Popul Ecol (2001) 43:213–220

ORIGINAL ARTICLE

Mark Broom · Graeme D. Ruxton

A model of dominance and resource division among a group of animals of differing quality

Received: April 9, 2001 / Accepted: September 16, 2001

Abstract Individuals of many species spend a large portion of their lives within groups of conspecifics. Within such groups, there can be considerable diversity in size and other traits, with some, perhaps larger or stronger, animals laying claim to a greater than fair share of available resources. We use the word quality as a single measure of individual animal phenotypes within such a group and develop a model of resource division through contests between animals of differing quality. We investigated the effect of varying environmental factors on the level of aggressiveness used in such contests and the division of resources among the group. A numerical example shows that maximum discriminations between individuals on the basis of quality occur for medium-sized costs of aggressive encounters, but resources are divided more equitably at either extreme, when costs are either high or low.

Key words Escalation · Fighting cost · Fixed reward · Evolutionarily stable strategy · Dominance hierarchy

Introduction

Within and between populations, there is great diversity in the form and intensity of aggressive conflicts between individuals over resources (Hand 1986). One particular puzzle is that apparently similar resource items can induce contests of very different intensity. The reasons behind this observation are two fold. First, it does not make sense for an individual always to fight for so long and hard as it possibly can, because there will be a cost to fighting (e.g., time, energy, or risk of injury) that will increase with the extent or intensity of a fight. Hence, individuals have an optimal level of investment in a contest, which will often be less than their physiological maximum. An important feature of the problem is that a contest occurs between two individuals, and the success of the strategy (in terms of investment in the contest) of one depends on the strategy played by the other. As such, this is a perfect situation for the application of game theory (see Dugatkin and Reeve 1998 for an overview of applications of game theory to biological questions). The situation becomes particularly interesting when individuals differ from each other in some respect. Sometimes, the situation is especially complicated because individuals do not have knowledge of the intrinsic qualities of their opponent and must try to assess these during a contest. In other circumstances, individuals are able to gauge both their own abilities and those of their opponent. Such situations may occur when differences are easily detected (e.g., size) or opponents have previous experience of each other. We consider this latter case, in which individuals have perfect knowledge of their opponents' abilities.

A related problem is how resources are divided among a group of animals. The spatial and temporal distribution of resources affects the degree to which they can be monopolized by a few dominant individuals and so may have an important effect on the strategies adopted by individuals (see Emlen and Oring 1977). Often such groups form dominance hierarchies in which there is a priority order among the individuals. How such dominance hierarchies are formed was considered by Mesterton-Gibbons and Dugatkin (1995) and Broom et al. (2000a,b). An important series of papers, starting with that by Vehrencamp (1983) and including those by Keller and Reeve (1994) and Reeve and Keller (1996), considered the concept of reproductive skew, which concerns the problem of how resources are divided within a dominance hierarchy. In particular, those authors suggested that dominant individuals grant subordinates "stay and peace incentives" and limited mating rights, to prevent them from either leaving the group or challenging for dominance.

M. Broom (✉)
Centre for Statistics and Stochastic Modelling, University of Sussex
School of Mathematical Sciences, Falmer, Brighton BN1 9QH, UK
Tel. +44-1273-877243; Fax +44-1273-678097
e-mail: M.Broom@sussex.ac.uk

G.D. Ruxton
Institute of Biomedical and Life Sciences, University of Glasgow,
Glasgow, UK

We consider a particularly simple situation in which each contestant (independently) chooses between two strategies: the cautious "dove" or aggressive "hawk" (defined below). Such a situation for phenotypically different individuals playing repeated hawk–dove games has been previously investigated by Maynard Smith and Parker (1976), who considered a hawk–dove contest between pairs of individuals, each of which has a 50% probability of taking one of two phenotypes or roles (e.g., territory holder and invader), such that the opponents always take opposite roles. We extend their model in a number of ways: we remove the limit on the number of different phenotypes in the population, and we assume that the phenotype of an individual is a fixed intrinsic property of the individual, rather than being determined by coin-toss. This approach is generally realistic for many phenotypic components, for example, size; if one individual is bigger than another in one contest, it is likely to remain so in future contests. Further, although Maynard Smith and Parker assumed that contests in which both individuals play dove are decided by the toss of another unbiased coin, we retain this stochasticity but allow the coin to be biased by the phenotypes of the two contestants. Last, previous studies assumed that the full cost of an escalated (hawk versus hawk) contest is paid by the loser with no cost to the winner, whereas we consider that both may pay a penalty for escalation, which may still be different for winner and loser.

Our aim is to find the most general set of evolutionarily stable strategies (ESSs) for individuals of all phenotypes in contests with individuals of all phenotypes. In this simple model, we assume that an individual's strategy depends on its own state and that of its opponent in a simple manner. In every contest, each individual aims to maximize its payoff in that contest with no expectation of the future, although it may use knowledge of previous contests between the two to do this. Thus, any complicated behavior based upon a sequence of games is prohibited, but if there is more than one stable solution for the single game, history can influence which solution is reached. We then use the strategies that we have found to consider two questions. First, how are the resources split between different individuals in a group? In particular, we consider whether this split is equitable or uneven. Second, we consider to what extent there is a clear dominance relationship between individuals; we say that individual A dominates B if and only if, in a contest between the two, A always plays hawk and B always plays dove. We implicitly assume a large, well-mixed population, and that any changes in the size of the population have no bearing on the ESS. For a more general approach, which integrates evolutionary and population dynamics, see Rand et al. (1994).

