

## SUPPORTING INFORMATION

Johnstone RA, Cant MA, Cram D, Thompson FJ

1. An extended model
2. Video Legends

### 1. An extended Model

#### *Persistent groups*

In the simple model described in the main text and methods, we assumed a well-mixed population in which groups are repeatedly formed at random to contest each resource item (so that a given individual will be associated with different group mates in every encounter), adopting a classical game theoretical approach similar to that of the original Hawk-Dove model. Here, we consider instead the possibility of persistent groups.

We focus on an infinite, asexual population, divided into discrete groups of size  $n$  (an ‘infinite island’ model), with non-overlapping generations. In each generation every individual produces a large number of offspring, of which a fraction  $h$  remain in their natal group, while the remaining fraction  $1-h$  disperse, each to a random other group in the population. After dispersal, the current generation of adults die, and offspring in a group (both native and immigrant) compete for the  $n$  breeding vacancies created thereby. Those that successfully claim a breeding position become the adults of the next generation (while the remainder die).

An individual’s fecundity reflects the outcome of inter-group conflict. In each generation, every group engages in a large number of pairwise interactions with other, randomly chosen groups. In each encounter, as in the preceding model, the two groups contest ownership of a resource, with a single, randomly-chosen leader in each determining whether the group in question collectively adopt Hawk or Dove tactics. Payoffs from an interaction, for both leaders and followers, are as described in the preceding model. Fecundity is equal to a baseline value  $w_B$  plus an individual’s average payoff from the group interactions in which it participates. For an individual that plays Hawk with probability  $p_i$ , in a local group that otherwise plays Hawk with mean probability  $p_{loc}$ , in a population that plays Hawk with mean probability  $p$ , this average payoff  $\bar{w}(p_i, p_{loc}, p)$  is given by

$$\begin{aligned} \bar{w}(p_i, p_{loc}, p) = & \frac{1}{n} \left( p_i p \left( \frac{v_L - c_L}{2} \right) + p_i (1 - p) v_L + (1 - p_i) (1 - p) \frac{v_L}{2} \right) \\ & + \frac{n - 1}{n} \left( p_{loc} p \left( \frac{v_F - c_F}{2} \right) + p_{loc} (1 - p) v_F + (1 - p_{loc}) (1 - p) \frac{v_F}{2} \right) \end{aligned}$$

To model the evolution of aggression, i.e. the probability with which an individual plays Hawk when acting as leader, we adopt an adaptive dynamic approach, assuming that evolution proceeds through the successive substitution of mutations of small effect. Given that selection is weak, the fitness of an individual that plays Hawk with probability  $p_i$ , in a local group that otherwise plays Hawk with mean probability  $p_{loc}$ , in a population that plays Hawk with mean probability  $p$ , can be approximated as

$$\begin{aligned}
& W(p_i, p_{loc}, p) \\
& \cong \frac{h(w_B + \bar{w}(p_i, p_{loc}, p))}{h\left(w_B + \bar{w}\left(\frac{1}{n}p_i + \frac{n-1}{n}p_{loc}, \frac{1}{n}p_i + \frac{n-1}{n}p_{loc}, p\right)\right) + (1-h)(w_B + \bar{w}(p, p, p))} \\
& \quad + \frac{(1-h)(w_B + \bar{w}(p_i, p_{loc}, p))}{(w_B + \bar{w}(p, p, p))}
\end{aligned}$$

where the first term on the right-hand side of the above equation reflects the contribution to fitness from young that claim a breeding vacancy in the local group, and the second term from young that claim a breeding vacancy in other groups. Using a neighbour-modulated, direct fitness approach to capture the impact of kin selection, the rate and direction of evolutionary change in  $p$  in such a population is then proportional to the selection gradient

$$S_p = \left. \frac{\partial W(p_i, p_{loc}, p)}{\partial p_i} + r \frac{\partial W(p_i, p_{loc}, p)}{\partial p_{loc}} \right|_{p_i=p_{loc}=p}$$

where  $r$  denotes the mean coefficient of relatedness between two distinct individuals chosen at random from the same group.

