Evolutionary Ecology Research, 2007, **9**: 395–408

ESS distribution of display duration in animal contests to assess an opponent before fighting or fleeing

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ABSTRACT

Questions: What determines the duration of conventional display in animal contests?

Mathematical method: Evolutionarily stable probability distribution of display duration is calculated mathematically.

Key assumptions: Display lasts until one of the contestants chooses to fight or flee. The outcome of fighting between two contestants is determined by their relative strength, which is unknown at the beginning but becomes more and more apparent to both contestants with time.

Conclusions: The ESS population may include individuals with very different display durations. The more valuable the contested resource and the greater the cost of losing a contest, the longer the display lasts. Animals that assess their opponents with very high or very low efficiency will engage in shorter displays than animals with intermediate assessment efficiency.

Keywords: assessment, contest behaviour, display duration, evolutionarily stable state.

INTRODUCTION

Animals fight over food, territory, and mates with conspecific individuals. But in many species, a violent attack does not begin immediately upon an encounter; there are first non-aggressive interactions. For example, red deer *Cervus elaphus* roar and walk in parallel with each other (Clutton-Brock and Albon, 1979), and cichlid fish *Nannacara anomala* show parallel orientation and tail-beating (Enquist and Jakobsson, 1986). These displays are thought to exchange information about fighting abilities or resource holding potential (physical fighting ability irrespective of motivation for fighting) (Parker, 1974), which may be related to body size, health, motor ability, and fighting skills (Morton, 1977; Davies and Halliday, 1978). Weaker animals can realize their inferiority by the display and can flee before the fight escalates. Thus, displays prevent animals from suffering serious injuries.

On the other hand, displays are costly (Hack, 1997a). Both contestants must pay the cost during the display in the form of time, energy or increased exposure to predators. So the length of the display or entire contest is important for behavioural ecologists. Empirical studies have identified several factors that affect contest duration. Contest duration

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increases when both opponents are of similar size or weight (e.g. Enquist and Jakobsson, 1986; Enquist *et al.*, 1990; Leimar *et al.*, 1991; Faber and Baylis, 1993; Hack *et al.*, 1997; Ladich, 1998; Panhuis and Wilkinson, 1999; Andersen *et al.*, 2000; Pratt *et al.*, 2003). These reports support the hypothesis that contestants assess each other during the display. However, other researchers have reported that the absolute resource holding potential of the loser, not of the winner, determines the contest duration (Bridge *et al.*, 2000; Taylor *et al.*, 2001; Jennings *et al.*, 2004; Morrell *et al.*, 2005), which supports the self-assessment hypothesis (Gammell and Hardy, 2003; Taylor and Elwood, 2003; Gherardi, 2006). An enhanced resource value increased the display duration in the study of Enquist and Leimar (1987) but reduced it in that of DiMarco and Hanlon (1997). Increasing residence duration increases contest duration (Johnsson and Forser, 2002; Takeuchi, 2006). Age, experience, and pre-exposure to the present opponent also affect the duration of the contest (Jensen and Yngvesson, 1998; Jennings *et al.*, 2004; Kemp *et al.*, 2006).

Mathematical models have been developed to study contest duration and ferocity in animal encounters (reviewed by Jennings *et al.*, 2005). The sequential assessment game assumes that animals repeatedly engage in costly assessments and decision making as to whether to continue the conflict or retreat (Enquist and Leimar, 1983). In cumulative assessment models, each contestant persists until the total physical costs surpass some threshold (Payne, 1998). In war-of-attrition games, each contestant displays for a prefixed length of time that can differ between individuals (Parker, 1974; Bishop and Cannings, 1978; Sjerps and Haccou, 1994; Haccou *et al.*, 2003). The objective of these models has been interpreted to be the acquisition of information about the opponent. However, in all of these models, the contestant that persists the longest is automatically assumed to be the winner of the contest. Hence in these games persisting longer is intended not purely to acquire information on relative strength, but is an option for the animal to win the contest.

We need to determine whether animals invest in information acquisition separately from fighting itself. To do this, we consider that the display is purely to accumulate information on the relative strength of two contestants. An individual strongly motivated to win might start a costly fight without first engaging in a conventional display. Individuals that continue to display may still be undecided about whether to fight or retreat. In such a case, we can clearly separate the display for assessment from the fighting itself, and discuss the role of information acquisition in animal contests.

