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A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*

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Abstract. Many species have a repertoire of behaviour patterns that are used in contests over resources. It is likely that the function of these behaviour patterns is the assessment of asymmetries between contestants in physical variables (e.g. size or strength). Theoretical models of fighting behaviour such as the war of attrition and the hawk–dove game do not incorporate any behavioural mechanisms allowing assessment, and, therefore, yield no predictions about the use of behaviour patterns. In a sequential assessment game, on the other hand, the assessment of asymmetries is a major activity during a fight. Recently, a version of the sequential assessment game with several behavioural options has been developed, and here predictions from this model are tested using data from 102 staged fights between males of the cichlid fish *Nannacara anomala*. The model predicts that the sequence of behaviour patterns in a fight should be maximally efficient in assessing relative fighting ability. Specific predictions are that (1) the sequence should be organized into phases consisting of one or several behaviour patterns with constant rates of behaviour within a phase, (2) the division into phases should be independent of relative fighting ability, and (3) contests with great asymmetry in relative fighting ability should end in an early phase, whereas matched individuals may proceed through a series of escalations reaching a final phase of more dangerous fighting. The results show that the fighting behaviour of *N. anomala* is rather well predicted by the model.

During the last 15 years the evolution of fighting behaviour has been studied quite extensively using evolutionary game theory (see Maynard Smith 1982 for a review). Two models have been basic in most theoretical analyses: the hawk–dove game and the war of attrition. Using models of this kind one has tried to understand how non-strategic factors (fighting ability, resource value, role asymmetry, kinship, etc.) affect the evolution of combat behaviour. A number of predictions relating non-strategic variables to the cost of fighting and probability of winning have been put forward. However, the hawk–dove game, the war of attrition and similar games are not based on realistic behavioural mechanisms, i.e. mechanisms that produce sequences of behaviour patterns as a result of internal and external stimulation. This means that much of the behavioural diversity found in fighting behaviour, like the use of different behavioural elements, cannot be analysed with such models.

The sequential assessment game (Enquist & Leimar 1983, 1987, 1990; Leimar & Enquist 1984) represents an attempt to introduce plausible behavioural mechanisms into a game theoretical model of fighting. In this kind of model the assessment of asymmetries, like differences in size or strength, is a major activity during a contest. In the first version of the sequential assessment game only one type of behaviour was available to the contestants. Recently, we have extended the model to include several behavioural options (O. Leimar & M. Enquist, unpublished data).

Our aim in this paper is to test the sequential assessment game. In the present study we used males of the small South American cichlid fish *Nannacara anomala*. One reason for choosing this species is that, as is common among cichlids, males of *N. anomala* use several different behavioural elements during contests.

The sequential assessment game tested here is the first evolutionary game theory model yielding evolutionarily stable strategies (ESSs) with a bout structure of the kind often observed in real contests. Predictions from the model have also prompted us to analyse contest data in new ways. For instance, the model predicts that the number of occurrences of a behaviour pattern (e.g. tail beating) in a fight should be negatively correlated with the size difference, whereas the number of occurrences of the pattern before the first appearance of another

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pattern (e.g. mouth wrestling) is predicted to be independent of the size difference.

We first give a brief presentation of the sequential assessment game with several behavioural options (O. Leimar & M. Enquist, unpublished data) and list a number of predictions from this model. After describing the experiment and the results, we compare the predictions with the results.

THE MODEL

Empirical data generally show that asymmetries in physical variables are of importance in determining the outcome of a fight. For instance, one often finds that the difference in size between contestants correlates with decisions about continuing or giving up, and this is also the case in species where injuries due to fighting are rare. Since aggressive interactions often take place between strangers, assessment must occur during the contest itself. Furthermore, the fact that behavioural elements are often repeated many times suggests that assessment of the opponent is a gradual process. This is also supported by the common observation that the duration of a fight tends to increase when the asymmetry in physical characteristics (e.g. size) decreases, indicating that more information must be obtained, through repetition of behaviour, to settle a contest when the difference between the opponents is small.