Assuming haploid inheritance for simplicity (though a diploid model yields identical results given additive allelic effects), this coefficient of relatedness is equivalent to the probability of identity by descent between gene copies sampled from two distinct females chosen at random from the same group, which satisfies

$$r = h^2 \left( \frac{1}{n} + \frac{n-1}{n} r \right)$$

since the females were born to the same group with probability  $h^2$ , in which case with probability  $1/n$  they derive from the same individual in the previous generation and are therefore identical by descent, while with probability  $(n-1)/n$  they derive from distinct individuals in their natal patch, and are therefore (at demographic equilibrium) identical by descent with probability  $r$ . This yields

$$r = \frac{h^2}{n - (n-1)h^2}$$

Substituting the above expression for  $r$  into the expression for  $S_p$  we can then solve for an equilibrium level of aggression  $p^*$  for which  $S_p = 0$  (or identify conditions for which  $S_p$  is negative or positive over the whole range  $0 < p < 1$ , implying that selection favours an extreme level of aggression  $p^* = 0$  or  $p^* = 1$ ). This yields the unique solution

$$p^* = \begin{cases} 1 & \text{for } c_L \leq v_L \\ \frac{v_L}{c_L} & \text{for } c_L > v_L \end{cases}$$

which is identical to that of our earlier analysis of a game in which groups are randomly assembled in each interaction (and which leads to identical mean payoffs from inter-group contests). In other words, allowing for persistent groups does not affect our conclusions in any way, regardless of the level of philopatry  $h$  in the population. This is to be expected given Taylor's (1992) general result that in a structured population of the kind we have considered, the effects of local relatedness and of local kin competition 'cancel out', with the result that selection is unaffected by the rate of dispersal of offspring between groups.

### *Consistent leadership*

In our analysis of persistent groups, we have continued to assume that one member of a group is selected at random to act as leader during each encounter (so that all members of the group lead equally often). Here, by contrast, we shall assume consistent leadership within each generation; that is, one member of a group is selected at random to act as leader during every encounter in that generation. Under these circumstances, the average payoff  $\bar{w}_L(p_i, p)$  to a leader that plays Hawk with probability  $p_i$ , in a population that plays Hawk with mean probability  $p$ , is given by

$$\bar{w}_L(p_i, p) = p_i p \left( \frac{v_L - c_L}{2} \right) + p_i (1 - p) v_L + (1 - p_i) (1 - p) \frac{v_L}{2},$$

while the average payoff  $\bar{w}_F(p_L, p)$  to a follower whose leader plays Hawk with probability  $p_L$ , in a population that plays Hawk with mean probability  $p$ , is given by

$$\bar{w}_F(p_L, p) = p_L p \left( \frac{v_F - c_F}{2} \right) + p_L (1 - p) v_F + (1 - p_L) (1 - p) \frac{v_F}{2}$$

The fitness of a leader that plays Hawk with probability  $p_i$ , in a population that plays Hawk with mean probability  $p$ , can then be approximated as

$$\begin{aligned} W_L(p_i, p) & \\ \cong & \frac{h(w_B + \bar{w}_L(p_i, p))}{h\left(w_B + \frac{1}{n}\bar{w}_L(p_i, p) + \frac{n-1}{n}\bar{w}_F(p_i, p)\right) + (1-h)\left(w_B + \frac{1}{n}\bar{w}_L(p, p) + \frac{n-1}{n}\bar{w}_F(p, p)\right)} \\ & + \frac{(1-h)(w_B + \bar{w}_L(p_i, p))}{\left(w_B + \frac{1}{n}\bar{w}_L(p, p) + \frac{n-1}{n}\bar{w}_F(p, p)\right)} \end{aligned}$$

