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Do male orangutans play a hawk–dove game?

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ABSTRACT

Background: (1) The hawk–dove game has been invoked to explain animal fighting. (2) Orangutans (*Pongo pygmaeus*) have two forms of reproductively competent males: (a) The matured adult male (MA) has wide cheek pads and a well-developed throat sac used for emitting loud cries. The average weight of matured adult males is more than twice that of adult females. (b) The arrested adult male (AA), although it is old enough to be a matured adult male, remains comparable in size to an adult female and lacks the wide cheeks and throat sacs of matured adult males. Matured adult males are behaviourally dominant, whereas arrested adult males are sneakers and forcibly copulate with females. When the population density of matured adult males is low, sub-adult males develop to matured adults by the age of 5–7 years. When the density of matured adults is high, males become arrested adults.

Question: Might game-theoretic models similar to the hawk–dove game explain male dimorphism in orangutans?

Models: (1) A modified density-independent hawk–dove game. In each, MA is the hawk and AA is the dove. The value of winning (pay-off) for an MA is larger than that for an AA. But only MAs pay a combat cost. (2) A density-dependent hawk–dove game similar to the first but with pay-offs that decline as population size grows.

Results: Density-independent: If an MA's combat cost is smaller than its payoff when it wins, then AA males always have less fitness than MAs. There should be no dimorphism. But if an MA's combat cost exceeds its pay-off when it wins, a stable mixed ESS proportion (less than 100%) of males should contain AAs (doves). In the density-dependent model, AAs are part of the ESS even in some circumstances in which the cost is smaller than the pay-off to MA. As population size increases, we see an increase in the breadth of mathematical conditions supporting a stable mixed evolutionarily stable strategy (ESS).

Keywords: alternative mating tactics, arrested adults, density effect, hawk–dove game, male dimorphism, orangutan, *Pongo pygmaeus*.

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INTRODUCTION

Maynard Smith and Price (1973) introduced the hawk–dove game to evolutionary ecology. It has become a major theme of the science (Krebs and Davies, 1987; Bulmer, 1994). Despite its development, few have applied it to real-life situations. Yet the hawk–dove game was introduced to explain courtship fights in animals. Here, using models very similar to the hawk–dove game, we return to the roots of the game and use it to explore the reasons for alternative mating tactics in orangutan (*Pongo pygmaeus*) males.

Many authors have studied male dimorphism (e.g. Gadgil, 1972; Hamilton, 1979; Stoltz and Neff, 2006). Gross (1982), in particular, realized the value of game theory in such study, and applied it to the evolution of sneaker males (i.e. males that mate when dominant males are, in some sense, not looking). Using 2×2 (four-parameter) games, he discovered that some parameter values of the game would lead to an evolutionarily stable strategy (ESS) in which aggressive and sneaker sunfish males would co-exist. However, he did not use hawk–dove games of any form, nor did he elucidate the actual conditions for sneaker evolution.

We build on Gross's work by using a modified hawk–dove game to explain male dimorphism in orangutans. We analyse its parameter space to determine the conditions that can lead to an ESS. Finally, we consider population size (N) as a variable, thus exploring how different population sizes will impinge on the possibility of the ESS.

Fogel *et al.* (1998), Claussen and Traulsen (2005), and Nowak (2006) all examined game theories with finite population size as a parameter. They showed that the finiteness of the population affects the game's equilibrium. Taylor *et al.* (2004), using a Moran Process, also explored the effect of population size. If population size is ignored, game theory predicts that doves and hawks can co-exist only if a losing hawk's cost is larger than a winning hawk's pay-off. But if population size is considered, even if a losing hawk's cost is smaller than its pay-off, genetic drift may allow the dove to co-exist with the hawk. Thus, small populations of players lead to an expanded opportunity for an ESS. However, our work found the opposite: the opportunity expands when N is large. The expansion comes not from genetic drift, but from a deterministic density effect.

