

225 ~~Pages~~ with note from "conventional" to "isolated" conflict. If contest carries no info
RHP, selection will favor persistence: SMS status is expected distribute. In contest
where display convey info; tendency toward deception. "conventional" fighting is a
assessment technique. ^{critical} threshold for escalation.
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Assessment Strategy and the Evolution of Fighting Behaviour

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The view is examined that the adaptive value of conventional aspects of fighting behaviour is for assessment of relative RHP (resource holding power) of the combatants. Outcomes of aggressive disputes should be decided by each individual's fitness budget available for expenditure during a fight (determined by the fitness difference between adoption of alternative strategies, escalation or withdrawal without escalation) and on the rate of expenditure of the fitness budget if escalation occurs (determined by the RHPs of the combatants). Thus response thresholds for alternative strategies ("assessments") will be determined by natural selection on a basis of which opponent is likely to expend its fitness budget first, should escalation occur. This "loser" should retreat (before escalation) and the winner should stay in possession of the resource. Many aggressive decisions depend on whether one is a resource holder, or an attacker. Assuming the RHP of the combatants to be equal, there are many instances of fitness pay-off imbalances between holder and attacker which should weight the dispute outcome in favour of one or other opponent by allowing it a greater expendable fitness budget. Usually the weighting favours the holder; the attacker therefore needs a correspondingly higher RHP before it may be expected to win. This is not invariably the case, and much observed data fits the predictions of this sort of model. If assessments are perfect and budget expenditure rates exactly predictable, then there would never seem to be any case for escalation. Escalation can be explained in terms of injury inflictions (expenditures) occurring as discrete events; i.e. as "bouts" won or lost during fighting. Assessment can give only a probabilistic prediction of the outcome of a bout. A simple model is developed to investigate escalation situations. Each combatant assesses relative RHP; this correlates with an absolute probability of winning the next bout (c_{abs}). The stake played for is infliction of loss of RHP and is determined by the fitness budgets of the opponents. (Each individual plays for the withdrawal of its opponent.) This defines a critical probability of winning (c_{crit}) for each combatant, above which escalation is the favourable strategy ($c_{abs} > c_{crit}$) and below which withdrawal is favourable ($c_{abs} < c_{crit}$). Escalation should occur only where $c_{abs} - c_{crit}$ is positive for both combatants. This model gives predictions compatible

with the observations, indicating that RHP loss alone can be adequate to explain withdrawal: escalation behaviour. Withdrawal tendency will be increased by low searching costs. Escalations should be restricted to closely matched RHP opponents if RHP disparity is the major imbalance. Outside the "escalation range" of a given individual, the higher RHP individual wins and the lower one loses (i.e. it should withdraw after conventional display). RHP disparity and holder: attacker imbalance should both interact to shape the observed pattern, though their relative importances will depend on species and situation. In some instances selection may favour immediate withdrawal from an occupied territory even without assessment of RHP.

1. Introduction

There is much in favour of viewing a great deal of animal behaviour as optimum strategies for maximizing the rate of extraction of "fitness gain" from the available series of "fitness gain parameters" (resources) present in its environment. One consequence of the occurrence of discontinuously distributed resources is that they may be in short supply. Animal aggression (in the form of resource guarding) will be favoured by selection when there are less resources than competitors and where an individual can achieve an immediate gain in fitness by forcibly ousting one of its fellows. Selection for aggression will be more intense the more discrete the resource (i.e. the easier it is to guard) and the higher its yield as a fitness gain parameter (a function both of its absolute effect and its shortness of supply). It is not surprising therefore that most of animal aggression relates to food fighting and especially to mating. Territoriality is often merely an adjunct to these two situations—e.g. an area is guarded because it has a high probable yield of food or mates, or both. Fighting tendency will be much modified by the probable relatedness of the two competing individuals, an effect studied by Hamilton (1964).

Darwin (1871) was very well aware of the individual advantages of aggression when he founded the theory of sexual selection. Since then it has become fashionable amongst certain ecologists and ethologists to view aggression and territory in terms of advantages it may confer upon groups or species, rather than on individuals (see Wynne-Edwards, 1962). The fact that much aggression is highly ritualized (as displays, pushing contests, etc.) and does not involve damage (termed "conventional fighting" Maynard Smith, 1972) has fuelled "group selectionism" because it can be argued that an immediate advantage would be conferred on any individual which indulged in damaging or escalated fighting. Group selection poses major problems in terms of modern population genetics, and it seems likely to be a very weak selective agent compared to individual selection (see Williams, 1971). An excellent

account of the position of fighting in relation to group selection and individual selection can be found in Maynard Smith (1972).

Recently (Maynard Smith, 1972; Maynard Smith & Price, 1973) it has become abundantly clear that there is no conflict between observed fighting strategy and individual selection. Of a number of possible strategies, it can be shown that the only one to form an evolutionary stable strategy (ESS—i.e. where, if most of the individuals in the population adopt it there is no other strategy which would give higher reproductive fitness) is one where individuals start conventionally but escalate to damaging fights later, especially when the opponent escalates. These “limited war” strategies appear stable against “total war” or “total peace” strategies when analyzed in relation to game theory.

In the present paper, fighting strategy is again considered in relation to individual selection. The view that the “retaliate if opponent escalates” will initially form an ESS is accepted. Further adaptations, once this strategy has stabilized, are examined, in particular the theory that relative strengths of combatants are estimated during displays: a suggestion which recurs continually in the literature (see Ewer, 1968) but which has attracted very little consideration in evolutionary terms.

2. Conventional Fighting as Assessment of RHP (Resource Holding Power)

Once “retaliator” has stabilized as an ESS, any mutant individual able to assess from the conventional fighting stage how its own RHP (resource holding power) compares with that of its opponent would have a selective advantage, since it could withdraw without damage when the RHP of its opponent exceeds its own by a sufficiently large amount. It is assumed that RHP is a measure of the absolute fighting ability of a given individual. If this character spreads, we may end up with a “total peace” strategy, where all disputes are settled conventionally. In this case, provided that the characteristic of retaliation is not lost, a mutant deficient in responding to the signals of RHP during conventional fighting will not spread—it will be disadvantageous since it will not gain any extra resources and will be beaten in encounters with individuals of higher RHP. Thus our “conventional assessor/retaliator” becomes the ESS.