In this paper, we focus on the duration of conventional displays that are made to assess the contestants' fighting abilities. In this game, a contest is divided into a display stage and a fighting stage. The duration of an animal's display is its strategy, and when the display duration of either contestant ends, both decide whether to fight or flee. We derive the ESS distribution (Maynard Smith and Price, 1973) of display duration analytically and discuss the condition in which all animals sustain a display longer than a certain minimum. We also examine the parameter dependence of the mean duration and the variability of the ESS display duration.

THE GAME MODEL

We consider the following situations. A contest consists of two stages: conventional display and escalation to fighting. When two individuals first meet, they do not have information about each other's fighting abilities. Once they start to display, the contestants' relative fighting abilities begin to be revealed. We also assume that the true fighting abilities of the contestants become clearer as the display progresses.

Consider a player with display duration t. He displays until t after the encounter begins, as long as the opponent has a display duration longer than t. When t has passed, he chooses to fight or flee based on the information he has just obtained. Once one of the contestants decides to fight, then the opponent must decide immediately whether to engage or flee. If one contestant chooses to flee, no fighting occurs and the individual that remains wins the contested resource V. Only when both contestants choose to fight does fighting occur. Then, one wins V and the other incurs the cost of losing (injury or a reduced chance of obtaining other resources). Due to the sequential nature of decision making, there is no possibility that both contestants will flee. The realized display duration is equal to the shorter display duration of the two contestants. This display duration t is the animal's strategy and can vary between individuals.

For the sake of explanation, we label the contestant with the shorter display duration S and the other contestant L. Their display duration is thus $t_S < t_L$. In a contest, S and L start displaying when they meet and, at t_S, S finishes its display and decides whether to attack or retreat. If S chooses to flee and leaves, L has won the contest and stops its display. In contrast, if S chooses to fight, L is forced to either fight or flee. Hence the realized duration of display is t_S.

We assume that the outcome of a fight is determined by relative fighting abilities. In any pair of contestants, one is stronger than the other, and the stronger contestant wins when fighting occurs. Hence if the animals know their relative strength clearly, the stronger should choose to fight and the weaker should choose to flee. However, animals cannot accurately know relative fighting abilities. Rather, they learn as much as they can by investing time in display.

We assume the probability that the stronger chooses to fight equals the probability that the weaker chooses to flee and call them, together, 'the probability of correct decision'. We denote this by $\phi(t)$, which increases monotonically with time once the encounter begins. For the analysis in this paper, we use the following simple saturation curve for the probability of a correct decision:

$$\phi(t) = \tfrac{1}{2}\left(1 + \sqrt{1 - e^{-\alpha t}}\right)$$

The probability of an incorrect decision – that is, the stronger chooses to flee or the weaker chooses to fight – is $1 - \phi$. When they first encounter each other, the contestants do not know each other's fighting abilities, and the probabilities are both 1/2 at time $t = 0$. As time passes, the probability of a correct decision increases to 1 and that of an incorrect decision decreases to 0. It is plausible that more information about fighting ability is presented early in the display rather than later, and that the slope of ϕ becomes less steep as the contestants sustain their displays, as illustrated in Fig. 1. The parameter α determines the slope of the curve and is called the 'assessment efficiency of the display'. If α is large, the animals will quickly understand the difference between their fighting abilities. In contrast, if α is small, they need longer to obtain accurate information about the difference.

Figure 2 shows the game tree of the model. We here assume that the true fighting ability is independent of the display duration, and that the probabilities that S is the stronger and that L is the stronger are both 1/2. Two animals fight over a resource of value V. The payoff matrix is shown in Table 1. Both contestants spend the duration t_S on the display, and pay the cost of it $f(t_S)$. We assume the cost of display is proportional to the display duration, as $f(t) = \beta t$, where β is the cost of display per unit time.

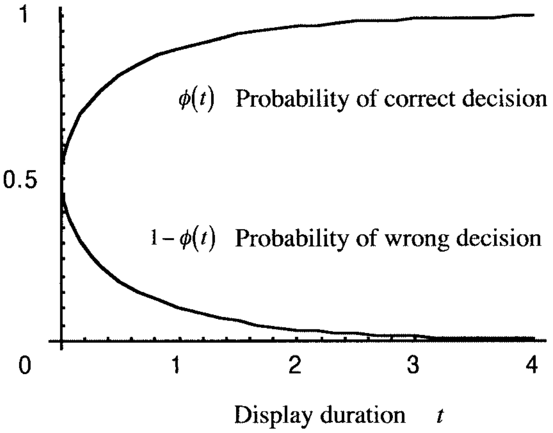

Fig. 1. Probabilities of correct decisions and wrong decisions change with time as contestants improve their decision making. We assume the probability of correct decisions $\phi(t)$ increases monotonically from 0.5 to 1, and that the probability of wrong decisions $1 - \phi(t)$ decreases monotonically from 0.5 to 0. In this figure, we show a set of examples of the probabilities when $\alpha = 1$.