The model

We consider a population of individuals that interact in a series of contests, each over identical individual resource items. Each contest occurs between two individuals. The outcome of the contest depends on a number of factors. One factor is chance; outcomes of contests are determined stochastically, thus in the following we think in terms of the long-term average outcome of a large number of contests. Individuals can, however, influence the outcome of a contest through the strategy they adopt in each contest. Here we characterize strategy very simply; each player can choose either to play aggressively (hawk) or defensively (dove). When two individuals enter into a contest, both select one or the other of these strategies. They do this simultaneously, without knowledge of the strategy adopted by the other contestant. We also assume that individuals can differ in some univariate parameter that we call quality, the value of which indicates an individual's ability to compete in both escalated contests when both individuals choose to be aggressive and play hawk and nonescalated contests when both play dove. When selecting the strategy to employ in a given contest, each contestant can use knowledge of both their own and their opponent's quality. This study considers how an evolutionarily stable method of strategy selection depends on an individual's quality, the quality of the opponent, the value of the resource being contested, and the cost of either winning or losing an escalated contest.

Consider a contest between two individuals of intrinsic qualities s and t, respectively. We assume that each contest is over a resource item of value V, where $V > 0$. If both individuals play dove then neither pays any cost and the winner obtains reward V. We assume that the probability of the player of quality t winning against an opponent of quality s is given by $0.5 + d(t,s)$. If one individual plays dove and the other hawk, then the dove gets nothing and the hawk gets the full prize (V). In the final case, where both play hawk, then we again assume that the winner gets the full prize (V); however, both winner and loser each incur a cost of the extended contest: the winner pays αC and the loser $(1 - \alpha)C$: $C > 0, 0 \le \alpha \le 0.5$. We assume that the probability of the player of quality t winning is given by $0.5 + r(t,s)$.

The rules of probability imply that the functions $r(t,s)$ and $d(t,s)$ have the following properties:

$$r(t,t) = 0, \quad d(t,t) = 0$$
$$-0.5 \le r(t,s) \le 0.5, \quad -0.5 \le d(t,s) \le 0.5$$
$$r(s,t) = -r(t,s), \quad d(s,t) = -d(t,s)$$

Let us define P as the strategy of playing hawk with probability P and dove with probability $(1 - P)$ in any given contest.

Evolutionarily stable strategies

When two players of intrinsic qualities s and t meet in a contest, we wish to specify the strategy that each should adopt, such that if the whole population of s and t individuals play these strategies, then no individual of either quality would increase their expected gain from s versus t contests by switching to any other strategy. We define the expected gain of an individual of quality t playing strategy T against an individual of quality s playing strategy S as $E_{ts}[T,S]$. Then

$$\begin{aligned} E_{ts}[T,S] = TS\left[\frac{V-C}{2} + r(t,s)\left(V+(1-2\alpha)C\right)\right] \\ + T(1-S)V + (1-T)(1-S)V\left(\frac{1}{2}+d(t,s)\right) \end{aligned} \tag{1}$$

Consider a situation where the population of quality s individuals is made up of $1-\varepsilon$ P_2 players and εQ_2 players. Similarly, the population of quality t individuals is made up of $1-\phi$ P_1 players and ϕQ_1 players; where ε and ϕ are very small. We assume that both $Q_1 \neq P_1$ and $Q_2 \neq P_2$; effectively, this assumption indicates that there is always a nonzero rate of mutation producing new strategies throughout all parts of the population. We wish to find the conditions for which $\{P_1,P_2\}$ is an evolutionarily stable pair: the conditions for this are Eqs. A1–A4 in Appendix A.

Selten (1980) showed that such a system could not have a mixed ESS unless $s = t$. If we assume that $s = t$, then this reduces our problem to the standard hawk–dove model with no asymmetry between competitors. The ESS for this is well known:

$$P_1 = P_2 = \begin{cases} \dfrac{V}{C}, & V \leq C \\ 1, & V > C \end{cases} \tag{2}$$

Hence, we concentrate on the case where $s \neq t$, where Selten has shown that the ESS values of P_1 and P_2 can only be 0 or 1.

We now consider all the possible pairs of $\{P_1,P_2\}$ in turn, starting with the case where both individuals always play hawk and we always have escalated contests: i.e., $\{P_1,P_2\} = \{1,1\}$, which (using Eqs. A6–A8 from Appendix B) is an ESS if and only if

$$\left|r(t,s)\right| \leq \frac{V-C}{2\left(V+(1+2\alpha)C\right)} \tag{3}$$

Substituting {0,0} into Eq. A5a implies that $V < 0$, which is not true. Hence, {0,0} is never an ESS.