and the fitness of a follower in a group with a leader that plays Hawk with probability  $p_L$ , in a population that plays Hawk with mean probability  $p$ , as

$$\begin{aligned} W_F(p_L, p) & \\ \cong & \frac{h(w_B + \bar{w}_F(p_L, p))}{h\left(w_B + \frac{1}{n}\bar{w}_L(p_L, p) + \frac{n-1}{n}\bar{w}_F(p_L, p)\right) + (1-h)\left(w_B + \frac{1}{n}\bar{w}_L(p, p) + \frac{n-1}{n}\bar{w}_F(p, p)\right)} \end{aligned}$$

$$+ \frac{(1-h)(w_B + \bar{w}_F(p_L, p))}{\left(w_B + \frac{1}{n}\bar{w}_L(p, p) + \frac{n-1}{n}\bar{w}_F(p, p)\right)}$$

The rate and direction of evolutionary change in  $p$  in such a population is then proportional to the selection gradient

$$S_p = \frac{1}{n} \frac{\partial W_L(p_i, p)}{\partial p_i} + \frac{n-1}{n} r \frac{\partial W_F(p_L, p)}{\partial p_L} \Big|_{p_i=p_L=p}$$

where  $r$  again denotes the mean coefficient of relatedness between two distinct individuals chosen at random from the same group.

In this model with consistent leadership,  $r$  satisfies

$$r = h^2 \left( L^2 + 2L(1-L)r + (1-L)^2 \left( \frac{1}{n-1} + \frac{n-2}{n-1}r \right) \right)$$

where  $L$  denotes the probability that a randomly chosen offspring born in a group derives from the leader, and is given by

$$L = \frac{w_B + \bar{w}_L(p, p)}{nw_B + \bar{w}_L(p, p) + (n-1)\bar{w}_F(p, p)}$$

This yields

$$r = h^2 \frac{1 - 2L + nL^2}{(n-1) + h^2(1-L)((1+L)n-2)}$$

and substituting the above expression for  $r$  into the expression for  $S_p$  we can derive the selection gradient for any given parameter values and thus again solve for the equilibrium level of aggression  $p^*$ . As the model does not yield simple, closed-form solutions in this case, we present illustrative numerical results in the figure below. As is apparent from the graphs, the introduction of consistent leadership has only a small quantitative impact on the model's predictions, favouring a slightly higher level of aggression at equilibrium (an effect that is more pronounced when leaders gain a greater share of benefits or pay a smaller share of costs, when groups are small, and when the probability of philopatry is high).

