) = \left(1,1\right)$ is the only invasion proof equilibrium strategy.

Let us therefore from now on assume $0 < V < \delta$, which implies $T_h < 1$. Now $z^* = \left(1,1\right)$ is no longer an invasion proof equilibrium, since $z_h^* = z_l^* = 1$ implies $\hat{\pi} = 1 > T_h$, which in view of (13) implies that a mutant with $z_h = 0$ could invade the population. $z^* = \left(0,0\right)$ is also not invasion proof, since $\hat{\pi} = 0 < T_h < T_l$ implies that the hawk strategy could invade irrespective of the exploration strategy. Any mixed strategy with $0 < z_h^* = z_l^* < 1$ can also not be an invasion proof equilibrium, since equality would have to hold in both (13) and (16) (i.e., $\hat{\pi} = T_h = T_l$), which is impossible in view of $T_h < T_l$. We can conclude that z_h^* and z_l^* differ at equilibrium. In view of (13) and (16), superficial explorers have a higher tendency to play hawk than thorough explorers. Hence, we can conclude that $z_l^* > z_h^*$. Summarising, we have shown that

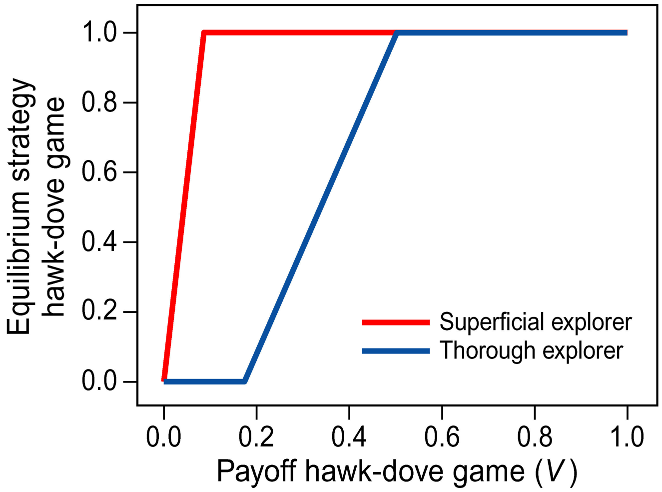
$$\begin{aligned} V > \delta \quad &\Rightarrow \quad z_l^* = z_h^* = 1 \\ V < \delta \quad &\Rightarrow \quad z_l^* > z_h^* \end{aligned} \tag{17}$$

which establishes Result 3.

With similar arguments as those given in the proof above one can furthermore show that there exist two thresholds $0 < S_1(V,\delta) < S_2(V,\delta) < \delta$ with the following properties:

$$\begin{aligned} S_2 < V < \delta \quad &\Rightarrow \quad z_l^* = 1,\ z_h^* < 1 \\ S_1 < V < S_2 \quad &\Rightarrow \quad z_l^* = 1,\ z_h^* = 0 \\ 0 < V < S_1 \quad &\Rightarrow \quad z_l^* > 0,\ z_h^* = 0. \end{aligned} \tag{18}$$

The explicit characterisation of these thresholds is rather intricate, but they are readily calculated numerically. This is illustrated by Supplementary Figure 1, where the equilibrium structure of the hawk-dove game is represented as a function of V.



Supplementary Figure 1. Equilibrium strategies in the hawk-dove game as a function of V, for $f_h = 3.5, f_l = 3.0$ and $\delta = 0.5$. Superficial explorers (red line) are always at least as risk-prone as thorough explorers (blue line). For $V < \delta$ superficial explorers play hawk with a strictly higher probability than thorough explorers, for $V > \delta$ playing the pure strategy hawk is a dominant strategy.

4. Evolution of behavioural correlations

Up to now our analysis has confirmed the life-history principle that individuals with higher fitness expectations (in our case: thorough explorers) should behave in a more cautious way. We here show that the same principle gives rise to the evolution of behavioural syndromes, i.e. correlated behavioural traits across two different games.