Using Eqs. A9 and A10, we find that {0,1} is an ESS if

$$r(t,s) < \frac{C-V}{2\left(V+(1-2\alpha)C\right)} \tag{4}$$

Similarly, we can show that the only condition for $\{P_1,P_2\} = \{1,0\}$ to be an ESS is

$$r(t,s) > \frac{-(C-V)}{2\left(V+(1-2\alpha)C\right)} \tag{5}$$

Note that the form of the ESS pair $\{P_1,P_2\}$ depends not on the absolute values of V and C independently, but on their ratio. For convenience, we define $R = \dfrac{V}{C}$.

In summary, there are two cases (see Fig. 1):

(i) $0 < R < 1$

$$\{P_1,P_2\} = \begin{cases} \{1,0\}, & \dfrac{1-R}{2(R+1-2\alpha)} \leq r(t,s) \leq \dfrac{1}{2} \\ \{0,1\}\{1,0\}, & \dfrac{R-1}{2(R+1-2\alpha)} < r(t,s) < \dfrac{1-R}{2(R+1-2\alpha)}, \quad s \neq t \\ \{R,R\}, & s = t \\ \{0,1\}, & -\dfrac{1}{2} \leq r(t,s) \leq \dfrac{R-1}{2(R+1-2\alpha)} \end{cases}$$

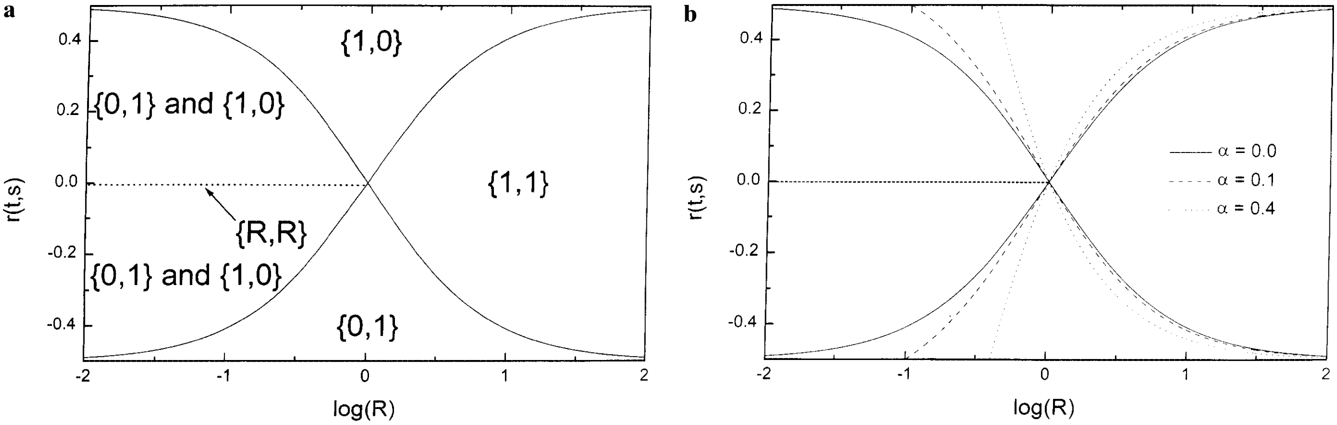

Fig. 1. **a** The ESS (evolutionarily stable strategy) pairs for different values of R and $r(t,s)$ when $\alpha = 0.0$. **b** As **a**, for three different values of α

(ii) $R \geq 1$

$$\{P_1,P_2\} = \begin{cases} \{1,0\}, & \dfrac{R-1}{2(R+1-2\alpha)} < r(t,s) \leq \dfrac{1}{2} \\ \{1,1\}, & \dfrac{1-R}{2(R+1-2\alpha)} \leq r(t,s) \\ & \leq \dfrac{R-1}{2(R+1-2\alpha)} \\ \{0,1\}, & -\dfrac{1}{2} \leq r(t,s) < \dfrac{1-R}{2(R+1-2\alpha)} \end{cases}$$

Every contest involves one (or both) of the players playing pure hawk, and so the mechanism with which dove versus dove contests are decided has no influence on the strategies that individuals adopt, and optimal play is independent of $d(t,s)$. Hawk versus hawk contests occur only if two conditions are satisfied; namely, the cost of losing is relatively small (it must be less than the reward) and the two individuals are relatively evenly matched, although the range of such opponents can become large if V is much greater than C. When there is a large difference between competitors, the superior individual plays hawk and the inferior dove, so that the superior individual is dominant over the other and always receives the reward. If the cost is large, but the individuals are not too dissimilar in ability, then both {1,0} and {0,1} are ESSs. Which of the two alternate ESSs occurs is a function of chance and the history of the system. Thus, it is possible that the inferior individual will dominate the superior one. This paradoxical ESS may occur when the relative ability of two individuals have reversed over time; i.e., a juvenile grows older and more able to compete with a mature individual but continues to back down.