It has certain problems to face, however. Firstly, there is the obvious difficulty that selection will immediately favour exaggeration of those cues used to assess RHP. The selective advantage of this form of “evolutionary cheating” is simple: if (for example) size is used as the cue for RHP, then where for other reasons it is disadvantageous to increase absolute size (and RHP), what will be favoured are mechanisms to increase apparent size (and

All cheating

therefore apparent RHP). That this has happened often seems very likely. The canid threat posture involves raising the neck hair and standing erectly (Darwin, 1872), so does that of many other groups including rodents (Eibl-Eibesfeldt, 1970). Lions have manes, fish often raise fins, birds fluff out feathers. Certain species have inflatable pouches (e.g. the lizard *Phenacosaurus richteri*; Kästle, 1963). Examples are legion. Another cue very commonly used could be weaponry. Much of threat display involves exaggeration and display of teeth, antlers, claws (e.g. in crabs; Crane, 1966) or even hind legs, which are the main defensive weapons in locusts (Parker, Hayhurst & Bradley, 1974). It seems quite likely that these features might initially have given good indices of RHP. Where there is this type of drive for "evolutionary cheating", a counter-selective compensatory adjustment of the assessment mechanism would continually follow in its wake.

More reliable measures of RHP might be provided by direct trials of strength between combatants. Pushing and pulling contests, on head and/or tail beating clashes abound in all groups from fish to ungulates (for many classic examples see Eibl-Eibesfeldt, 1970). Very often conventional fighting consists of combinations of "unreliable" display and "reliable" contests of strength, implying that many cues may be used to assess relative RHP. An independent analysis has been made of contests carrying no information of RHP by Maynard Smith (1974). He shows that selection will here mainly favour persistence during displays. Persistence durations should stabilize at a negative exponential distribution, but should all be of constant intensity. The present paper mainly concerns contests which provide RHP information. Though the "conventional assessor-retaliator" theory ascribes a definite selective advantage to the display behaviour, it poses an alternate problem—why do damaging fights ever occur? With a nearly perfect assessment mechanism one would predict escalation only where combatants are very closely matched, and there is no clear-cut predictive outcome. We shall consider this problem later (section 4) but first let us consider how assessment might operate and whether the simple comparison of RHPs provides a satisfactory solution for aggressive behaviour.

Clearly, this model is a naive one, and certain behavioural observations do not conform to its prediction. Very often the odds appear heavily weighted in favour of the resource holder, and the absolute RHP (as judged by human eyes) of the attacker apparently has to exceed that of the holder very considerably before a take-over occurs. There are several possible reasons why this effect operates:

(1) Suppose that the "resource structuring" is near perfect; i.e. by the assorting action of disputes, the population is perfectly truncated with the highest RHP individuals occupying all the resources. In this case, restructur-

ing can only occur by inputs and outputs of competitors and resources or by changes in RHP status of individuals in one or both of the two groups (holders or non-holders). Here most of the observed disputes would obviously be won by the holders.

(2) The tenure of the resource may well itself increase RHP, especially where the resource is a food source. Also the outcome of a fight may involve experience of the local environment, hence tenure of the resource may increase RHP in this way. Position of the holder in guarding the resource may be very important, for instance, in the female-guarding behaviour where the male clings to the female (see Parker, 1974) because the attacker must prise the holder off before a take-over can occur.

(3) Pay-offs may be different for the holder and attacker. Supposing that the holder will lose more than the attacker will gain, it might be expected that the holder could afford to sacrifice more units of fitness in the fights than the attacker could afford to expend. Hence where the combatants are of equal RHP, the attacker should withdraw because it will run out of expendable fighting units before the holder. Hence an attacker must be of higher RHP before it can win.

The last suggestion causes us to modify our suggestion about the type of assessment favoured by selection, and leads to a less naive model. Individuals will be favoured which respond appropriately to the correct threshold of RHP prediction before they withdraw. This threshold, which will be set by evolution, will not be simply "does his RHP exceed mine?"; rather, it will be "given that his RHP is x and mine y , and that in this situation I have a units available to expend and he has b units, will I run out of expendable fitness units before he does?" It will be the probable relative rates at which the combatants will expend fitness during an interaction which will (via selection) set the appropriate thresholds for withdrawal, since this will determine which individual will expend its fighting budget first (and hence lose). We shall consider this less naive model more fully in section 4, but first we shall consider how pay-offs depend on whether one is a holder or attacker, and circumstances in which imbalances in pay-offs arise.

3. Pay-off Imbalances between Holder and Attacker

Let us assume for the present section that we are considering two average individuals of equal RHP, and that one has held a resource for a certain time (t) before it is encountered by an attacker. What we wish to estimate is the change in fitness sustained by each individual as a result of a possible change in state (i.e. a take-over or a withdrawal). Where the holder's loss in fitness exceeds the attacker's gain, then the attacker should show a greater

tendency to withdraw because it will have less fitness units available to expend in the fight. This model is compatible with an adaptive interpretation of motivation. It is suggested that motivational state will be a function of the "fitness change effect" achieved by shifting from one motivational state to another.