RESULTS

Now we analyse the model to find an evolutionarily stable state (ESS) for the distribution of display duration. From Fig. 2 and Table 1, the expected payoffs for S and L are

$$W_S = \tfrac{1}{2}\{V - \phi(t_S)(1 - \phi(t_S))(V + C) - 2f(t_S)\} \tag{1a}$$

and

$$W_L = \tfrac{1}{2}\{V + \phi(t_S)(1 - \phi(t_S))(V - C) - 2f(t_S)\} \tag{1b}$$

respectively. Please note that W_L is always larger than W_S for all t (see equation A1 in the Appendix). The more patient animal has an advantage in one round. However, this does not imply that having a longer display is always beneficial, because the longer the display lasts, the greater its cost is.

Evolutionarily stable distribution of display duration

Consider the expected payoff of an animal that has a strategy to display for t' in a population in which display duration has the distribution $p(t)$. Using equation (1), the expected payoff is

$$E[W(t')] = \int_0^{t'} W_L(t)p(t)\mathrm{d}t + W_S(t')\int_{t'}^{\infty} p(t)\mathrm{d}t \tag{2}$$

Note that $W_L(t)$ and $W_S(t)$ are given by equation (1) as functions of the shorter display duration of the two animals. Suppose that the opponent has a shorter t than the focal animal, denoted by t', hence $t < t'$. Then the display stops at t, and the focal animal will play L. On the other hand, when $t' \leq t$, the display will continue until t', and the animal plays S.

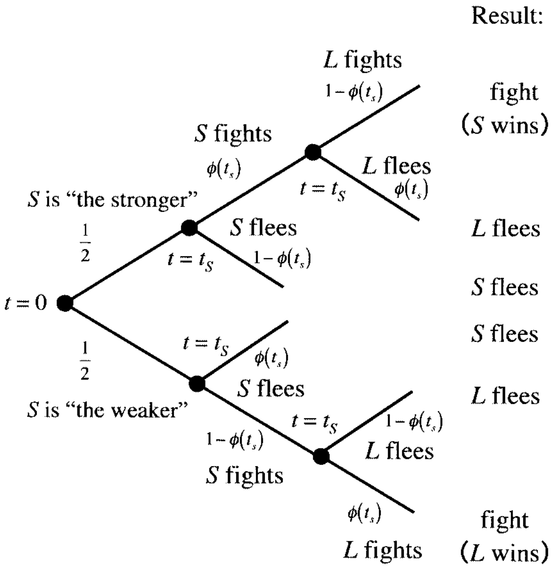

Fig. 2. The game tree of the model. Two contestants, S and L, meet at time $t = 0$. The probabilities that S is the stronger and that L is the stronger are both 1/2. First S chooses the correct decision with $\phi(t_S)$ or the wrong decision with $1 - \phi(t_S)$ at $t = t_S$. When S chooses to fight, L makes its decision at $t = t_S$. A fight occurs if both choose to fight, and the stronger one always wins.

For the ESS $\rho(t')$, the time axis from 0 to infinity is composed of two kinds of time interval: that in which $\rho(t') > 0$ holds and that in which $\rho(t') = 0$ holds. For the former, some individuals adopt the display duration t', whereas in the latter no individuals have a display duration of t'. In the ESS, animals with different t' have the same payoffs. [For examples of similar conditions used in deriving an ESS probability distribution of the emergence dates for insects, see Iwasa *et al.* (1983) and Iwasa and Haccou (1994).] In the interval of $\rho(t') > 0$, we have

$$\frac{\mathrm{d}E[W(t')]}{\mathrm{d}t'} = 0 \qquad \text{for any } t' \text{ satisfying } \rho(t') > 0 \tag{3a}$$

which is a condition necessary for $\rho(t)$ to be an ESS (Bishop and Cannings, 1978).

In addition, we have

$$E[W(t')] < E[W(t)] \qquad \text{for } \rho(t') = 0 \text{ and } \rho(t) > 0 \tag{3b}$$

which implies that the fitness of a mutant who happens to have t' that is not included in the ESS ($\rho(t') = 0$) must be lower than the fitness of residents.