The value of α has little effect when R is high but acts to increase the range of $r(t,s)$ values where both ESS pairs coexist. A nonzero value for α means that, for sufficiently low R values, coexistence occurs for all possible values of $r(t,s)$. This relationship can be seen clearly from Fig. 1b, because increasing α penalizes winners of contests; hence, the more asymmetric the quality of the two individuals, the more extreme the value of $r(t,s)$ will be, the more often the better-quality competitor will win, and so the more it will be "punished" by increasing α. Thus, increasing α will decrease the likelihood of the better competitor playing hawk and the poorer one playing dove being the only ESS.

An example of the function of *r*(*t*,*s*)

We now specify the exact form of $r(t,s)$ of Mesterton-Gibbons (1994):

$$r(t,s) = \begin{cases} \dfrac{\exp(\lambda(t-s)) - 1}{2} & t \leq s \\ \dfrac{1-\exp(-\lambda(t-s))}{2}, & t > s \end{cases} \tag{6}$$

where λ is a positive constant. Note that r is not a function of the two competitive abilities t and s separately but only of the difference between them. Where such a "quality" is an arbitrary measure, then λ is a mere scaling factor of no importance. We envisage, however, that the quality in question is some obvious physical trait (Mesterton-Gibbons 1994 used the example of horn size), so that λ has a natural meaning. The higher the value of λ, the more effectively any advantage that one individual has over another in quality is translated into success in contests. Hence, from the explanation just given, it is no surprise that the larger λ becomes, the smaller the range of differences in quality that lead to coexisting ESS pairs (Fig. 2).

When $R \geq 1$, if an individual of quality t plays one of quality s, then using Eqs. A11 and A12 we have the following:
It receives reward V if

$$s < t - \left(\frac{1}{\lambda}\right)\ln\left(\frac{R+1-2\alpha}{2-2\alpha}\right) \equiv X \tag{7}$$

It receives reward zero if

$$s > t + \left(\frac{1}{\lambda}\right)\ln\left(\frac{R+1-2\alpha}{2-2\alpha}\right) \equiv Y \tag{8}$$

Otherwise, it receives reward

$$\frac{V-C}{2} + r(t,s)\left[V + (1-2\alpha)C\right] \tag{9}$$

Division of resources among a population of animals

Let us assume that the distribution of individual quality in a population is normal with mean μ and variance σ^2. Thus, an

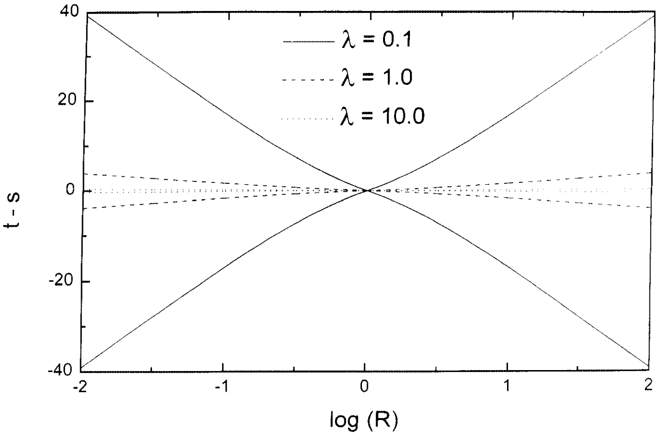

Fig. 2. The ESS pairs for different values of R and $t - s$ when $\alpha = 0.0$ and λ takes on three different values, when $r(t,s)$ is defined by Eq. 6. Between the two *lines*, both ESS pairs where one individual plays hawk and the other dove coexist for $\log(R) < 0$, and {1,1} is the only ESS when $\log(R) > 0$; outside these regions, the ESS pair always has the higher-quality individual playing hawk and the poorer-quality individual playing dove

individual of quality t receives reward V against a proportion of opponents:

$$\Phi\left(\frac{X-\mu}{\sigma}\right) \tag{10}$$

where Φ is the cumulative distribution function of the standard normal distribution.

Using the function of Mesterton-Gibbons (1994) and the Eqs. A13–A15, the reward to an individual of quality t is evaluated as

$$\begin{aligned}
&\alpha C\Phi\left(\frac{X-\mu}{\sigma}\right)-(1-\alpha)C\Phi\left(\frac{Y-\mu}{\sigma}\right)\\
&\quad+\left(V+(1-2\alpha)C\right)\Phi\left(\frac{t-\mu}{\sigma}\right)\\
&\quad+\frac{\left(V+(1-2\alpha)C\right)}{2}\exp\left(\lambda(t-\mu)+\frac{\lambda^2\sigma^2}{2}\right)\\
&\quad\times\left[\Phi\left(\frac{Y-\mu+\lambda\sigma^2}{\sigma}\right)-\Phi\left(\frac{t-\mu+\lambda\sigma^2}{\sigma}\right)\right]\\
&\quad-\frac{\left(V+(1-2\alpha)C\right)}{2}\exp\left(\lambda(\mu-t)+\frac{\lambda^2\sigma^2}{2}\right)\\
&\quad\times\left[\Phi\left(\frac{t-\mu-\lambda\sigma^2}{\sigma}\right)-\Phi\left(\frac{X-\mu-\lambda\sigma^2}{\sigma}\right)\right]
\end{aligned} \tag{11}$$