Take a very simple case where a resource can be extracted at a constant rate of gain g fitness units through time 1, summing to g by the end of the extraction. The interaction occurs at time t during extraction, $(1-t)$ time units before the resource will finish. If there is an escalated fight, the individuals will be damaged and the winner's gain rate reduced to w for the rest of the time. (This arises mainly because the RHP will have declined, though other reproductive disadvantages may also have been incurred.) Let the search cost before finding the resource = s_h for the holder and s_a for the attacker (these values really summarize the fitness of each individual before it encountered the resource). If withdrawal occurs before an escalated fight, the withdrawing individual achieves a probable gain rate of p_g , if it occurs after an escalated fight, the probable gain rate is p_w . We can therefore summarize all the possible fitness outcomes to each individual (by the end of resource extraction) in the following way:

	Fitness if fights		Fitness if withdraws without damaging fight	
Holder				
Wins:	$gt + w(1-t) - s_h$	(1)	$gt + p_g(1-t) - s_h$	(3)
Loses:	$gt + p_w(1-t) - s_h$	(2)		
Attacker				
Wins	$w(1-t) - s_a$	(4)	$p_g(1-t) - s_a$	(6)
Loses:	$p_w(1-t) - s_a$	(5)		

Suppose that the combatants escalate. The change in fitness of the holder if it loses = $\Delta h = (1) - (2) = w(1-t) - p_w(1-t)$; and that for the attacker if it wins = $\Delta a = (4) - (5) = w(1-t) - p_w(1-t)$. Hence $\Delta h = \Delta a$; there is no imbalance in pay-offs and therefore no clearcut predictive outcome. If motivation to fight is proportional to Δh or Δa , both should be equally motivated.

We can ask a second question: are both individuals equally motivated to withdraw without fighting? Do both experience the same change in fitness for the choice between withdrawal without escalation rather than escalating? That is, what is the fitness change effect due to withdrawing during conventional fighting. For the holder, this is

$$\Delta hr = (1)/2 + (2)/2 - (3) = w(1-t)/2 + p_w(1-t)/2 - p_g(1-t),$$

and for the attacker $\Delta ar = (4)/2 + (5)/2 - (6)$, which is exactly the same value. Hence again the pay-offs are equal and there is no clearcut predictive outcome; motivations to withdraw will be equal. Both these conclusions are intuitively obvious from this simple model where the pay-off remaining after the interaction is of equal value to both combatants. For estimates of changes in fitness, it is obvious that the fitness of the individual *before* the interaction is irrelevant (values s_h , s_a , and gt cancel out). The best estimate of a "fitness budget for fighting" is undoubtedly $\Delta hr - \Delta ar$ since this considers the disparity between the alternative strategies of *escalate* versus *withdraw without escalation*. We can now consider some more realistic imbalance situations.

(A) CASE 1: INVESTMENT OCCURS BEFORE GAIN; FIXED INVESTMENT PERIOD

Many examples of guarding involve a period of investment (expenditure of fitness) before gain can be extracted from the guarded resource. Males of many groups show precopulatory female-guarding phases until the female becomes receptive and mates. These are especially common in crustaceans (e.g. *Asellus*, *Gammarus*, *Talitrus*, *Orchestria*, *Artemia*, and copepods) and in insects (reviewed by Parker, 1970a). In the vertebrates, a territory or mate may often be guarded for some time before any obvious gain can be recognized. A holder can be said to have entered the gain phase when it has a probability of offsetting some of its investment (e.g. when it has begun to transfer sperm—so it will have a probable fertilization gain). Take-over (when it occurs) usually happens during the investment phase, possibly because it is generally longer and because take-over is often easier then.

(a) Suppose that the investment rate is constant. If take-over occurs, the attacker simply supplies the remaining investment necessary before gain (= that which the holder would have put in after the interaction, had he won). It can be shown simply analytically after the method above that there is no imbalance here; $\Delta h = \Delta a$ and $\Delta hr = \Delta ar$, irrespective of whether take-over occurs during investment or gain. This may seem odd because the holder loses his existing investment as well as his possible gain. However, the attacker's net gain is correspondingly greater because he has to invest correspondingly less. Again the holder's possible loss = the attacker's possible gain.

(b) This will not be true where the investment rate is not constant. Suppose that if it won the holder would invest a total of j_i fitness units after the interaction and the attacker would invest a total of k_i units, before gain extraction. In this case, $\Delta h - \Delta a = k_i - j_i$ and $\Delta hr - \Delta ar =$ half this value. Clearly, when investment rate is highest at the start, $k_i > j_i$ and the holder has more expendable fitness units. This is not unfeasible for certain situations, e.g. where a territory must be elaborately marked and its characteristics learned,

or where nests must be rebuilt, or females re-courted etc. In the reverse case (investment rate increasing with time) then $j_i > k_i$ and the odds will be weighted in favour of the attacker. This is an interesting possibility in cases where, for example, female-guarding or territory-holding means that males are impaired in their feeding activity. If this is so they may lose condition (and increase investment) at an accelerating rate with time. In the kob, males holding TGs (small territories, continually contested, to which the females come for mating) sustain a higher takeover rate than males on STs (much larger territories, little contested, where females are reluctant to mate)—probably because food is in very short supply in the TGs (Leuthold, 1966). This is probably best regarded as an example of case 4 with $j(\text{net gain}, g-i) < k(\text{net gain}, g-i)$ because the gain rate (probability of insemination) will be constant but the investment rate accelerating. Note that when $g = i$, the male should leave anyhow, with or without any contest. In locusts there is a precopulatory female-guarding phase and the take-over rate is much higher during oviposition than earlier in guarding (Parker, Hayhurst & Bradley, 1974). Oviposition is usually the last stage of guarding investment before copulation. It is very difficult, however, to determine whether or not this effect results from a decline of absolute RHP, or merely from the change in posture during oviposition.

For arthropod precopulatory guarding phases, it seems very likely that the main feature heavily weighting the odds in favour of the holder is that it initially has a major postural advantage.

It seems unlikely that the $j_i > k_i$ case could ever exert a major effect. If the probability of take-over before gain gets too high then the existing investment strategy becomes disadvantageous. This is one of the features which may be expected to stabilize drive for investment earlier and earlier before the pay-off (Parker, 1974); in other words the $j_i : k_i$ relationship can never become heavily $j_i > k_i$ biased because this is not evolutionary stable. Note that this will not apply to the $j_i > k_i$ case.