Such observations are in accordance with the basic idea of a sequential assessment game: that assessment is a dominating activity in fighting, and that information accumulates during a fight in a way similar to statistical sampling. The outcome of a single act of fighting behaviour contains a random error, and to get a more accurate estimate of an asymmetry contestants must 'increase the sample size' by repeating the behaviour (see e.g. Enquist & Leimar 1983).

The particular sequential assessment game we aim to test in this paper models a situation similar to the one we find in *N. anomala*: several behavioural elements are available to the contestants, and the contested resource is sufficiently valuable for long interactions with much repetition of behaviour to occur. A brief and non-technical presentation of the model will be given here, together with a description of properties of an ESS for the game. A full description of the model, including technical arguments and details, is available from us (O. Leimar & M. Enquist).

A basic assumption of the model is that the behavioural diversity often found in fighting behaviour reflects different methods for assessing asymmetries between contestants. A closer examination of the behavioural elements used in fights shows that many of them are likely to make such information available. For instance, in *N. anomala* lateral display gives an opportunity to assess size, and tail beating and mouth wrestling yield information about aspects of relative strength. In the model, the following assumptions are made about behavioural elements. When an element is performed information is made available about an asymmetry unique to that element. These asymmetries may be correlated: information about one asymmetry may statistically contain information about other asymmetries. A single assessment of an asymmetry is not perfect, but has a sampling error, and, finally, there is a cost associated with the performance of a behavioural element. Both the sampling error and the cost may vary between behavioural elements.

An ESS for the model has the property that decisions about giving up or continuing are based on a single variable, which acts as an overriding asymmetry. In general, there may be ESSs with an arbitrarily defined overriding asymmetry, but if the contestants are able to inflict injury on each other and this ability varies between individuals, the overriding asymmetry will be determined with little ambiguity and be strongly related to the relative ability to inflict injury (relative fighting ability). Let us assume that one behavioural element can be singled out as particularly dangerous to the opponent and that, in contrast with other behavioural elements, the cost involved varies between individuals, so that for a pair of contestants there will be an asymmetry in the ability to inflict cost. The use of this behavioural element we call dangerous fighting and the corresponding asymmetry is referred to as relative fighting ability.

For *N. anomala*, severe injuries have not been observed, but minor injuries due to bites are common. Observations from related species suggest that *N. anomala* are physically able to inflict severe damage, and it is quite likely that this ability will vary with the size of an individual.

For an ESS, decisions to give up or continue are then based on estimates of relative fighting ability. Another basic property of an ESS is that, as long as an individual continues, behavioural elements are chosen to provide optimal assessment of relative fighting ability. This means that the behavioural element that most efficiently increases the information about relative fighting ability is selected. As a consequence, a behavioural element will be used only if the corresponding asymmetry is correlated with relative fighting ability. Provided that one knows the costs, sampling errors, and the correlations between all asymmetries (including relative fighting ability), a sequence of behaviours that is optimal for assessment of relative fighting ability is to a great extent determined. Generally speaking, a behavioural element is efficient in assessing relative fighting ability, and is then likely to be used, if the cost and/or the sampling error is low and if the correlation between the corresponding asymmetry and relative fighting ability is high.

When relative fighting ability is assessed through sampling of a correlated asymmetry, there will be a diminishing return of information with each repetition of the behavioural element. This creates a tendency for behavioural elements to replace each other during a fight. As a consequence, an optimal assessment sequence will be divided into different phases. Some of the phases may, however, consist of mixtures of several behavioural elements, and then these should be used in constant proportions relative to each other. During dangerous fighting, when relative fighting ability is assessed directly, there is no diminishing return of information, and a fight that has entered dangerous fighting will stay in that phase until the fight ends.

We illustrate the possibility of sequences with a few examples. Consider first a repertoire of two behavioural elements, A and D, the latter being dangerous fighting. An optimal sequence is either to repeat A a given number of times and then escalate to D, or, if A is initially less efficient than D, to start with D and never use A. When a third element B is introduced the situation becomes much richer. One possibility is that A is first repeated a number of times, then in the next phase A and B are mixed in some frequency, and finally only D is used (A–AB–D). Other possibilities with three behavioural elements are A–B–D, A–B–AB–D, A–D, and only D. If A and B provide complementary information about relative fighting ability (i.e. if the corresponding asymmetries covary with different aspects of relative fighting ability) both tend to be used, whereas if they provide similar or highly correlated information one of them may be more efficient and the other element will not be used at all. This suggests that contestants will use behavioural elements that allow assessment of rather different aspects of fighting ability, which in turn suggests that the repertoire will contain rather different types of behavioural elements.