The parameters λ and σ only affect this reward through the product $\lambda\sigma$. The proportion of contests in which it is involved, where one individual is not dominant, is

$$\Phi\left(\frac{Y-\mu}{\sigma}\right)-\Phi\left(\frac{X-\mu}{\sigma}\right) \tag{12}$$

The total proportion of nondominant contests is equal to the probability that two random individuals have a quality differing by less than

$$\beta=\left(\frac{1}{\lambda}\right)\ln\left(\frac{R+1-2\alpha}{2(1-\alpha)}\right) \tag{13}$$

If the qualities of the individuals are s and t, then $s-t \sim \mathrm{N}[0, 2\sigma^2]$. Thus,

$$P\left[|s-t|<\beta\right]=\Phi\left(\frac{\beta}{\sqrt{2}\sigma}\right)-\Phi\left(\frac{-\beta}{\sqrt{2}\sigma}\right)=2\Phi\left(\frac{\beta}{\sqrt{2}\sigma}\right)-1 \tag{14}$$

which is the proportion of nondominant contests. This proportion will be large if σ is small (if almost all individuals are evenly matched) or if R is large (the reward is large relative to the cost).

If $R < 1$, then all contests are of the hawk–dove form and for every pair of individuals one is dominant over the other. However, for individuals of sufficiently similar quality, it is not obvious which is the dominant one. We assume that this is decided by the historical relationship between the two; for example, the elder may be dominant because of past encounters unless the two have never met, in which case the "default" behavior may be for the larger to be dominant. The superior individual is thus dominant in a proportion $\gamma \geq 0.5$ of cases. Note that, in general, γ may depend on the degree of difference.

If $R > \alpha$, then, using Eqs. A16–A18, the payoff to an individual of quality t is shown to be as follows.
The payoff is V if

$$s \leq t-\frac{1}{\lambda}\ln\left(\frac{R+1-2\alpha}{2R-2\alpha}\right)\equiv x \tag{15}$$

The payoff is γV if

$$x<s<t \tag{16}$$

And, the payoff is $(1-\gamma)V$ if

$$t<s<t+\frac{1}{\lambda}\ln\left(\frac{R+1-2\alpha}{2R-2\alpha}\right)\equiv y \tag{17}$$

Thus, the overall reward to an individual of quality t is

$$\begin{aligned}
&V\Phi\left(\frac{x-\mu}{\sigma}\right)+\gamma V\Phi\left(\frac{t-\mu}{\sigma}\right)-\gamma V\Phi\left(\frac{x-\mu}{\sigma}\right)\\
&\quad+(1-\gamma)V\Phi\left(\frac{y-\mu}{\sigma}\right)-(1-\gamma)V\Phi\left(\frac{t-\mu}{\sigma}\right)
\end{aligned} \tag{18}$$

which simplifies to

$$\begin{aligned}
&V\left\{(1-\gamma)\Phi\left(\frac{x-\mu}{\sigma}\right)+(2\gamma-1)\Phi\left(\frac{t-\mu}{\sigma}\right)\right.\\
&\quad\left.+(1-\gamma)\Phi\left(\frac{y-\mu}{\sigma}\right)\right\}
\end{aligned} \tag{19}$$

If $R \leq \alpha$, then no individual is clearly dominant over another, so that the overall reward for an individual of quality t is

$$\begin{aligned}
&V\left\{\gamma\Phi\left(\frac{t-\mu}{\sigma}\right)+(1-\gamma)\left(1-\Phi\left(\frac{t-\mu}{\sigma}\right)\right)\right\}\\
&\quad=V\left\{(1-\gamma)+(2\gamma-1)\Phi\left(\frac{t-\mu}{\sigma}\right)\right\}
\end{aligned} \tag{20}$$

We shall now consider the division of resources for a range of values of R. Without loss of generality, we can use $\mu = 0$, $\sigma^2 = 1$, and $V = 1$. In addition, we shall set $\alpha = 0$, $\lambda = 0.1$, and $\gamma = 0.7$. The reward to an individual of quality t is given by Eqs. A19 and A20 (Fig. 3). From this figure, it is clear that when $R = 1$, the high-quality individuals perform a lot better than the lower-quality ones and that this advantage is more extreme than for either $R = 10$ or $R = 0.1$ and