(B) CASE 2: INVESTMENT OCCURS BEFORE GAIN; ATTACKER MUST REINVEST

Here there is an obvious imbalance in favour of the holder. If we assume a roughly constant investment rate summing to i by the end of investment, and that the attacker must complete a full i before collecting the gain, we find that $\Delta h - \Delta a = it + p_w t$ and $\Delta hr - \Delta ar = (it + p_w t)/2$. That is the holder has an extra number of expendable fitness units, equivalent to the difference between how much more he would have to invest until pay-off ($i(1-t)$ units) and the full investment (i units), plus the value of searching during the time (t) that the attacker is reinvesting ($p_w t$ units). If the interaction occurs during the gain phase, the imbalance is even greater, simply $i + p_w$ and $(i + p_w)/2$.

This case appears particularly relevant to postcopulatory guarding in insects (see Parker, 1970a). Here the male copulates and then guards the female during oviposition. In the dung fly the sperm transfer phase can really be considered the investment phase because the last male to mate fertilizes most of the eggs (80%) and the female would certainly be quickly remated if left unguarded during oviposition. Hence the gain phase is the pay-off of ensuring precedence of one's ejaculate while eggs are being laid. Here a full reinvestment (full copulation) occurs if there is a take-over. In interactions, struggles (escalated fights?) are rare (about 7%) and usually the holder wins. However, it is again difficult to estimate the positional advantage of the holder. Take-overs are more frequent during oviposition than copulation, although this model would predict the opposite, because the imbalance is most favourable to the holder during the gain phase. This effect certainly relates to a relatively greater positional advantage during copulation (Parker, 1970b). Positional advantage must be minimal in the non-contact post-copulatory guarding phases shown by many dragonflies, and though take-overs are relatively common, the odds are weighted in favour of the holder (Jacobs, 1955), as we would predict. A full recopulation occurs after take-over, and guarding continues until the end of oviposition, as in dung flies.

(C) CASE 3: DAMAGE FROM FIGHT PERMANENT; COMBATANTS DIFFERENT AGES

For many prolonged resource guarding situations (e.g. males in certain primate troops, lions, and certain ungulates, etc.) it seems very likely that the average age of holders will exceed that of attackers. In this case if the combatants fight and the damage persists to some extent throughout life, then it seems likely that the overall fitness of the younger combatant will be reduced more than that of the older one; it will have a longer part of its reproductive life in the reduced RHP condition. Suppose that y and z represent the proportions of reproductive life spent before the interaction by the holder and attacker respectively. They have therefore $(1-y)$ and $(1-z)$ left. p_g and p_w again represent the gain rates due to searching time in the undamaged and damaged states respectively. We know by the present analysis that what happens beforehand is irrelevant (i.e. $p_g y, p_g z$) because it cannot alter the *change* in fitness arising from the interaction. If we add $p_w(1-y)$ to equations (1) and (2) and $p_w(1-z)$ to (4) and (5) though $\Delta h = \Delta a$, there is a clear imbalance with $\Delta hr - \Delta ar = p_w(1-y) - p_w(1-z) + p_g(1-z) - p_g(1-y)$. This example indicates why $\Delta hr - \Delta ar$ gives the best indication of disparity in fitness budgets; it takes into account the value of the alternative strategy, *withdrawal without escalation*. If we signify the difference between the attacker's and holder's remaining reproductive life as a [i.e. $(1-z) - (1-y)$], then $\Delta hr - \Delta ar$ is simply $p_g a - p_w a$ which is clearly positive if the

attacker is younger than the holder. Thus the odds are again weighted in favour of the holder, because of the more disastrous effect of damage on the younger attacker. This certainly fits observed data if we assume that there will generally be older holders and younger attackers. Note that there will be no imbalance if the damage does not persist until the death of the older individual.

(D) CASE 4: NON-CONSTANT EXTRACTION RATE FROM TIME OF START OF EXTRACTION

This is the converse of case 2(b). Suppose that if it won the holder would extract a total of j_g fitness units after the interaction and the attacker would extract k_g units. Here $\Delta h - \Delta a = j_g - k_g$, $\Delta hr - \Delta ar = (j_g - k_g)/2$, and so where $j_g > k_g$ the holder has the higher budget (i.e. where gain increases with time a given individual has been extracting). If the rate of gain is greatest at the start ($j_g < k_g$), the attacker has the edge.

Now, for prolonged guarding as for example in certain feeding territories, it seems likely that learning the characteristics of the resource will increase the rate of uptake from the resource. Hence the remainder of the resource may be worth more to the holder than to the attacker, and so $j_g > k_g$ and the holder wins. However, this will not be true for temporary feeding resources, e.g. food-fighting situations. It seems highly likely here that the first few units of food intake will affect fitness disproportionately more than subsequent units. Thus the value of the extractable remainder of the resource will be higher to the attacker than to the holder ($j_g < k_g$). This time the odds should be weighted towards the attacker. In many species there is a clear cut ordering of feeding with dominant male feeding first, then females, then young. This ordering corresponds exactly to the expected absolute RHPs of the individuals—highest first. There is some evidence that where the disparity between RHPs is not so obvious, the "holder has precedence" effect does not apply. An example is the intra-specific food-fighting found in some birds. Often, if it is a single food item that is being contested, there is no obvious precedence and the interaction is a mixture of fighting and snatching. We would predict this if neither individual has yet extracted from the resource and both are equally hungry ($j_g = k_g$). Even more interesting is the case of sparrows around pieces of bread (D. Barnes & G. A. Parker, unpublished observations). A "holder" (the hungriest?) guards all or part of the resource some time while feeding and giving threat displays to contestants. However, even after a few pecks the odds become heavily weighted in favour of an attacker—which usually takes over the resource for a time until it itself is ousted. The same sort of pattern also appears to apply to starlings. Group selectionists would probably interpret this as a mechanism which overall gives an even share out

of the resource to all individuals and which therefore has an adaptive advantage at the species level. The individual selection interpretation is favoured since it is likely to form the greater selective agent.