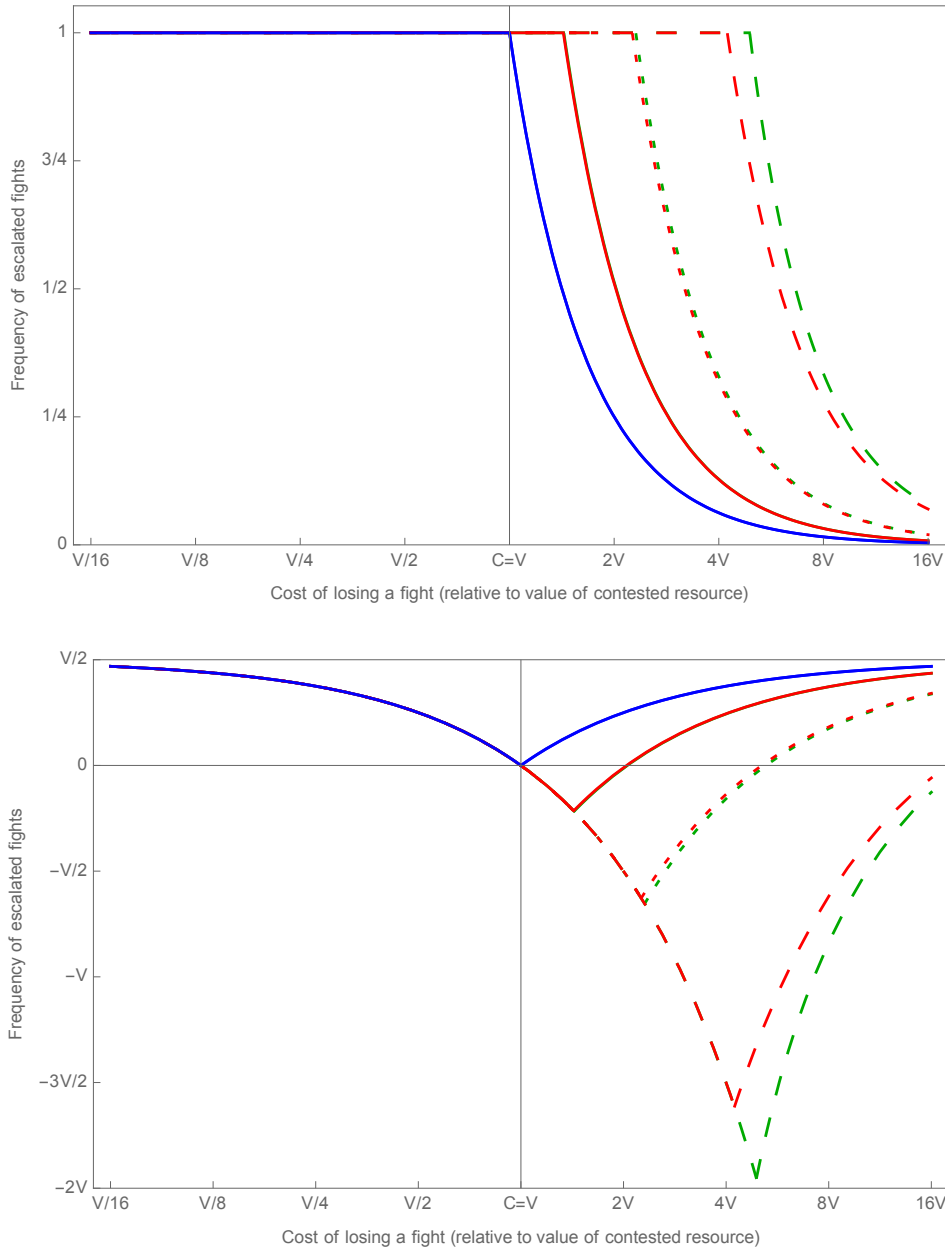


Figure S1. Evolutionarily stable probabilities of escalated fighting (upper panel) and mean payoffs (lower panel), as a function of the total cost  $c$  of losing a fight relative to the value of the contested resource  $v$  (plotted on a log scale), in the original pairwise-interaction Hawk-Dove game (blue curves), in the group-interaction game with persistent groups but no consistency in leadership (red curves), and in the group-interaction game with persistent groups and consistent leadership (green curves). For the group-interaction results, leaders are assumed both to claim a disproportionately large share of resources and to suffer a disproportionately small share of the cost of losing a fight (solid red and green curves,  $d_v = d_c = 0.2$ ; dotted red curves,  $d_v = d_c = 0.4$ ; dashed red curves  $d_v = d_c = 0.6$ ). In all cases  $w_b = 4$ ,  $n = 5$  and  $h = 0.9$ . Note that the solid red and green curves overlap so closely that the latter are not clearly visible in the figure.

## **2. Video Legends**

**Video 1 Battle lines.** After detecting each other, groups bunch together and advance toward one other in tight 'battle lines'.

**Video 2 Intergroup violence.** Fights between groups involve repeated waves of attack and retreat. Individuals that become separated from their group are surrounded and attacked on all sides.

**Video 3 Intergroup mating.** In the confusion and chaos of battle, females mate with males from the opposing group.