It is possible that opponents will differ in which behaviour they prefer at some point of a contest. For instance, an individual that estimates itself to have high relative fighting ability stands less of a risk and should be more willing to escalate to dangerous fighting. There are two conditions that result in agreement in choice of behaviour: information about relative fighting ability should be obtained gradually, and the cost of performing behavioural elements should be similar for the two opponents. Note that if escalation to dangerous fighting takes place only for opponents that are fairly well matched (due to assessment in previous phases), the difference between them in cost of fighting will be small. For *N. anomala* both these conditions ought to hold reasonably well.

A lack of conflict in choice of behaviour facilitates cooperation in assessment. In fact, many behavioural interactions observed in fighting behaviour are meaningless without cooperation. For instance, tail beating in *N. anomala* requires that one fish is the beater and the other is the recipient, and the recipient must stay still so that the beater can direct its behaviour. Similarly, mouth wrestling requires that both fish grip each other's jaws.

An example of an ESS for a case with three behavioural elements is shown in Fig. 1. There are three phases of fighting (A–AB–D), and the figure depicts a causal factor space with two causal factors: the current estimate of relative fighting ability and the accuracy of the estimate. The accuracy increases as the contest continues, and the abscissa may loosely be identified as a time-axis. An individual gives up when the estimate of relative fighting ability goes below the switching line in Fig. 1. The state of an individual during a contest is illustrated in the figure as a trajectory through the causal factor space. In the case shown the individual has lower fighting ability than the opponent and gives up in the second phase.

If the parameters in the model (such as costs, sampling errors and correlations) are known one can determine an ESS. When comparing the model with real contests it might not be possible to estimate the parameters, and this is the case for fights between

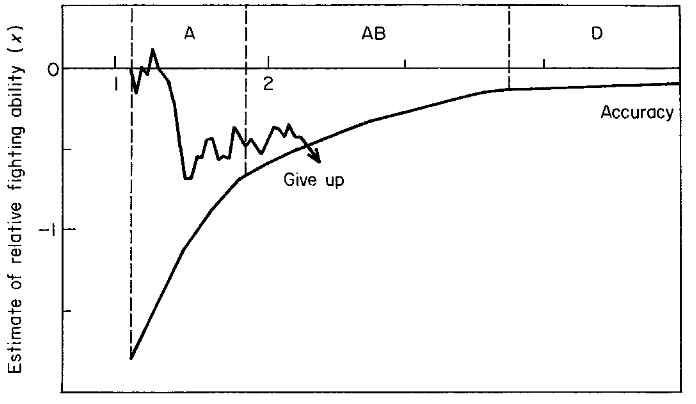

Figure 1. A causal factor space with two causal factors: the estimate of relative fighting ability (x) and the accuracy of the estimate. An ESS is illustrated as three phases of fighting (using behavioural element A, using a mixture of A and B, and using dangerous fighting, D), and a switching line for giving up. The trajectory illustrates a contestant's successive estimates of the relative fighting ability during a fight. The contest ends when a contestant's trajectory crosses the giving up switching line. In the case illustrated, the fight ends without escalation to dangerous fighting.

N. anomala. However, there are a number of qualitative predictions from the model that can be tested. First, concerning choice of behaviour, the model predicts that contests are divided into phases in a way that is (approximately) independent of the relative fighting ability of contestants. Second, concerning decisions to give up, a switching line of the kind depicted in Fig. 1 has a number of consequences. In fights with a clear asymmetry in fighting ability, the trajectory of the estimate of the weaker contestant tends to stay well below the time-axis and to cross the switching line after a short interaction, whereas for matched opponents trajectories tend to stay closer to the time-axis. This leads to longer fights on average when the asymmetry in fighting ability decreases. Similarly, more phases of fighting will on average be entered when the asymmetry in fighting ability decreases. There must be a considerable amount of randomness in an individual's trajectory, resulting in variation in the duration of fights that is not due to variation in relative fighting ability. Concerning probabilities of winning, the individual with higher fighting ability usually wins, but in fights with a small asymmetry in fighting ability, the weaker animal has a chance of winning due to the random errors in the estimate of relative fighting ability.