(E) SUMMARY OF IMBALANCES

Most of the cases considered are very inadequate for a given natural situation, which often consists of elaborate combinations of the above effects. Apart from the last example ($j_g < k_g$), holders should generally maintain tenure of their resources unless the attacker is of sufficiently higher RHP to offset the imbalance. Predictions from holder: attacker imbalances appear to fit observed data reasonably well, suggesting that a combination of assessment of absolute RHP (during conventional fighting) with an appropriate imbalance threshold, could be operative in aggressive decisions. The model as proposed so far depends on an assessment from these two parameters of the relative rates at which each combatant will lose fitness and therefore which will run out first. Because there is a single "I will win—he will win" outcome to this problem, then the model based on relative rates of loss of fitness predicts "never escalate" for a perfect assessment mechanism. Let us now consider a more realistic model.

4. Why Escalate?

Clearly, if the combatants can predict exactly their relative rates of loss of fitness during a subsequent damaging fight, they should never escalate. This is unrealistic as a model because there will be a strong element of chance involved. Assessment will give only a probabilistic prediction of winning, not an absolute one. Instead of a precisely ordered rate of fitness loss, a much more valid description of observed escalations would be a series of bouts in which either combatant can score an injury inflicted upon his opponent. Injuries will occur as discrete events. Let us now revise the model as follows:

(1) As before, the function of conventional fighting is to assess relative RHPs. This will give an absolute probability (c_{abs}) for each individual to win the first bout of an escalated fight (score the first injury against his opponent).

(2) Suppose that the loss in fitness due to an injury in the first bout would be l . For this possible loss, there will be a critical minimum probability of winning the first bout (c_{crit}) below which retreat (rather than escalation) is the more favourable strategy. c_{crit} is greater the greater the search cost for an alternative resource.

(3) Now, only where $c_{abs} > c_{crit}$ for both individuals does escalation occur. Where the sign is reversed for one individual, it retreats rather than be

damaged. Where the sign is reversed for both, the winner is the one with the lesser negative score; it can afford to persist without escalation longer.

(4) Should escalation occur, a reassessment should occur immediately after the end of the first bout (first injury) because the RHP of the loser will have decreased and so will its c_{abs} for the next bout (also c_{abs} for the winner has actually increased). Thus the chance that withdrawal (before the next bout) will be advantageous to the loser is likely to be considerably increased, depending on I (greater I , greater the probability that withdrawal will be favourable before the next bout). It is a common feature of damaging fights that as soon as a combatant sustains an obvious injury, it retreats; an observation which fits the model.

(5) The "game" being played is that of reversing the opponent's $c_{abs} > c_{crit}$ to become $c_{abs} < c_{crit}$; i.e. playing for the withdrawal of one's opponent. Thus fighting in disputes over resources is regarded as a form of resource assessment strategy in that the probable gain from a given resource is weighed against the probable search cost for an alternative. In the present case the withdrawal point is defined by the changing nature of probability of winning and its cost, measured against the cost of withdrawal for searching for an alternative resource (i.e. one which is unguarded or has a holder with a lower RHP, more favourable to attack).

It is interesting to attempt a quantification of the above model to examine its characteristics. A rigorous examination becomes extremely complex, so only a first order approximation will be attempted here. Evolution's job is in a sense a much simpler one—selection merely favours individuals showing the optimum withdrawal/escalate thresholds, out of a series of "threshold variants". Let us assume a normal distribution of RHP in the competing population, so that frequencies of individuals in relation to RHP will therefore be summarized by:

$$f(r) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(r-\mu)^2}{2\sigma^2}}$$

where the variable r = RHP, σ = standard deviation and μ = mean RHP for the competitors. Integrating this distribution between $r = 0$ and r_x (r_x is a given RHP individual being considered) we get

$$F(r_x) = \int_0^{r_x} f(r) dr$$

which gives the proportion of the competing population with an absolute RHP below r_x if we set $F(r_\infty) = 1.0$. $F(r_x)$ can be calculated from tables of integrals of variable $\pm\sigma$ limits of the normal distribution.

Consider an individual without a resource searching in a locality where all resources are guarded, but by a random sample of the competing popula-

tion. The time taken to come across a resource held by an individual of lower RHP will be on average $t/F(r_x)$, where t = the mean time between successive encounters of different resources. Obviously, where t is low relative to the resource life, an "imperfect structuring" of the resources (resources held randomly) cannot persist; there will be a change towards "perfect structuring" (resources held by truncated top end of RHP distribution) at a rate inversely related to t . To make a gross simplification, we could assume that a proportion s of the resources are perfectly structured, and that $(1-s)$ are held randomly. There are many more competitors than resources. A less naive approach (e.g. where there is an increase in the average level of structuring with encounters through resource life) is complex and is not justified until other aspects of the model are also elaborated. All that is required of s : $(1-s)$ is that it gives an approximate index of structuring so that we can assess roughly how long it will take a given individual to find a takeable resource. For the present model we will assume that no holder: attacker imbalance operates, other than disparity in RHP.

(A) VALUE OF SEARCH TIME IF WITHDRAW WITHOUT FIGHTING

We shall assume that the advantage of high RHP is related to the lower search time to find a resource, and that a "takeable" resource (from the viewpoint of estimating the value of search time) is simply one occupied by an individual of lower RHP. This is obviously a reasonable approximation only when the range of opponent RHP which will result in escalation with a given searcher (the "escalation range"—see later) is narrow. On average a searcher will come across a lower RHP holder once in every $t/F(r_x)(1-s)$ time units from the non-structured resources, i.e. $t/F(r_x) \times 1/(1-s)$. Of all structured resources, a proportion $[F(r_x) - (1-s)]/s$ will be occupied by lower RHP individuals. Hence the time to take a "structured" resource will be:

$$\frac{t}{F(r_x) - (1-s)} \times \frac{1}{s} = \frac{t}{F(r_x) - (1-s)}$$

If $F(r_x) - (1-s)$ is negative, the value is taken as 0 (none of the structured resources held by lower RHP individuals).