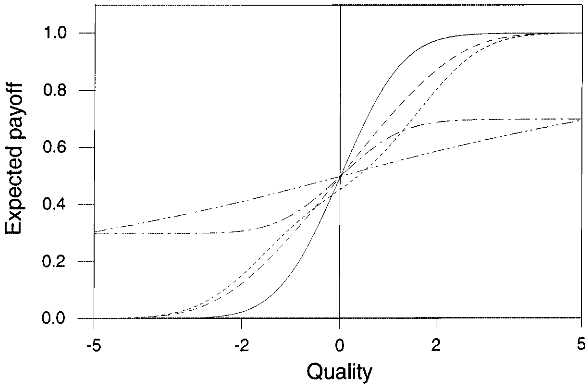

Fig. 3. The expected payoff to individuals of differing quality in a population where quality is $N(0,1)$, $\alpha = 0$, $\lambda = 1$, $V = 1$, and $\gamma = 0.1$, for different values of R. *Alternate long and short dashes*, $R = 0$; *long dashes*, $R = 0.1$; *solid line*, $R = 1$; *short dashes*, $R = 10$; *long dashes and two short dashes*, $R = \infty$

considerably more extreme than in the asymptotic cases $R = 0$ and $R = \infty$. When R is large, there are many hawk versus hawk contests so that the average payoff for the population is lower than for low or medium-sized R (the mean payoff for the population is 0.5 for both $R = 0.1$ and $R = 1$, and is ≈ 0.4 for $R = 10$). However, it is the medium- to higher-quality individuals that suffer from this; low-quality individuals do better here than they do with low- or medium-sized R. Note that when $R = \infty$ there are no longer any costs to contests, yielding the most even distribution of resources.

Discussion

Two aspects of our results are worth discussion in a wider context: the predicted strategies and the consequential division of resources. A mixed strategy is one where an individual's probability of playing a given strategy in a contest is neither zero nor one. In our model, mixed strategies can only occur in the very restrictive circumstance in which both competitors are identical. Previous workers (e.g., Maynard Smith and Parker 1976; Mesterton-Gibbons 1994) have raised concerns about the potential heritability of such strategies. Mesterton-Gibbons concluded that "an ESS in pure strategies is a very much more convincing solution to an evolutionary game than an ESS in mixed strategies." This is not to say, however, that we would expect such purity in the real world. Natural situations are always much more complicated than the model situations described in theory, and we would not expect perfect matching. However, this conclusion may suggest that we would expect the behavior of real individuals to be close to pure strategies and that we should be slow to assume that any deviation from the pure strategy is necessarily the result of natural selection for a mixed strategy.

For some contests between individuals of different but similar qualities, we show that two very different ESSs are possible: in one, the better competitor always plays hawk and the other dove; in the other, the better competitor always plays dove and the poorer one always plays hawk, and so always wins. This second ESS is surprising and was termed "paradoxical" by Maynard Smith and Parker (1976), who considered that it was unlikely to occur in nature. Their argument was that in their model (and ours) this ESS always coexists with another ESS that "has a larger 'zone of attraction' and hence is more likely to arise." We agree that such paradoxical ESSs are unlikely to be widespread in nature but suggest that they may be possible in circumstances where the relative "quality" of individuals changes over time. For example, adult animals are generally stronger than juveniles, who would be expected to be submissive to them. However, over time the juveniles will grow stronger whereas adults may decline in quality with age, leading eventually to a reversal in relative strength. However, it appears at least possible that the strategy of juvenile submission may persist for a time after it has become strictly "paradoxical" because of the history of the system (Matsumura and Kobayashi 1998 and references therein). Such situations in which the competitive abilities of individuals change over time are worthy of further empirical and theoretical effect.

Using a particular function for $r(t,s)$ and making the simplifying assumption of a normally distributed population of qualities, we find a number of interesting results. The proportion of nondominant contests is zero if $R \leq 1$, but it can be large for sufficiently large R or if the variance in individual qualities is small. In particular, the relative frequency of highly aggressive contests is high when the cost of losing an escalated contest is small.

In practice, estimating the value of R for a given ecological system is challenging, especially because the costs and benefits of a contest are often measured in different currencies. However, it is clear that R can vary greatly in size. For example, blackbirds in winter often feed on worms in groups and attempt to steal from each other. These contests last a few seconds, and an individual can be involved in hundreds each day. The costs of these contests must be low. In spring, these birds form territories and the contest over possession of a territory is generally only slightly longer lasting and no more intense than contests over food items, yet the benefit from obtaining a feeding territory is much greater than from obtaining a single worm. Thus, individuals of this species will experience different types of contest that differ in R by several orders of magnitude.

Figure 3 shows how resources are divided in a population for a given set of parameter values for varying values of R. When R is low ($R = 0.1$), the probability of contests where both ESSs (1,0) and (0,1) occur is high, so that lower-quality animals win some contests for historical reasons. If R is high ($R = 10$), then many hawk–hawk contests occur and, as the cost of losing is low, lower-quality animals can win contests and do better than for medium R. Overall, the expected reward is lower due to costs incurred, and medium- to high-quality animals are hardest hit; thus, for high R the split of resources is relatively equitable. For medium R (close to unity), neither of these situations occur and low-quality animals do poorly and high-quality ones well. Perhaps surprisingly, maximum discrimination between qualities occurs here rather than at either of the extremes, as is emphasized by the asymptotic cases where R is set to equal either 0 or ∞ where the division of resources is at its most equitable.

Acknowledgment M.B. acknowledges the help of Nuffield Foundation (grant reference SCI/180/97/125/G) in the production of this paper.