Summary of Predictions

The first prediction, if fulfilled, tells us that variation in fighting ability exists and can be measured empirically. The second and third are about the characteristics of phases, i.e. how behaviour patterns are used during a fight. The fourth deals with decisions to give up in relation to fighting ability. The last prediction concerns costs of fighting. Note that predictions about fight duration assume that there is a close correspondence between amount of behaviour performed (e.g. number of repetitions of behaviour patterns) and time.

(1) An individual's probability of winning should increase when its fighting ability increases relative to that of the opponent.

(2) The behavioural sequence should be organized into phases, each characterized by the appearance of a new behavioural element. A phase may contain one or several behavioural elements. If it contains several elements, these should be used at constant rates relative to each other throughout the phase.

(3) The behavioural sequence should be approximately independent of relative fighting ability. From this it follows that the duration of completed phases should be independent of relative fighting ability. Thus, when considering all contests that enter a certain phase, the amount of behaviour (number of repetitions or total duration) prior to the start of the phase in question should not depend on relative fighting ability.

(4) Decisions to give up should be influenced by fighting ability: contests with a smaller asymmetry in fighting ability should proceed further along the behavioural sequence. For instance, the number of

different behavioural elements and phases observed in a fight should tend to increase when the asymmetry in fighting ability decreases. In parallel, the average number of repetitions of behaviour in a fight and the average fight duration should increase when the difference in fighting ability decreases. There should be additional random variation in these variables, resulting in only moderate correlations between number of repetitions or duration and differences in fighting ability.

(5) The total cost of fighting should tend to increase when the asymmetry in fighting ability decreases. The probability of injury in a contest should be higher for the individual with lower fighting ability. The final phase should correspond to direct sampling of relative fighting ability, i.e. dangerous fighting.

TEST OF PREDICTIONS

Material and Methods

We used fish from a stock bred at the department and originally obtained from local dealers. We raised them in tanks of volume 200–350 litres. For the experiment, individuals beginning to show male characteristics were immediately taken out from these tanks and isolated in holding aquaria ($50 \times 50 \times 30$ cm). All tanks contained a substrate of gravel 2 cm deep. The temperature was kept at 26°C and a 12:12 h light:dark cycle was maintained. We fed the fish twice daily (on midge larvae and dry fodder); they weighed between 1 and 9 g when tested.

The test aquaria ($90 \times 60 \times 40$ cm) could be divided in two by an opaque partition. In each part there was a box in which a fish could be enclosed (see Fig. 2). The boxes were opened and closed by a remotely controlled motor. All filming and also the operation of the boxes took place behind a screen.

On the evening prior to a test, a selected pair of fishes were weighed and transferred from their holding aquaria to the test aquarium, now divided in two with an opaque partition. Thirty minutes before the test the fish were enclosed in their boxes and the opaque partition was removed. We then started the test by slowly opening the boxes, allowing the pair to interact. The interaction was video filmed until one of the fish gave up. After a fight we measured the fish and inspected them for injuries. These injuries were invariably slight (e.g. the loss of a few scales), and rather careful inspection was needed to detect them. They seemed not to hamper or affect the fishes in their normal activities (the study was carried out in accordance with current Swedish regulations concerning animal welfare).

The social context in which male *N. anomala* fight differs from what one usually finds among cichlids. Investigations using large tanks have shown that the males are not territorial. The social system that develops, in both small and very large tanks, is a dominance system with one alpha-male and a number of beta-males. These males move around in search of females, which are territorial. On finding a female ready to spawn, the alpha-male will court her and attack other males if they try to court. The alpha-male also challenges any unknown male. In our study, a pair of males started interacting as soon as they saw each other, and the contested resource would then be the alpha-position.

A fight ended as soon as one fish signalled that it gave up, by folding its fins and changing coloration. After giving up, the loser did not try to hide or escape from the winner. It often stayed nearby and was tolerated by the winner.