In the next section, we describe male dimorphism in orangutans (Maggioncalda *et al.*, 1999; Maggioncalda and Sapolsky, 2002). Then we introduce two models of the hawk–dove game. One is independent of orangutan population size (N). The other does depend on N. In the final section, we discuss the difference between the effect of genetic drift and that of large population sizes.

DIMORPHISM IN MALE ORANGUTANS

Adult male orangutans have obvious secondary sexual traits such as wide cheek pads and a well-developed throat sac, enabling them to emit loud cries. The average matured adult male weighs more than twice as much as an adult female. In contrast, a sub-adult male weighs about the same as an adult female. When the population density of matured adult males is low, sub-adults develop into matured adults by the age of 5–7 years. However, if the density of matured adult males is high, then sub-adults develop into reproductively competent males without the male secondary sexual traits. In addition, they retain their sub-adult size for a long period. Such males are called arrested adults.

For example, in one zoo enclosure, all arrested adult males remained developmentally arrested as long as there was a matured male. But when the matured adult male was

removed, many arrested adult males began (simultaneously) to develop into matured adults (Maggioncalda *et al.*, 1999; Maggioncalda and Sapolsky, 2002).

Researchers had believed that stress induced the delay of full maturation: they hypothesized that adolescent males stopped developing owing to the physiological effects of their fear of matured adult males (Kingsley, 1988). However, Maggioncalda and colleagues (Maggioncalda *et al.*, 1999; Maggioncalda and Sapolsky, 2002) discovered that arrested adolescence is not a pathology but a male strategy. They found that arrested adult males have quite low concentrations of stress hormones, whereas matured adult males have high concentrations. Meanwhile, arrested adult males can reproduce as sneakers. Sneakers force females to copulate with them, essentially raping the females. Hence, males have one of two strategies for reproduction: matured adult (MA) – the dominant, boss strategy – and arrested adult (AA) – the sneaker strategy.

DENSITY-INDEPENDENT MODEL

Now we apply a modified hawk–dove game to the orangutan males. The male MA dominates the male AA. So let the MA be the hawk and the AA be the dove. If a matured adult (MA) opposes an arrested adult (AA), the MA gains the pay-off (mating value), V, while the AA receives the pay-off 'zero'. Zero represents the base fitness ($V > 0$).

However, an MA has to pay a combat cost when it challenges another MA. Let this cost be C. If two MAs oppose each other, the loser pays the combat cost and the winner receives the net pay-off V. Hence each MA gains the average pay-off $(V - C)/2$.

On the other hand, in the eyes of MA males, an AA is not a target of aggression. So the AA mates with far fewer females but pays little or no challenger's cost. As do other students of the hawk–dove game, we will neglect the cost of an AA × AA encounter. Hence, if two AAs oppose each other, each one gains the average pay-off $U/2$, where U is the pay-off (mating value) to an AA, and $V > U$.

Table 1 shows the pay-off matrix of the hawk–dove game of orangutan males. The pay-offs in this table differ from those of the usual hawk–dove game in that $V \neq U$.

Now we assume a constant population size of orangutan males and study the effect of changing the proportion p that are hawks (MAs). When the proportion of hawks is p, then the fitness of each individual hawk $W(H)$ is

$$W(H) = (1 - p)V + p(V - C)/2 \tag{1}$$

Thus:

$$W(H) = V - p(V + C)/2 \tag{2}$$

Table 1. Pay-off matrix of hawk–dove game as applied to orangutan males

	Opponent	
Player	Hawk (MA)	Dove (AA)
Hawk (MA)	$(V - C)/2$	V
Dove (AA)	0	$U/2$

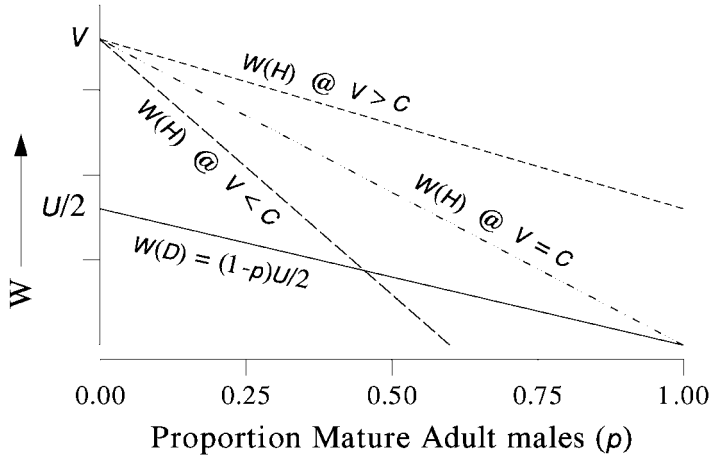

Fig. 1. The average net pay-offs (W) of hawk and dove for the modified density-independent model. The values of $W(H)$ and $W(D)$ are depicted against the ratio p of hawk (matured adult males). The figure illustrates three cases: $V > C$, $V = C$, and $V < C$. The intersection for the case of $V < C$ determines a stable, mixed evolutionarily stable strategy.

On the other hand, the fitness of a dove $W(D)$ is expressed by

$$W(D) = (1 - p)U/2 \tag{3}$$

Recalling that $V > U$, and $0 \leq p \leq 0$, we now examine $W(H, p)$ and $W(D, p)$ as V varies from more than C to less than C (see Fig. 1).

The W-intercepts of equations (2) and (3) do not depend on p. They are V and $U/2$ respectively. Moreover, $V > U$; therefore, $W(H)$ is always greater than $W(D)$ when $p = 0$.

The slope of $W(H) = -(V + C)/2$. The slope of $W(D) = -U/2$. Both slopes are negative. Because $(V + C) > U$, the slope of $W(H)$ is always steeper than that of $W(D)$. So if there exists a value of p for which $W(H) = W(D)$, it will be an ESS. Let this value be p^*.

If $V = C$ and $p = 1$, $W(H) = W(D)$. So $p^* = 1$ and all males should be MAs. If $V > C$, $W(H) > W(D)$ for all p and, again, all males should be MAs. But if $V < C$, then $p^* < 1$ and some males ought to be doves (AAs).

If $V < C$, we obtain p^* by setting $W(H) = W(D)$ and solving

$$p^* = (2V - U)/(V - U + C) \tag{4}$$

If $V < C$ and $p > p^*$, AA is a better strategy than MA. New males should become AAs until p declines to p^*. If $p < p^*$, AA is a poorer strategy. New males should become MAs. Thus p^* is an ESS.

As V declines farther below C, the slope of $W(H)$ rotates clockwise around its W-intercept and p^* declines. p^* also decreases with increasing U.

In summary: (i) when $V < C$, only MA (hawk) wins the game; (ii) when $V < C$, both MA and AA are stable strategies. These results closely resemble the results of a standard hawk–dove game.

EFFECT OF DENSITY

The value of matings should depend on population size, N. As N increases, individuals may compete more for limited resources or space (Tainaka *et al.*, 2006). As a consequence, the mating values, V and U, may decrease. Let us assume that they do decrease and that each does so according to a simple function of density, $B/(B + N)$, where B is constant. By multiplication, we obtain V_{eff} and U_{eff}, the density-reduced, effective values of mating:

$$V_{\text{eff}} = VB/(B + N) \tag{5a}$$

$$U_{\text{eff}} = UB/(B + N) \tag{5b}$$

The average net pay-off for hawk and dove individuals would be:

$$W(H) = V_{\text{eff}} - p(V_{\text{eff}} + C)/2 \tag{6}$$

$$W(D) = (1 - p)\ U_{\text{eff}}/2 \tag{7}$$

Equations (6) and (7) are similar to equations (2) and (3). Given any constant value of N, they are negatively sloped, straight lines in W vs. p space. Moreover, equation (6) declines more steeply than equation (7) and intersects it at $p^* < 1$ if and only if $V_{\text{eff}} < C$. The latter is seen by solving the p^*-equation for 1:

$$p^* = (2V_{\text{eff}} - U_{\text{eff}})/(C + V_{\text{eff}} - U_{\text{eff}}) \tag{8}$$

So $p^* = 1$ if and only if $V_{\text{eff}} - U_{\text{eff}} = C$.