References

Broom M, Cannings C, Vickers GT (2000a) Evolution in knockout conflicts. The fixed strategy case. Bull Math Biol 62:451–466

Broom M, Cannings C, Vickers GT (2000b) Evolution in knockout conflicts. The variable strategy case. Selection 1:5–21

Dugatkin LA, Reeve HK (1998) Game theory and animal behaviour. University Press, Oxford

Emlen ST, Oring LW (1977) Ecology, sexual selection and the evolution of mating systems. Science 197:215–223

Hand JL (1986) Resolution of social conflicts: dominance, egalitarianism, spheres of dominance and game-theory. Q Rev Biol 61:201–220

Keller L, Reeve HK (1994) Partitioning of reproduction in animal societies. Trends Ecol Evol 9:98–103

Matsumura S, Kobayashi T (1998) A game model for dominance relations among group living animals. Behav Ecol Sociobiol 42:77–84

Maynard Smith J, Parker GA (1976) The logic of asymmetric contests. Anim Behav 24:159–175

Mesterton-Gibbons M (1994) The Hawk-Dove game revisited: effects of continuous variation in resource-holding potential on the frequency of escalation. Evol Ecol 8:230–247

Mesterton-Gibbons M, Dugatkin LA (1995) Towards a theory of dominance hierarchy: effects of assessment, group size and variation in fighting ability. Behav Ecol 6:416–423

Rand DA, Wilson HB, McGlade JM (1994) Dynamics and evolution: evolutionary stable attractors, invasion exponents and phenotype dynamics. Philos Trans R Soc Lond B Biol Sci 343:261–283

Reeve HK, Keller L (1996) Relatedness asymmetry and reproductive sharing in animal societies. Am Nat 148:764–769

Selten R (1980) A note on evolutionarily stable strategies in asymmetric animal conflicts. J Theoret Biol 84:93–101

Vehrencamp SL (1983) A model for the evolution of despotic versus egalitarian societies. Anim Behav 31:667–682

Appendix A: General conditions

The conditions for P_1 and P_2 to constitute an ESS pair are

$$\text{(a) } E_{ts}[P_1,P_2] \geq E_{ts}[Q_1,P_2] \tag{A1}$$

and

$$\text{(b) if } E_{ts}[P_1,P_2] = E_{ts}[Q_1,P_2] \text{ then } E_{ts}[P_1,Q_2] > E_{ts}[Q_1,Q_2] \tag{A2}$$

for all $Q_1 \neq P_1$ and $Q_2 \neq P_2$
and

$$\text{(c) } E_{st}[P_2,P_1] \geq E_{st}[Q_2,P_1] \tag{A3}$$

and

$$\text{(d) if } E_{st}[P_2,P_1] = E_{st}[Q_2,P_1] \text{ then } E_{st}[P_2,Q_1] > E_{st}[Q_2,Q_1] \tag{A4}$$

for all $Q_2 \neq P_2$ and $Q_1 \neq P_1$

Equation A1 can be reexpressed as

$$(P_1 - Q_1)V\left(\frac{1}{2} - d(t,s)\right) + P_2(P_1 - Q_1) \times\left(\frac{-C}{2} + r(t,s)\left(V + (1-2\alpha)C\right) + d(t,s)V\right) \geq 0 \tag{A5a}$$

Similarly, we require that $E_{st}[P_2,P_1] \geq E_{st}[Q_2,P_1]$, which gives

$$(P_2 - Q_2)V\left(\frac{1}{2} - d(s,t)\right) + P_1(P_2 - Q_2) \times\left(\frac{-C}{2} + r(s,t)\left(V + (1-2\alpha)C\right) + d(s,t)V\right) \geq 0 \tag{A5b}$$

Appendix B: The different ESS possibilities

Substituting the values $P_1 = P_2 = 1$ into Eq. A5a gives

$$(1 - Q_1)\left(\frac{V - C}{2} + r(t,s)\left(V + (1-2\alpha)C\right)\right) \geq 0 \tag{A6}$$

Because $Q_1 < 1$, this is only satisfied when

$$r(t,s) \geq \frac{C - V}{2\left(V + (1-2\alpha)C\right)} \tag{A7}$$

If $r(t,s)$ is greater than the right hand side of Eq. A7, then $E_{ts}[P_1,P_2] > E_{ts}[Q_1,P_2]$, but if equality holds then $E_{ts}[P_1,P_2] = E_{ts}[Q_1,P_2]$, and so (for P_1 to be an ESS), we require $E_{ts}[P_1,Q_2] > E_{ts}[Q_1,Q_2]$. Substituting into Eq. 1, we obtain

$$(1 - Q_1)(1 - Q_2)V\left(0.5 - d(t,s)\right) > 0$$

which is true for $Q_1 < 1$ and $Q_2 < 1$.

Substituting in Eq. A5b gives

$$r(s,t) \geq \frac{C - V}{2\left(V + (1-2\alpha)C\right)} \tag{A8}$$

Thus, by similar reasoning, {1,1} is an ESS if Eqs. A7 and A8 hold.

However, because $r(t,s) = -r(s,t)$, this simplifies to {1,1} is an ESS if and only if Eq. 3 holds.