Tape analyses

The analyses of the videotapes focused on behaviour patterns of interest for testing the sequential assessment game. The following behaviour patterns were recorded throughout a fight: tail beating, biting, mouth wrestling and circling. Before the start of mouh wrestling the number of frontal orientations and attemps at mouth wrestling were also recorded. Orientation movements, fin position and body coloration were not sampled. The behaviour patterns analysed are described below. For further description of these behaviour patterns see e.g. Baerends & Baerends Van Roon (1950), Oehlert (1958), Jakobsson et al. (1979) and Enquist & Jakobsson (1986). Time of occurrence was noted for all behaviour patterns recorded and for mouth wrestling we also recorded the duration of each bout. The duration of a fight was measured from the first tail beat to the end of the fight. The first time the fish approached each other with erected fins and aggressive body coloration was noted when this event was clear. Giving up is associated with clear changes in both behaviour and coloration (Jakobsson et al. 1979; Enquist & Jakobsson 1986).

Tail beating

One fish, the actor, beats with its tail and water is pushed, usually in the direction of the other fish.

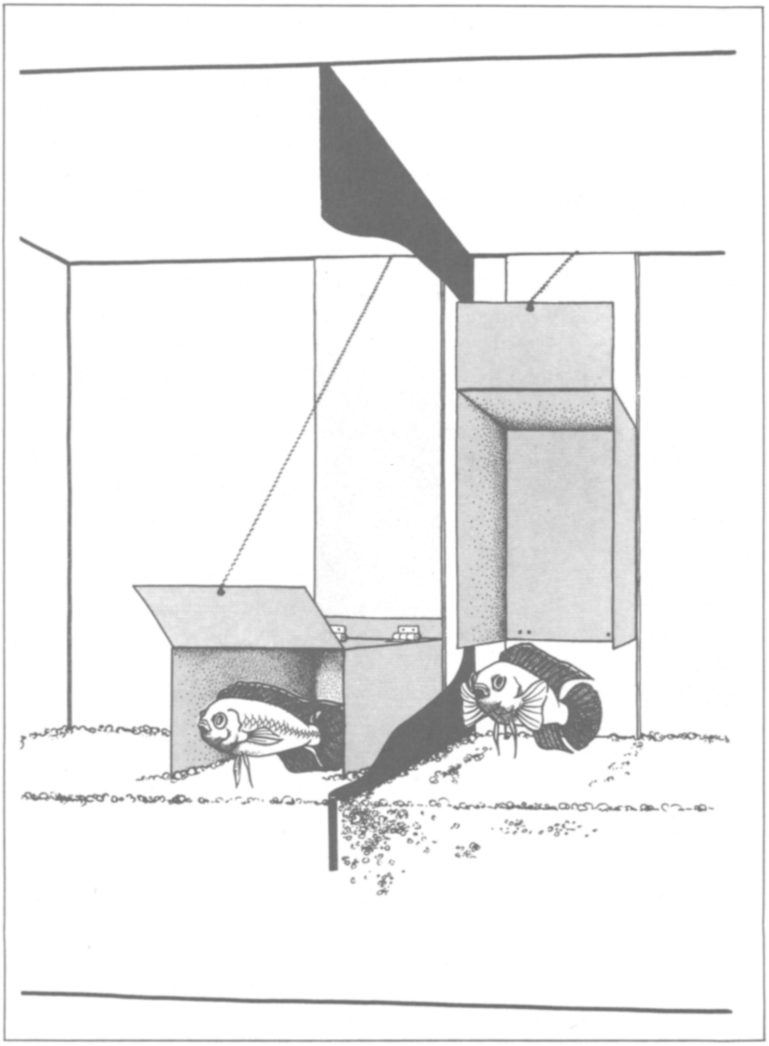

Figure 2. The experimental tank with its starting boxes at the time when the boxes are being opened (the indicated opaque partition has already been removed at this time).

The animals constantly change position and usually orient laterally to each other. One function of these orientation movements may be to allow a change of roles, from beater to recipient and vice versa, and to coordinate the actor and the recipient so that the water stream hits the latter. Tail beating has its peak of occurrence shortly after the beginning of a fight.