Now, in one (long) time unit of searching, the total encounters of takeable resources is therefore

$$\{1/[t/F(r_x)(1-s)]\} + \{1/[t/F(r_x) - (1-s)]\} = \frac{F(r_x)(1-s) + [F(r_x) - (1-s)]}{t}$$

Thus the mean search time taken to find a resource held by a lower RHP individual will be the reciprocal of this value (i.e. total time divided by total

fruitful encounters, and hence the overall gain rate for a gain G with gain extraction time h

$$= \frac{G}{\left\{ F(r_x)(1-s) + [F(r_x) - (1-s)] \right\} + h} \quad (7)$$

(B) PROBABILITY OF WINNING A BOUT IF ESCALATE

In a bout between any two given combatants the probability of winning (c_{abs}) will be assumed to be directly proportional to the relation between their RHPs. For individual x fighting y , this is $r_x/(r_x + r_y)$.

(C) FITNESS BUDGETS FOR FIGHTING

A withdrawal point in resource assessment strategy is set by the stage in investment where

(a)	=	(b)
Probable future fitness gain rate due to continued investment in the resource (in gain extraction, fighting, courtship persistence, etc.)		Probable future fitness gain rate due to withdrawal for resumption of searching for an alternative resource.

(see Parker, 1974). Obviously the optimum strategy is to continue investment when (a) > (b), but to withdraw when the sign is reversed. The theoretical withdrawal point for each combatant depends on how much fitness it can afford to lose (during fighting) before withdrawal becomes the favourable strategy; i.e. on its "fitness budget" for fighting. For the present analysis, we shall measure fitness loss entirely in terms of reduction in RHP; the actual fitness loss will be greater than this for a variety of reasons, but (especially for sexually selected fighting) RHP loss may often form the major component. (The model to be developed can be modified quite simply to include, say, an increased probability of mortality as a result of fight damage; however, it is interesting to examine whether RHP loss on its own can account for observed behaviour). We shall consider the effect of a loss l in RHP. Hence an individual of RHP r_x falls to RHP = $r_x - l$ if it loses a bout of escalated fighting.

Now, the winner will gain from the resource at a rate G/h . When he leaves the resource (after extraction is complete), the value of search time is equivalent to (7). For the loser, the search time gain rate will be reduced to

$$\frac{G}{\left\{ F(r_x - l)(1-s) + [F(r_x - l) - (1-s)] \right\} + h} \quad (8)$$

Supposing that loss l persists for time n , and then the individual recovers to RHP r_x . For each combatant, the fitness budget (maximum permissible loss l) can now be calculated roughly as:

$$c_{\text{abs}}\{hG/h + (n-h)(7)\} + (1 - c_{\text{abs}})n(8) = n(7) \quad (9a)$$

for the condition where $n > h$, the evaluation is roughly:

$$c_{\text{abs}}hG/h + (1 - c_{\text{abs}})\{n(8) + (h-n)(7)\} = h(7) \quad (9b)$$

In (9a) and (9b) above, the parts (a) and (b) correspond quantitatively to (a) and (b) in the descriptive equation for withdrawal point.

(D) CALCULATION OF c_{crit} : WHEN SHOULD ESCALATION OCCUR?

We can make a major simplification if we ensure that the model operates as a "one step game", i.e. there is a definite solution after one bout—the loser withdraws. This can be done by adjusting the stake played for by the combatants. We can find the minimum value of l in a combat which will ensure that the lower will withdraw.

We know that the withdrawal point at any stage in the interaction is set by (9a) and (9b). Stake l is determined as follows. Assume a given individual loses at the first bout. On reassessment of $c_{\text{abs}2}$ (c_{abs} for the second bout), will it fight for a further bout assuming that the stake played for will be the same as in the first bout (i.e. escalation is maintained at the same level)? A second bout will be favourable if

$$c_{\text{abs}2} > c_{\text{crit}2} = \frac{n(7) - n(8)}{[G + (n-h)(7)] - n(8)} \quad (10a)$$

where $n > h$, or if

$$c_{\text{abs}2} > c_{\text{crit}2} = \frac{h(7) - [n(8) + (h-n)(7)]}{G - [n(8) + (h-n)(7)]} \quad (10b)$$

for the condition $n < h$. The value of c_{crit} above follows from substituting $c_{\text{crit}2}$ for c_{abs} in (9a) or (9b). Thus by supplying a range of values for l in (10a) or (10b) we can plot $c_{\text{crit}2}$ against l . The intercept of this curve with one for $c_{\text{abs}2}$ against l gives the minimum injury (l_{crit}) which will ensure withdrawal if the individual loses the first bout (i.e. where $c_{\text{abs}2} = c_{\text{crit}2}$). We calculate two stakes, one for each combatant, and use the higher value to determine whether or not escalation should occur after a period of "conventional assessment". Escalation should occur only when $c_{\text{abs}1} - c_{\text{crit}1}$ is positive for both opponents; $c_{\text{crit}1}$ is calculated from (10a) or (10b) above using the higher value for l_{crit} as the stake this time for both opponents for the *first* bout.

The above procedure for deciding the stake I_{crit} is by no means as arbitrary as it may at first appear. It relies entirely on the relative fitness budgets of the two opponents; and integral part of the proposed model. It assumes that each combatant is playing for the retreat of its opponent and that this demands the infliction of a certain critical level of injury. It also assumes that the level of escalation necessary (higher I_{crit}) to ensure the withdrawal of one's opponent renders oneself vulnerable to the same possible danger. The opponent with the lower fitness budget must play for a higher stake than would be necessary to ensure his own withdrawal if he lost; this automatically escalates the fight to the same level for both opponents.