According to the calculation in the Appendix, we can derive the following from equation (3):

(i) When $8\beta/\alpha > V + \mathrm{C}$ holds,

$$\rho(t) = h(t)e^{-\int_0^t h(s)\mathrm{d}s} K \qquad \text{for } 0 \le t < \infty \tag{4a}$$

Table 1. The payoff matrix of the model

(A) When S is the stronger

		L	
		fight	flee
S	fight	$-C-f(t_S)$ $V-f(t_S)$	$-f(t_S)$ $V-f(t_S)$
	flee	$V-f(t_S)$ $-f(t_S)$	$V-f(t_S)$ $-f(t_S)$

(B) When L is the stronger

		L	
		fight	flee
S	fight	$V-f(t_S)$ $-C-f(t_S)$	$-f(t_S)$ $V-f(t_S)$
	flee	$V-f(t_S)$ $-f(t_S)$	$V-f(t_S)$ $-f(t_S)$

Note: The payoff of S is written in the bottom left and that of L is written in the top right in each box. (A) The payoff matrix when S is the stronger. (B) The payoff matrix when L is the stronger. V = the contested resource value, C = the cost of losing an escalated fighting, $f(t_S)$ = the cost of display depending on S's display duration t_S.

where $h(t)$ is given by

$$h(t) = -\frac{\mathrm{d}}{\mathrm{d}t} W_S(t) \Big/ (W_L(t) - W_S(t)) \tag{4b}$$

K is a normalization constant and is determined to satisfy $\int_0^\infty \rho(t)\mathrm{d}t = 1$. Here the distribution is positive for all t. The ESS population includes players of all different display durations.

(ii) When $8\beta/\alpha < V + C$ holds, there is a minimum duration of display denoted by t^*, and all the players at the ESS should play longer than or equal to t^*. The distribution is given by

$$\rho(t) = 0 \qquad \text{for } 0 \le t < t^* \tag{5a}$$

$$\rho(t) = h(t)e^{-\int_{t^*}^{t} h(s)\mathrm{d}s} K \qquad \text{for } t^* \le t < \infty \tag{5b}$$

$h(t)$ is given by equation (4b). K is again the normalization constant. The minimum duration of display t^* is given by

$$t^* = \frac{1}{\alpha} \cdot \ln\left(\frac{\alpha(V+C)}{8\beta} \right) \tag{5c}$$

At $t = t^*$, $h(t^*) = 0$ holds. Hence $\rho(t)$ given by equation (5b) is connected with $\rho(t) = 0$ continuously at the boundary. In the Appendix, we prove that these are the only ESS distributions that satisfy the conditions in equations (3a) and (3b).

Parameter dependence of display duration

Figure 3 shows the evolutionarily stable distribution $\rho(t)$ of display duration, which is spike-shaped. We here examine how the ESS distribution changes with parameters.

1. *Value of winning*. Examples in Fig. 3A differ in the contested resource value V. For small V, some animals make their decisions with a short display, whereas for large V, all animals display longer.
2. *Cost of losing in an escalated fight*. Figure 3B shows examples with various values of C. When the cost of losing a fight C is small, an animal attacks immediately as the encounter begins. As C increases, the mean display duration grows and the variance of the duration shrinks.
3. *Assessment efficiency*. Figure 3C shows the dependence of the ESS on assessment efficiency α. The mean display duration is longest for an intermediate α. With very large or very small α, the mean duration is short.

In some examples in Fig. 3, some individuals sustain very long displays, whereas others show no display. Duration varies widely when the assessment efficiency of the display is low. We can see that, as α increases, the variance in display duration narrows.

4. *Cost of a long display*. Figure 3D shows how the cost of display β affects the ESS. If the display cost per unit time is small, an animal lengthens the display. If β is large, the display will be shorter.
5. *Rescaling variables and combinations of parameters*. We rescale the time variables. Using $t' = \alpha t$ as a new variable for time, we find the model includes only two parameters: $V' = (\beta/\alpha)V$ and $C' = (\beta/\alpha)C$, as explained in the Appendix. Then the fitnesses are also multiplied by a common factor β/α. Hence the ESS distribution over time $\rho(t')$ has only two parameters (V' and C'), if time is rescaled by the factor α. The rescaled duration would be expressed in terms of V' and C'.
6. *Sensitivity of the mean display duration*. We examined how the mean display duration at the ESS depends on different parameters. In Fig. 4, we set parameter values fixed to the standard ones except for a single parameter that is in the horizontal axis. The increase in V, C, or β simply prolongs or shortens the mean duration. However, the assessment efficiency α gives a different result. In some cases, especially with small resource value V and large cost of losing C, intermediate α results in a long display.