Let us now consider the conditions under which $\{P_1,P_2\} = \{0,1\}$ is an ESS. Substitution into Eq. A5a gives

$$r(t,s) \leq \frac{C - V}{2\left(V + (1-2\alpha)C\right)} \tag{A9}$$

Substitution into Eq. A5b gives the condition

$$V\left(\frac{1}{2} - d(s,t)\right)(1 - Q_2) \geq 0 \tag{A10}$$

the left hand side of which is strictly positive for all $Q_2 < 1$.

We must again consider the case where equality holds. Substituting into Eq. A2 we obtain $(-Q_1)(1 - Q_2)V(0.5 - d(t,s)) > 0$, which is not satisfied.

Appendix C: Rewards received

When $R \geq 1$, using Eq. 6 an individual receives reward V if

$$r(t,s) = \frac{1 - \exp(-\lambda(t-s))}{2} > \frac{R-1}{2(R+1-2\alpha)} \tag{A11}$$

which rearranges to give Eq. 7.

It receives 0 if

$$r(t,s) = \frac{\exp(\lambda(t-s)) - 1}{2} < \frac{1-R}{2(R+1-2\alpha)} \tag{A12}$$

which rearranges to give Eq. 8. Otherwise, it receives the reward shown in Eq. 9.

An individual with quality t receives V against opponents with quality less than X. Against opponents whose quality is between X and Y, it receives the following rewards:

$$\begin{cases} \dfrac{V-C}{2} + (V + (1-2\alpha)C)\dfrac{\exp(\lambda(t-s)) - 1}{2} \\ \quad t \leq s \leq Y \\ \dfrac{V-C}{2} + (V + (1-2\alpha)C)\dfrac{1 - \exp(-\lambda(t-s))}{2} \\ \quad t > s \geq X \end{cases} \tag{A13}$$

Otherwise, it receives 0. The overall reward to an individual of quality t is thus

$$\left\{ \begin{aligned} & V\Phi\left(\frac{X-\mu}{\sigma}\right) + \int_t^Y \left(\frac{V-C}{2} + (V + (1-2\alpha)C) \right. \\ & \left. \times \frac{\exp(\lambda(t-s)) - 1}{2}\right) \frac{1}{\sqrt{2\pi}\,\sigma} \exp\left(\frac{-(s-\mu)^2}{2\sigma^2}\right) ds \\ & + \int_X^t \left(\frac{V-C}{2} + (V + (1-2\alpha)C)\frac{1 - \exp(-\lambda(t-s))}{2}\right) \\ & \times \frac{1}{\sqrt{2\pi}\,\sigma} \exp\left(\frac{-(s-\mu)^2}{2\sigma^2}\right) ds \end{aligned} \right. \tag{A14}$$

Considering the moment-generating function of a $N(\mu,\sigma^2)$, the following equation holds:

$$\begin{aligned} & \int_a^b \exp(cs) \frac{1}{\sqrt{2\pi}\,\sigma} \exp\left(\frac{-(s-\mu)^2}{2\sigma^2}\right) ds = \\ & \exp\left(\mu c + \frac{c^2\sigma^2}{2}\right)\left[\Phi\left(\frac{b-\mu-c\sigma^2}{\sigma}\right) - \Phi\left(\frac{a-\mu-c\sigma^2}{\sigma}\right)\right] \end{aligned} \tag{A15}$$

These results together can be used to show Eq. 11.

When $\alpha < R < 1$, the payoff to a quality t individual is V if

$$r(t,s) = \frac{1 - \exp(-\lambda(t-s))}{2} \geq \frac{1-R}{2(R+1-2\alpha)} \tag{A16}$$

which rearranges to give Eq. 15. The payoff is γV if

$$0 < \frac{1 - \exp(-\lambda(t-s))}{2} < \frac{1-R}{R+1-2\alpha} \tag{A17}$$

which rearranges to give Eq. 16. Finally the payoff is $(1 - \gamma)V$ if

$$\frac{R-1}{R+1-2\alpha} \leq \exp(\lambda(t-s)) - 1 < 0 \tag{A18}$$

which rearranges to give Eq. 17.

Appendix D: Equations for Fig. 3

$$\begin{aligned} & \frac{R+1}{R}\Phi(t) - \frac{1}{R}\Phi\left(t + \ln\left(\frac{R+1}{2}\right)\right) + \exp(0.1t + 0.005) \\ & \times \frac{R+1}{2R}\left[\Phi\left(t + 0.1 + \ln\left(\frac{R+1}{2}\right)\right) - \Phi(t + 0.1)\right] \\ & - \exp(0.005 - 0.1t)\frac{R+1}{2R}\left[\Phi(t - 0.1)\right. \\ & \left. - \Phi\left(t - 0.1 - \ln\left(\frac{R+1}{2}\right)\right)\right] \end{aligned} \tag{A19}$$

if $R \geq 1$, or

$$0.3\Phi\left(t - \ln\left(\frac{R+1}{2R}\right)\right) + 0.4\Phi(t) + 0.3\Phi\left(t + \ln\left(\frac{R+1}{2R}\right)\right) \tag{A20}$$

if $R < 1$.