(E) SOME PREDICTIONS OF THE MODEL

Obviously escalation tendency will be inversely related to damage cost. Where the effects of damage persist less than the encounter time ($n < t$), damage costs nothing in the present model because the loser will have recovered before the next resource is encountered. Hence RHP loss as the sole fitness cost of fighting damage can operate only where $n > t$. Note that in (9) and (10) n is used to apportion relative loss; this is used in conjunction with extraction time h to relate all situations to the same time base (when $n > h$ we use overall time base n , and vice versa). However, the model is to some extent "buffered" against relative differences in t , h , and n because of the means of determining I_{crit} —the stake played for.

The effects of different levels of RHP disparity between extremes of the population are difficult to estimate accurately from the present model because of the assumption that the value of search time can be estimated directly from the proportion of resources held by lower RHP individuals. Clearly, however, the less the extent of RHP disparity across the competitor population, the closer the c_{abs} values for combatants and the closer the c_{crit} values (because there will be less search time disparity if the value of search time is only weakly influenced by RHP disparity). From the results obtained below, this might be expected to result in a wider "escalation range" (see below).

Most animal conflict involves relatively little escalation and much conventional display, implying that the cost of damage and the degree of RHP disparity are both higher rather than lower, so that withdrawal is commonly the favourable strategy. An experimental computation was investigated using $t = 0.1$, $h = 1$, $n = 10$, $G = 1$; c_{crit} calculated after (10a). This ranking should give a moderately high incentive for withdrawal (search time short, damage prolonged). Because $h = 10t$ and the number of competitors is assumed to be considerably in excess of the number of resources, then s might be expected to be fairly high and was taken as 0.7. RHP was arranged

so that $r = \sigma$ (standard deviation) and where the mean $\mu = 2\sigma$. Hence $r_x = 1$ for a low ranking individual -1σ below the mean, and $r_x = 3$ for a high ranker $+1\sigma$ above the mean. A combat between two such individuals gives c_{abs} values of 0.25 and 0.75 respectively; a moderate disparity. We shall consider the optimum strategy (escalate or withdraw) of a low, medium, and a high ranker ($r_x = 1, 2, 3$ respectively) in combats with a range of opponents within $\pm 2\sigma$ of the mean, and also consider the optimum strategy for the opponent.

Results are shown in Fig. 1. Each combatant shows a relatively narrow "escalation range" (range of RHP opponents for which both individuals

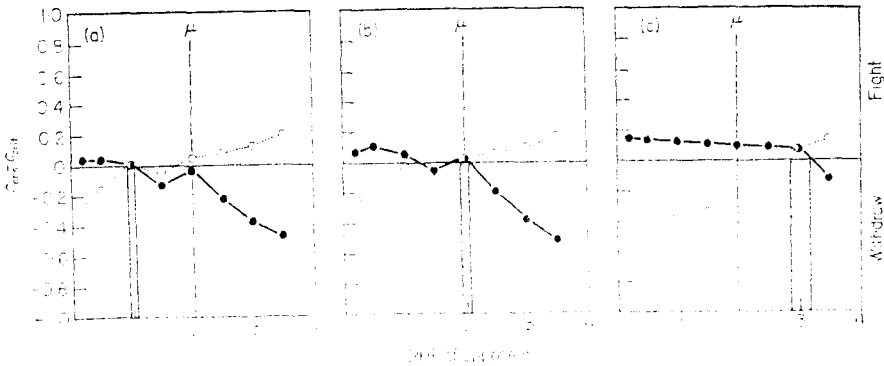


FIG. 1. Outcome of aggressive encounters of various combinations of RHP combatants using the model described in section 4 with $t = 0.1$, $h = 1.0$, $n = 10$, $G = 1$, $s = 0.7$, $r = \sigma$, $\mu = 2\sigma$. ● and solid lines = $c_{abs} - c_{crit}$ for combatants of $r_x = 1$ (a), $r_x = 2 = \mu$ (b), $r_x = 3$ (c); ○ and dotted lines = $c_{abs} - c_{crit}$ for range of opponents between $r_2 = 0.2$ to 3.5 (abscissa) fighting each of these three combatants. In a fight the individual with the highest score for $c_{abs} - c_{crit}$ stays in possession of the resource and the loser withdraws, except where both opponents have positive scores in which case there is escalated fighting to determine the winner. Shaded zones = escalation ranges (ranges of opponent RHPs which will result in escalation with each of the three combatants considered).

show a positive value for $c_{abs} - c_{crit}$). Outside this range the favourable strategy is withdrawal for the lower RHP individual and generally escalation for the higher one. However, both the low and medium rankers show withdrawal as the favourable strategy for *both* combatants when the opponent has $r_x = 1.5$. Because $F(r_x)$ is sigmoidal with the maximum gradient at the mean, a unit drop in r_x affects an average RHP individual more than an extreme one (the number of takeable resources falls more). Hence the relation between l and c_{crit2} is steeper the closer to the mean RHP. In Fig. 1(b) the $r_x = 1.5$ opponent has a higher fitness budget (l_{crit}) than the $r_x = 2$ combatant, even

accounting for the difference in c_{abs} ; however, $c_{crit} > c_{abs}$ for both individuals. For Fig. 1(a), though the I_{crit} for $r_x = 1.5$ is higher than that for $r_x = 1$, its c_{abs} value is still too low to allow escalation. These effects probably arise because for a short range of RHP close to the mean, the I_{crit} is greater for the theoretical bout 2 than for bout 1 because the RHP disparity does not fully offset the effect of the steeper $F(r_x)$ gradient. Note, however, that the higher RHP individual still "wins" in such cases (has less motivation to withdraw and can afford to be more persistent in conventional display).

The model also indicates a wider escalation range with the high ranking combatant [Fig. 1(c)]. Because of the steeper gradient in $F(r_x)$ at the mean one might expect a narrower escalation range there than at the extremes. However, the escalation range of the low ranker is even smaller than that of the average one. This is probably because c_{abs} disparity increases towards $r_x = 0$; obviously the disparity is greater between $r_x = 0.3$ and 0.5 than between $r_x = 3.3$ and 3.5 .