Minimum duration of display

As shown in equations (4) and (5), the ESS distribution includes players with different patterns of display duration. There are two parameter regions. In one region all animals

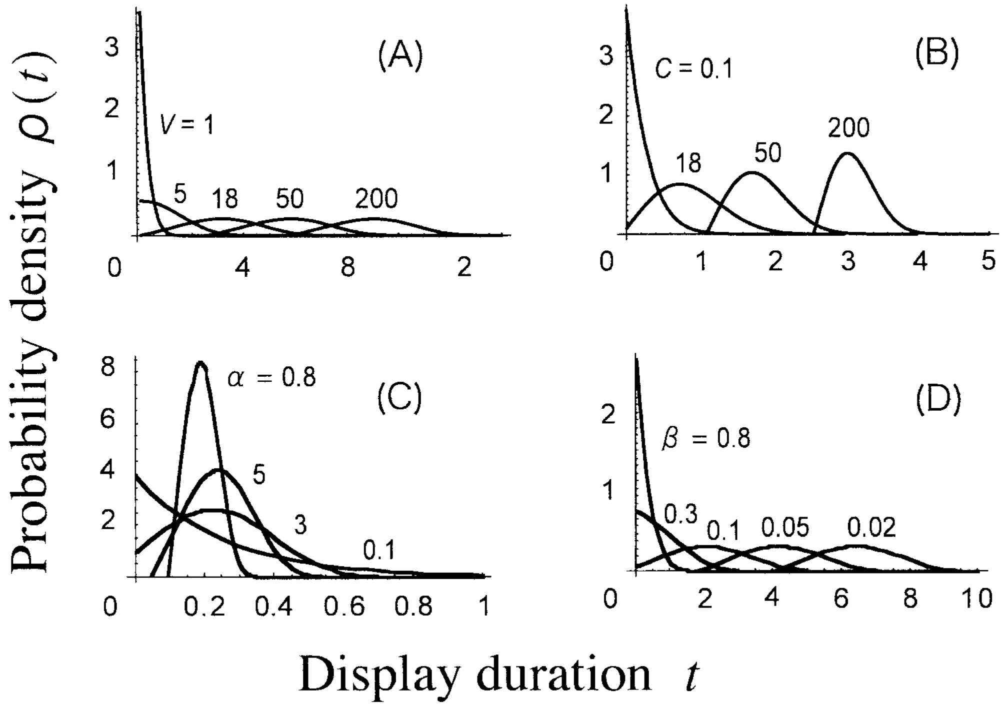

Fig. 3. Examples of evolutionarily stable state for distribution of display duration. The horizontal axes are the duration of display t and the vertical axes are the probability density of the individuals taking the display duration as their strategy. (A) Each example varies in the contested resource value. The numbers in the figure show the resource value of each example. Other parameter values are $C = 1$, $\alpha = 0.4$, and $\beta = 1$. (B) Each example varies in the cost of losing a fight. The numbers in the figure show the cost for each example. Other parameter values are $V = 1$, $\alpha = 0.4$, and $\beta = 1$. (C) Each example varies in the assessment efficiency. The numbers in the figure show the assessment efficiency for each example. Other parameter values are $V = 1$, $C = 1$, and $\beta = 1$. (D) Each example varies in the display cost per unit time. The numbers in the figure show the cost for each example. Other parameter values are $V = 1$, $C = 1$, and $\alpha = 0.4$.

display for longer than the minimum period, and in the other region there is no minimum duration. The minimum duration of display is positive if $8\beta/\alpha < V + C$. This inequality implies that the ratio of the display costs per unit time to the assessment efficiency of display is smaller than the sum of the contested resource value and the cost of losing the escalated fighting. If an animal need not pay a heavy cost to obtain accurate information on his opponent's fighting ability, and if the winner acquires valuable resources or the loser incurs a heavy cost, all animals should make their decisions carefully at the end of their displays.

DISCUSSION

We studied the distribution of display duration in animal contests. Unlike the traditional war-of-attrition models, we considered when animals decide whether to escalate to fighting