Consider the scenario where each individual sequentially plays one anti-predator game and one hawk-dove game between years 1 and 2. Individuals can condition their behaviour on their exploration intensity and a strategy is now a quadruple of the form $s=(y_h, y_l, z_h, z_l)$. We here only sketch how to derive the invasion proof equilibrium strategies of the model. To this end, we consider a resident population with strategy $\hat{s}=(\hat{y}_h, \hat{y}_l, \hat{z}_h, \hat{z}_l)$ at its population dynamical equilibrium $(\hat{F}_h, \hat{F}_l, \hat{\pi})$, where $\hat{\pi}$ is the frequency of hawks in the population. Then we consider four types of rare mutants, each differing in only one component from the resident strategy $\hat{s}$. Take, for example, a mutant of the form $s=(y_h, \hat{y}_l, \hat{z}_h, \hat{z}_l)$. As above, we may assume without loss of generality that the mutant is a thorough explorer. The population dynamics of this mutant is then given by

$$n(t+1)=n(t-1)\left(y_h\hat{E}_{bold}+\left(1-y_h\right)\hat{E}_{shy}\right) \tag{19}$$

where $\hat{E}_{bold}$ and $\hat{E}_{shy}$ is the expected reproductive success of a thoroughly exploring individual given that it plays bold or shy, respectively. The expected payoff from the hawk-dove game is $\hat{z}_h(1-\frac{1}{2}\hat{\pi})V+(1-\hat{z}_h)(1-\hat{\pi})\frac{1}{2}V=(1+\hat{z}_h-\hat{\pi})\frac{1}{2}V$. Therefore these expectations are given by

$$\begin{aligned}\hat{E}_{bold}&=(1-\gamma)\left((1-\tfrac{1}{2}\delta\hat{\pi}\hat{z}_h)(\hat{F}_h+b)+(1+\hat{z}_h-\hat{\pi})\tfrac{1}{2}V\right)\\ \hat{E}_{shy}&=(1-\tfrac{1}{2}\delta\hat{\pi}\hat{z}_h)\hat{F}_h+(1+\hat{z}_h-\hat{\pi})\tfrac{1}{2}V.\end{aligned} \tag{20}$$

The growth rate of the mutant

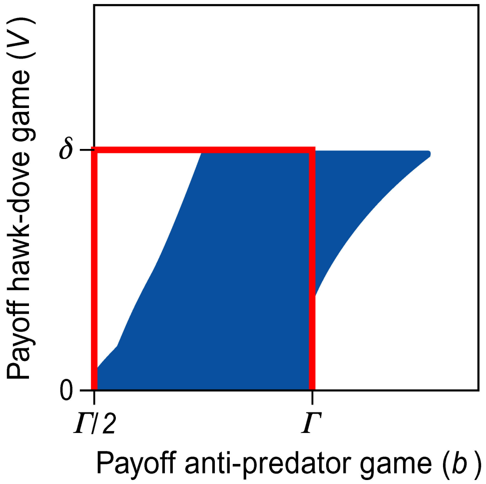
$$\lambda(s,\hat{s}) = \sqrt{y_h \hat{E}_{bold} + (1 - y_h)\hat{E}_{shy}} = \sqrt{\hat{E}_{shy} + y_h(\hat{E}_{bold} - \hat{E}_{shy})} \tag{21}$$

is again a strictly monotonic function in the mutant trait y_h. If $\hat{E}_{bold} > \hat{E}_{shy}$, $y_h = 1$ is the best response to $\hat{s}$, while $y_h = 0$ is the best response if $\hat{E}_{bold} < \hat{E}_{shy}$. Analogous considerations characterise the best responses with respect to the other three traits.

Having derived the best response structure, all invasion proof equilibrium strategies can be calculated. Each such equilibrium s^* has to be a best response to itself, i.e. each of the four strategy components of s^* has to be a best response to the resident environment $\hat{s} = s^*$.

Based on these conditions we numerically calculated the evolutionary equilibria $s^* = (y_h^*, y_l^*, z_h^*, z_l^*)$ as a function of the payoff in the hawk-dove game V and the payoff in the anti-predator game b (Supplementary Figure 2). First note that behavioural correlations across the two games are only possible if there is behavioural variation in both games. We know from Results 2 and 3 that variation in a single anti-predator game occurs for $\frac{1}{2}\Gamma < b < \Gamma$ and in single hawk-dove game for $V < \delta$. The corresponding area in parameter space is bordered by red lines in the figure. The blue area indicates the parameter combinations for which we find behavioural syndromes, i.e. behavioural correlations across the two games. The white area in the figure corresponds to payoff configurations where all individuals play the same pure strategy in at least one of the two games, irrespective of their exploration behaviour.