5. Discussion

In summary, the main predictions of the type of model developed in section 4 are that there should be an escalation range of closely matched combatants and that on either side of the range for a given individual, the higher ranking opponent should usually be prepared to escalate and the lower one to withdraw. Much fighting follows this pattern. Size, strength, weaponry, and experience all seem involved in RHP. There are innumerable examples where the outcome of disputes depends to a large extent on the relative size of the opponents. For instance, large individuals dominate over small ones in green sunfish (Greenberg, 1947; Hale, 1956), crayfish (Bovbjerg, 1953, 1956), mice (Ginsberg & Allee, 1942), New Forest ponies (Tyler, 1972) and a host of other species. Matched individuals often show the greatest tendency for escalation; mirror images are often very effective stimuli (e.g. Figler, 1972). Though pushing contests are apparently commonplace as estimates of relative strengths, there are several examples where visual cues or physiological ones are used as indicators of weaker individuals. Chickens which are moulting (and hence likely to be weaker) are usually submissive (Collias, 1943); crayfish avoid combat until the cuticle has hardened after moulting—newly-moulted specimens are less mobile and sustain greater damage and risk as a result of fights (Bovbjerg, 1953). Antler and horn size appear to be judged directly in many deer and sheep and fights occur only between closely matched combatants (see Eibl-Eibesfeldt, 1970); there seems little doubt from the literature that assessment of RHP is occurring in most cases of

animal combat. To avoid any implications of teleology, it must be stated that "assessment" in this context means only that the individual responds differentially to opponents on a basis of their RHP relative to its own; the only assessment of what is the appropriate response is the unconscious one performed by selection.

It is interesting that during a display, selection should mainly favour presenting an opponent with a maximal impression of one's RHP. Until a "strategic decision" is reached, no information should be displayed to an opponent concerning withdrawal intentions, since there is the possibility that the opponent may withdraw first (see Maynard Smith, 1974). In *Betta splendens* various display components increase in parallel for several minutes, and an outcome is not predictable until one individual finally gives up (Simpson, 1968). For a given action of the opponents, there may be an optimal retaliatory action. For food fights of blue tits Stokes (1962) has shown that correlations between display components and the subsequent outcome (attack, escape, stay) are sometimes significant, but not generally high. Hinde (1972) has argued that this may be interpreted on the view that the next action of the displaying individual is not predetermined but dependent on the behaviour of the opponent.

Prior conditioning and experience can also be very important in determining the outcome of aggressive disputes. In some cases this is related to the holder: attacker imbalances mentioned in section 3, where the holder has a higher fitness budget than the attacker for reasons other than mere RHP disparity. However in some cases it seems likely that successful fighting experience markedly increases the readiness for escalation (e.g. in mice and rats, Scott & Fredericson, 1951); an effect explicable in terms of experience increasing RHP.

Males are usually dominant over females. This often relates to RHP disparity because males are bigger; in some instances however secondary sexual characters are used as signals [e.g. comb size is a determinant of dominance in chickens (Collias, 1943)]. It seems possible that because of sexual selection male fitness may be increased by adopting a more dangerous strategy if this gives an overall increase in insemination rate. Thus males of the same RHP as females may have a higher fitness budget for fighting over, say, food—because being in peak condition may affect male fitness more because of intra-sexual competition (see Trivers, 1973, for a similar argument concerning male mortality). It is interesting in this context that females with young often (but not always) increase markedly in rank. They may have a higher fitness budget in such circumstances.

Prevention of damage during retreat is a common adaptation. Fish colour changes which accompany submission and retreat can often be explained on

a basis of crypsis. A trapped retreator (presumably $c_{\text{abs}} < c_{\text{crit}}$) when faced with a potential escalator (presumably $c_{\text{abs}} > c_{\text{crit}}$) is often very frantic in its attempts to escape (e.g. Sabine, 1949).

Much of RHP disparity must be environmental, due to experience, nutrition effects during development, accidental damage, etc. In insects adult size variation is very largely environmental in origin; if size is important in combats the main selective force acts on choice of oviposition site by the female (Prof. H. E. Hinton, personal communication). Selection will favour RHP increase until this is countered by opposing pressures; for sexual selection the selection coefficient of a competitively advantageous character actually accelerates as the character spreads throughout the population (Charlesworth & Charlesworth, in press).

If RHP variance is small, holder : attacker imbalances may be the main factors determining the outcome of aggressive disputes, and vice versa when RHP disparity is large and holder : attacker imbalances small. It is interesting that *within* social groups RHP disparity seems to be the main determinant of aggression and dominance rank. This fits the predictions because it is unlikely that (possibly food-fighting apart) holder : attacker imbalances will be of major importance within groups. The opposite may prevail for many *between* group (or single individual) territorial situations; probably mainly because of the considerable reinvestment imbalances of the type discussed in case 1(b) and case 2, section 3. A fascinating effect is predictable here. Where the holder : attacker imbalances are high, the RHP disparities small, and the value of search time high (e.g. if alternative territories are relatively abundant), it seems possible that RHP assessment need not occur before withdrawal is favourable; mere signs that the territory is occupied may be enough to favour retreat for further searching. This may well be the explanation of territory-marking scents, songs and visual cues which appear to give little indication of RHP. Baker (1972) gives an excellent discussion and evidence for this sort of effect in the territorial behaviour of male nymphalid butterflies. For instance, in *Aglais urticae* searching males become less reluctant to share occupied territories as the afternoon wears on (and the chances of finding an unoccupied territory become reduced).

The models developed in the present paper have many inadequacies. In section 4 we have not considered how RHP will modify tenure-time of a resource because of its relation with the chances of take-over. Nor do we have an accurate assessment of the value of search time; nor is the exact relationship between t , h and s properly explored. Though the mere loss of RHP alone is adequate to explain much of observed behaviour, it would be interesting to examine the interaction of RHP loss with other possible sources of fitness loss through damage. A much more rigorous analysis,

though very complex, might allow a more exact set of predictions and enable quantitative consideration of real data.

Perhaps the implications of assessment strategy for human aggression are better left for a future occasion.

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