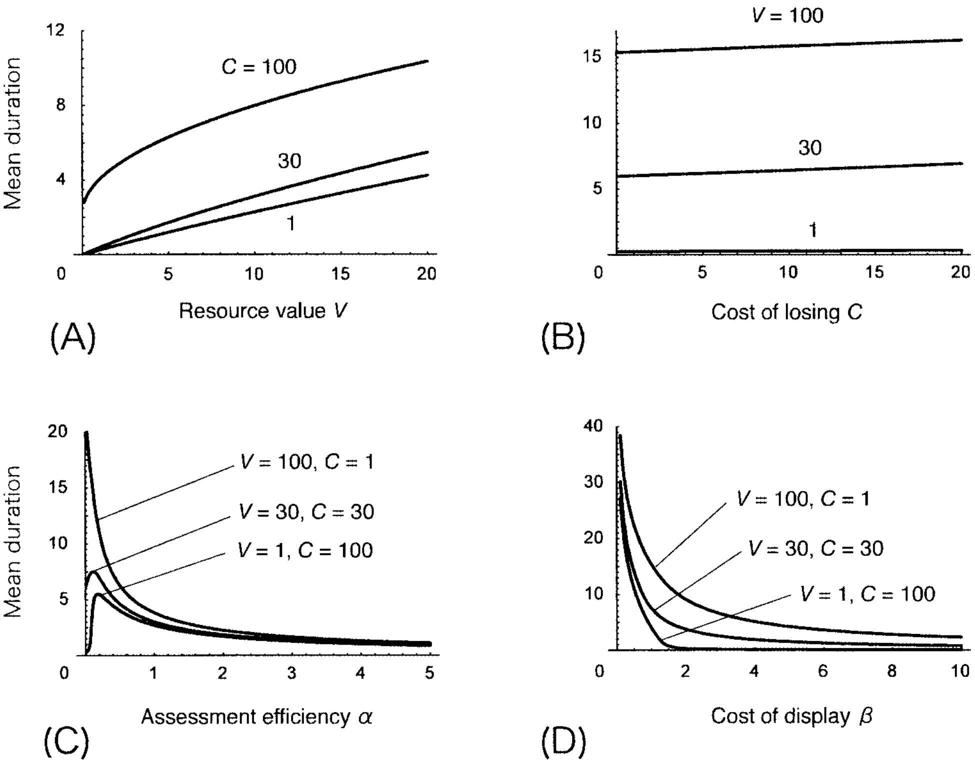

Fig. 4. Examples of the mean display duration at ESS. The horizontal axes show the values of the parameters, and the vertical axes are the mean display durations. (A) Dependence of the mean duration on the contested resource value. The three examples vary in the cost of losing a fight. The assessment efficiency and the cost of display per unit time are fixed as $\alpha = 0.1$ and $\beta = 1$. (B) Dependence of the mean duration on the cost of losing a fight. The three examples vary in the contested resource value. The assessment efficiency and the cost of display per unit time are fixed as $\alpha = 0.1$ and $\beta = 1$. (C) Dependence of the mean duration on the assessment efficiency. The three examples vary in the contested resource value and the cost of losing the fight. The costs of display per unit time are fixed as $\beta = 1$. (D) Dependence of the mean duration on the display cost per unit time. The three examples vary in the contested resource value and the cost of losing the fight. Values of the assessment efficiency are fixed as $\alpha = 0.1$.

or retreat when the display ends. Therefore, the player with the longer display does not necessarily win the game. During the display, both contestants obtain information on their relative fighting abilities by costly assessment, and after the display both contestants decide whether to fight for or to give up the resource. Here we treat the cost of display separately from the cost of losing an ensuing fight. Our model is an explicit modelling of the idea of 'display as assessment' (Enquist and Leimar, 1983), and is appropriate for treating contests in which animals show conventional displays as a way of assessing each other's fighting abilities before the conflict escalates to fighting.

Contested resource value and cost of escalation to fighting

We derived the ESS distribution of display duration mathematically, as in equations (4) and (5). Both a larger value of the contested resource V and a larger cost of loss in escalated fighting C increase the mean display time. Regarding the effect of resource value on display duration, the present results are consistent with those of sequential assessment (Enquist and Leimar, 1987) and the results of some experiments for several species (reviewed in Enquist and Leimar, 1987). A greater cost of losing will also make contestants cautious in the model. We should consider the effects of the cost of losing a fight and that of non-aggressive display separately.

Interestingly, changes in V and C clearly differ in their effect on the variance of display duration in the ESS. With enhanced V, the variance of the duration among individuals does not change much. In contrast, the larger C is, the smaller the variance becomes.

Cost and effectiveness of assessment

The mean duration of display in the ESS depends on the assessment efficiency of display α in a non-monotonic manner. If α is small, animals cannot quickly tell which contestant is the stronger. Then there is no minimum display duration, and the population includes players with very short displays, who make quick decisions. For a mildly high-efficiency α, more animals display, and the displays last longer. Enquist and Leimar (1983) predicted that the contest duration should increase as sampling uncertainty increases. However, as shown in Fig. 4C, the display becomes shorter if it is too vague (small α) when V is low and C is high. In contrast, at a very large α, animals need only a short display to obtain very accurate information, and almost all animals make correct decisions with the short display. Animals may show longer displays when the clarity of display is intermediate.