We stress that these results are in perfect agreement with the individual-based simulations that we performed.



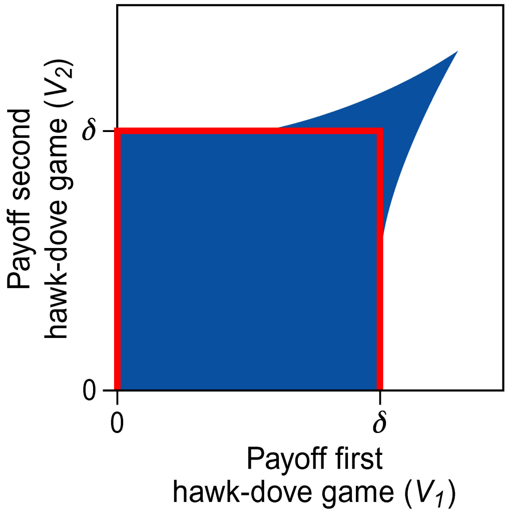
Supplementary Figure 2. The combinations of payoffs in the anti-predator and the hawk-dove game that result in the evolution of behavioural syndromes, i.e. positive behavioural correlations across two different games (blue area). For payoff combinations where we did not find positive correlations, at least one of the games had a dominant pure strategy, precluding behavioural variation in relation to exploration behaviour. Evolutionary equilibria were calculated numerically for $f_h = 3.5$, $f_l = 3.0$, $\gamma = 0.1$ and $\delta = \frac{1}{2}$, where $\Gamma = \gamma/(1-\gamma)$. The red lines border those payoff combinations for which thorough and superficial explorers differ in equilibrium behaviour in both of the individual games.

5. Evolution of time-consistent behaviour

Our approach for analysing the evolution of stable behavioural differences within the same game follows the approach described in the preceding section. We here consider the scenario where each individual plays two hawk-dove games between years 1 and 2. A strategy is now a quadruple of the form $s = (z_{h,1}, z_{l,1}, z_{h,2}, z_{l,2})$. The resident population at its population dynamical equilibrium is now characterised by $(\hat{F}_h, \hat{F}_l, \hat{\pi}_1, \hat{\pi}_2)$ where $\hat{\pi}_1$ $(\hat{\pi}_2)$ is the population frequency of hawks in the first (second) hawk-dove game. As above, we derive the best response structure by considering four types of rare mutants. Based on these conditions we numerically calculated the evolutionary equilibria

$s^* = (z^*_{h,1}, z^*_{l,1}, z^*_{h,2}, z^*_{l,2})$ as a function of the payoff V_1 in the first hawk-dove game and the payoff V_2 in the second hawk-dove game (Supplementary Figure 3).

First note that, analogously to the results in Section 4, stable behavioural differences are only possible if there is behavioural variation in each of the hawk-dove games. We know from Result 3 that variation in a single hawk-dove game occurs for $V < \delta$. The corresponding area in parameter space is bordered by red lines. The blue area indicates the parameter combinations for which we find stable behavioural differences, i.e. positive behavioural correlations across the two hawk-dove games. The white area in the figure corresponds to payoff configurations where all individuals play the same pure strategy in at least one of the two games, irrespective of their exploration behaviour. Again, these results are in perfect agreement with the individual-based simulations that we performed.



Supplementary Figure 3. The combinations of payoffs that give rise to stable behavioural differences within contexts, i.e. positive correlations in two subsequently played hawk-dove games (blue area). For payoff combinations where we did not find positive correlations, at least one of the games had a dominant pure strategy, precluding behavioural variation in relation to exploration behaviour. Evolutionary equilibria were calculated numerically for $f_h = 3.5$, $f_l = 3.0$ and $\delta = \frac{1}{2}$. The red lines border those payoff combinations for which thorough and superficial explorers differ in equilibrium behaviour in both of the individual hawk-dove games.

References

Edelstein-Keshet, L. *Mathematical Models in Biology* (Society for Industrial and Applied Mathematics, Philadelphia, 2005).