The above is well summarized by the hawk–dove game illustrated in Fig. 1. But there is an important difference. The added density term, $B/(B + N)$, does not influence C. So density exerts an asymmetrical effect on the point that determines whether AAs should be present. That point is $V_{\text{eff}} = C$. But $V_{\text{eff}} < V$, and therefore $C < V$ at the density-dependent values at which mixed evolutionarily stable strategies begin to become realistic solutions. So as N increases, the concomitant decline in V_{eff} allows a portion of the males to be AAs at the ESS even though $C < V$ – that is, even though the cost to an MA is less than the value to an MA. Moreover, the larger N becomes, the greater the ratio V/C at which AAs are a part of the ESS.

DISCUSSION

Sneakers (and other subordinate strategies) are alternative mating tactics in many animal species (Thornhill and Alcock, 1983; Kodric-Brown, 1986). Sneakers are usually considered the best of a bad job (Dawkins, 1980) because their pay-offs are lower than those of dominant males. But sneakers may not always be so unfit. Using game theory, Gross (1982) showed that the evolutionary relationship between sneakers and dominants might conceal a mixed ESS that would favour the maintenance of both strategies.

In this paper, we expanded on Gross's theme by applying game theory to the case of orangutan dimorphism. We began with a slightly modified hawk–dove model and found the conditions that would produce a mixed ESS. Our results showed that under some conditions, conventional wisdom would be correct. Any sneaker would be a poor strategy. But because dominants pay a combat cost that sneakers are largely exempt from, the individual average net pay-off to a dominant declines as the proportion of dominant males increases. Sometimes that is enough to make room for some sneakers in a stable mixed ESS.

The limiting condition that allows for an evolutionarily successful proportion of sneakers in the modified hawk–dove model is the ratio of pay-off (V) to cost (C). If $V/C \geq 1$, only hawks prevail. But if $V/C < 1$, natural selection makes room for some proportion of sneakers. The smaller the pay-off : cost ratio, the higher that proportion.

The news for sneakers is even better if pay-off values (to both sneakers and dominants) decline as a result of population growth. If they do, sneakers will be successful even when V/C exceeds 1 by some finite amount. That finite amount grows along with population size. Thus, the larger the orangutan population, the greater the opportunity for a mixed ESS.

Our population-size results are just the opposite to those of other game models of finite population size. Previous theories suggested that sneakers could evolve only as the result of the random genetic drift associated with very small populations (Taylor *et al.*, 2004). In our work, however, they evolve because of the competition associated with large populations.

We believe that our results could explain the dimorphic male strategies of orangutans. If dimorphism is an ESS whose value varies with population size and with the proportion of males that are dominant, then the model provides a reason for orangutan developmental flexibility. At times, when the pay-off : cost ratio of dominant males is high, dominance is the better strategy and arrested-growth sneaker males are a suboptimal morphology. But when that ratio falls far enough, selection will favour those males that can 'run in place', waiting for more propitious times and meanwhile accumulating whatever few mating events they can sneak in.

Of course, we cannot be sure that our model offers the correct explanation of orangutan dimorphism. And even if it does, a bigger question remains. How does the orangutan hawk–dove matrix evolve in the first place? Was a form of positive evolutionary feedback involved? ('That's not fierce, aggressive behaviour; I'll show you fierce, aggressive behaviour'.) Did orangutan conflict thus escalate in evolutionary history until it became so costly that it created the opportunity for furtive, docile sneakers? If that is true, then, whereas aggressive males do reduce the pay-offs to sneakers today, aggressive males would have been needed for sneakers to evolve in the first place! And if the optimal proportion of sneakers really is subject to profound temporal variation, what temporal regime will favour sneakers often enough and strongly enough to keep the sneaker strategy from extinction?

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