Hence display duration is short with both small and large α. However, the behaviour of animals differs between these two limits: animals are likely to make wrong decisions when α is small, whereas most animals make correct decisions when α is large. We may see frequent aggressive fights when animals cannot evaluate each other's fighting abilities: animals escalate to fighting frequently when displays are unclear or their perceptive ability is poor.

It is understandable that displays become shorter as display per unit time becomes more costly (large β). Animals stop displaying if doing so is very costly, and prolong displays when the cost of doing so is low. Displays that provide accurate information about animals' fighting abilities presumably result in heavier costs than mild interactions, such as parallel orientation in cichlid fish, which provide visual information only. Hence the cost and effectiveness of a display should be related to each other, although here we assumed they are not correlated.

The condition in which all individuals prolong their displays beyond the minimum is $8\beta/\alpha < V + C$. We can see that both the cost-effectiveness, defined as the increase in information accuracy per unit display cost, and the sum of V and C determine whether all individuals will prolong their display beyond the positive minimum, t^*. Naturally, an animal is willing to pay the cost of a long display when it can gain accurate information from it at a low cost or when escalation to fighting would be very dangerous. These predictions are testable experimentally.

Future research

To simplify our analysis, we ignored the effect of the magnitude of the difference between contestants' fighting abilities. We supposed that only a small difference between individuals could have a decisive effect on the outcome of a fight. However, a large difference is likely to have clearer outcomes than a small difference. In fact, asymmetry in resource holding potential is considered to be an important determinant of contest duration in many species (e.g. Enquist and Jakobsson, 1986; Enquist *et al.*, 1990; Leimar *et al.*, 1991; Faber and Baylis, 1993; Hack *et al.*, 1997; Andersen *et al.*, 2000). Furthermore, in some species the size of the loser has a greater effect on contest duration than the size of the winner (Bridge *et al.*, 2000; Taylor *et al.*, 2001; Jennings *et al.*, 2004; Morrell *et al.*, 2005), whereas we assumed that an animal's fighting ability and its display duration are independent. Moreover, size asymmetry is also related to the total cost of a contest in house crickets *Acheta domesticus* (Hack, 1997b). In the future, we will extend the model to more realistic situations considering payoff-relevant asymmetries that have been studied in war-of-attrition models (e.g. Hammerstein and Parker, 1982; Haccou and Glaizot, 2002). Fighting behaviours may also be affected by energy reserves, body condition, age, and experience of winning or losing (reviewed in Morrell *et al.*, 2005). Animals may use several displays in a contest (e.g. Enquist and Jakobsson, 1986), and these different displays may differ in costs and efficiency of resource holding potential assessment. However, the model presented here with its analytical results forms the basis of all these developments.

ACKNOWLEDGEMENTS

This work was made possible by Grants-in-Aids from JSPS to T.U., Y.I., and H.O. Comments by the following people were very helpful in developing this work: B. Adams, J.M. Greeff, P. Haccou, H. Ito, T. Kawai, E. Kasuya, M. Kondoh, O. Leimar, J.M. McNamara, J.A.J. Metz, and A. Sasaki.

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APPENDICES

Finding an evolutionarily stable state for display duration

From the game tree and the payoff matrix in Fig. 2 and Table 1, we can obtain the expected payoffs of the individual with the shorter display (S) and the individual with the longer display (L) by summing all cases. The results are given in equation (1) in the text. The difference between W_L and W_S is

$$W_L - W_S = \phi(t_S)(1 - \phi(t_S))V \tag{A1}$$

Here, $1/2 \le \phi(t_S) < 1$ holds for $0 \le t_S \le t_L < \infty$. Since the right-hand side of equation (A1) is positive, the expected payoff of player L is always greater than that of S.

In a population with a distribution of display duration $\rho(t)$, the expected payoff of an individual with t' display duration is given by equation (2) in the text. Equation (3a) holds for all t' with $\rho(t') > 0$, implying that if there are some individuals with display duration t' in the ESS, they should have the same expected payoffs (Bishop and Cannings, 1978). By differentiating $E[W(t')]$ with respect to t' and setting it equal to 0, we get

$$\frac{\mathrm{d}E[W(t')]}{\mathrm{d}t'} = \rho(t')(W_L(t') - W_S(t')) + \frac{\mathrm{d}W_S(t')}{\mathrm{d}t'}\int_{t'}^{\infty} \rho(t)\mathrm{d}t = 0 \tag{A2}$$

which is rewritten as

$$-\frac{\mathrm{d}W_S(t)}{\mathrm{d}t}\bigg/(W_L(t) - W_S(t)) = \rho(t)\bigg/\int_t^{\infty} \rho(s)\mathrm{d}s \tag{A3}$$

Let $h(t) = -\frac{\mathrm{d}}{\mathrm{d}t} W_S(t)\Big/(W_L(t) - W_S(t))$. We differentiate equation (A3) and we have $\rho'(t)/\rho(t) = h'(t)/h(t) - h(t)$. Then we have $\rho(t) \propto h(t)\exp[-\int^t h(t')\mathrm{d}t']$ for all t with $\rho(t) > 0$. The ESS distribution is composed of the interval in which this holds, and of another interval in which $\rho(t) = 0$ holds [for a similar condition for the ESS probability distribution, see Iwasa *et al.* (1983) and Iwasa and Haccou (1994)].

Then, from equation (A1), the sign of $h(t)$ depends on $\mathrm{d}W_S/\mathrm{d}t$. Using $\phi(t) = \frac{1}{2}(1 + \sqrt{1 - \exp(-\alpha t)})$ and $f(t) = \beta t$, $\mathrm{d}W_S/\mathrm{d}t$ then becomes

$$\mathrm{d}W_S/\mathrm{d}t = \tfrac{1}{8}(\alpha e^{-\alpha \cdot t}(V + C) - 8\beta) \tag{A4}$$

This is a monotonically decreasing function of t, and changes its sign from positive to negative. It becomes 0 at $t^* = (1/\alpha)\ln(\alpha(V + C)/8\beta)$. $h(t) > 0$ for all $t > t^*$, $h(t) < 0$ for all $t < t^*$, and $h(t^*) = 0$.

(i) When $t^* \leq 0$, $h(t) > 0$ for all $t > 0$. Hence the solution $\rho(t)$ given by equation (4) satisfies equation (3a). This is the case for equation (4).
(ii) When $t^* > 0$, $h(t) > 0$ for all $t > t^*$, $h(t) < 0$ for all $t < t^*$. Equation (5) satisfies equations (3a) and (3b). This is the case for equation (5).

Although equations (4) and (5) satisfy the condition for the ESS given by equation (3), we need to reject the possibility that other types of solution could also satisfy equation (3). The putative ESS distribution is composed of two kinds of intervals: [class 1] $\rho(t) > 0$ and equation (A2) hold; and [class 2] $\rho(t) = 0$ holds. For example, equation (5) is one interval of class 1 for $t > t^*$, and another interval of class 2 for $t < t^*$. Equation (4) has a single interval $t > 0$ of class 1. If there is an interval of class 2 ($\rho(t) = 0$), the mean fitness should not exceed the fitness in the interval of class 1 ($\rho(t) > 0$). If there are multiple intervals of class 1, the fitness must be the same between different intervals. By noting that $\mathrm{d}W_S/\mathrm{d}t < 0$ holds for $t > t^*$, and that equation (A2) holds for all $t > 0$, we can eliminate the possibility of a solution composed of a combination of class 1 and class 2 intervals other than those given by equations (4) and (5).

Rescaling of time and fitness

We can reduce the number of parameters by rescaling time and fitness. First include assessment efficiency in time as $t' = \alpha t$. Then the probability of making correct decisions is represented as a function of t', $\phi(t') = ½(1 + \sqrt{1 - e^{-t'}})$. Using this t', $\phi(t')$, the rescaled parameters $V' = (\beta/\alpha)V$ and $C' = (\beta/\alpha)C$, and rescaled fitness $\hat{W}_S(t') = (\beta/\alpha)W_S(t')$ and $\hat{W}_L(t') = (\beta/\alpha)W_L(t')$, we have

$$\hat{W}_S(t') = \tfrac{1}{2}\left\{V' - \phi(t'_S)(1 - \phi(t'_S))(V' + C') - 2t'_S\right\} \tag{A5a}$$

$$\hat{W}_L(t') = \tfrac{1}{2}\left\{V' + \phi(t'_S)(1 - \phi(t'_S))(V' - C') - 2t'_S\right\} \tag{A5b}$$

We can represent the ESS distribution $\rho(t')$ as a function of two parameters (V' and C'), and hence the shape of the ESS distribution in the original model is given by these two parameters and the time scaling parameter, α.