Biting

We define biting as an attack in which the mouth of the actor hits the other fish. Hits in the mouth area were not counted as bites since they frequently occurred in connection with attempts to mouth wrestle. Bites directed towards fins sometimes resulted in tears, but no other injuries could be seen directly after a bite. Biting seemed to have two peaks of occurrence. The first bite occurred after some tail beating and biting reached a small peak prior to the first bout of mouth wrestling. In very long fights the rate of biting increased again, in which case we did not only observe single bites, but instead the fish often tried to bite repetitively (see circling below).

Mouth wrestling

In mouth wrestling, the contestants grip each other's jaws and engage in a pushing or pulling contest. Mouth wrestling requires that both contestants cooperate, and it is possible for a fish to stop mouth wrestling by breaking loose from the opponent's grip. Before mouth wrestling starts the contestants orient frontally. Usually a series of bouts of mouth wrestling occurred in a fight, and each bout ranged from 1 to 144 s with an average of 10 s. The maximum amount of time of mouth wrestling observed in a fight was 52 min and the shortest time was 1 s.

Circling

When both fish repetitively try to bite each other a characteristic circling pattern appears, where both individuals swim fast in a small circle trying to bite the back of the opponent. Circling occurred only after quite a long period of mouth wrestling and was observed in only a few fights. After the first bout of circling behaviour mouth wrestling still occurred but at a low frequency.

Weight asymmetry as independent variable

We analysed the data using a measure of weight difference as the independent variable. Instead of using the weight ratio (an individual's weight/opponent's weight) we used the logarithm of this ratio, referred to as the weight asymmetry between the individual and the opponent. If the weight asymmetry is negative the individual is smaller than his opponent, if it is zero they are matched, and if it is positive the individual is heavier. We have classified contests according to the weight asymmetry from the point of view of the heavier fish and called this the contest weight asymmetry, which is always positive. Note that contest weight asymmetry was used in all correlation analyses. In some cases we analysed the behaviour of the heavier and the lighter fish separately using the individual weight asymmetry; the weight asymmetry of the lighter fish of a pair is then minus that of the heavier.

Instead of just collecting material for the whole range of possible weight asymmetries, we selected five particular values (by weighing 20–30 fish the likelihood of finding a pair with a particular value is high). Selected values and sample sizes are given in Table I. In total, the analysis was based on 102 fights.

It is known from earlier experiments with *N. anomala* that weight difference is a good predictor of the outcome of contests. Compared with the model we intended to test, such a result would be obtained if relative weight had a high correlation with the overriding asymmetry, and we have attempted this interpretation. The weight asymmetry was a strong predictor of outcome (Fig. 3). In only three cases did the lighter fish win. In the group with an asymmetry of 0·1 the heavier fish won 20 out of 22 fights, and when the asymmetry was 0·2 the heavier one won all but one of the 20 fights.

Table I. Classes of weight asymmetry and sample sizes

Weight asymmetry*	Deviation accepted	Weight ratio†	Sample size
0	0·01	1·0	19
0·1	0·01	1·11	22
0·2	0·01	1·22	20
0·4	0·02	1·49	15
0·8	0·05	2·23	20
1·6	0·1	4·95	6

*ln (weight ratio).
†Weight of heavier divided by weight of lighter fish.

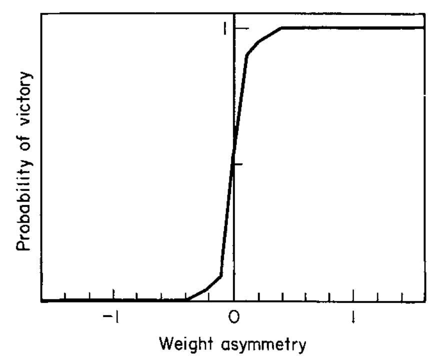

Figure 3. Estimated probability of winning as a function of weight asymmetry for the present experiment.

Absolute weight

To check whether there was an additional effect of absolute weight on the behaviour of the fish, we computed the correlation of fight duration with the average weight of a pair. No relationship was found for the total material ($r_s = 0{\cdot}02$, NS); the different weight asymmetry groups yielded some positive and some negative correlations without any clear pattern (all but one NS). Thus, absolute weight had little effect on fighting behaviour.

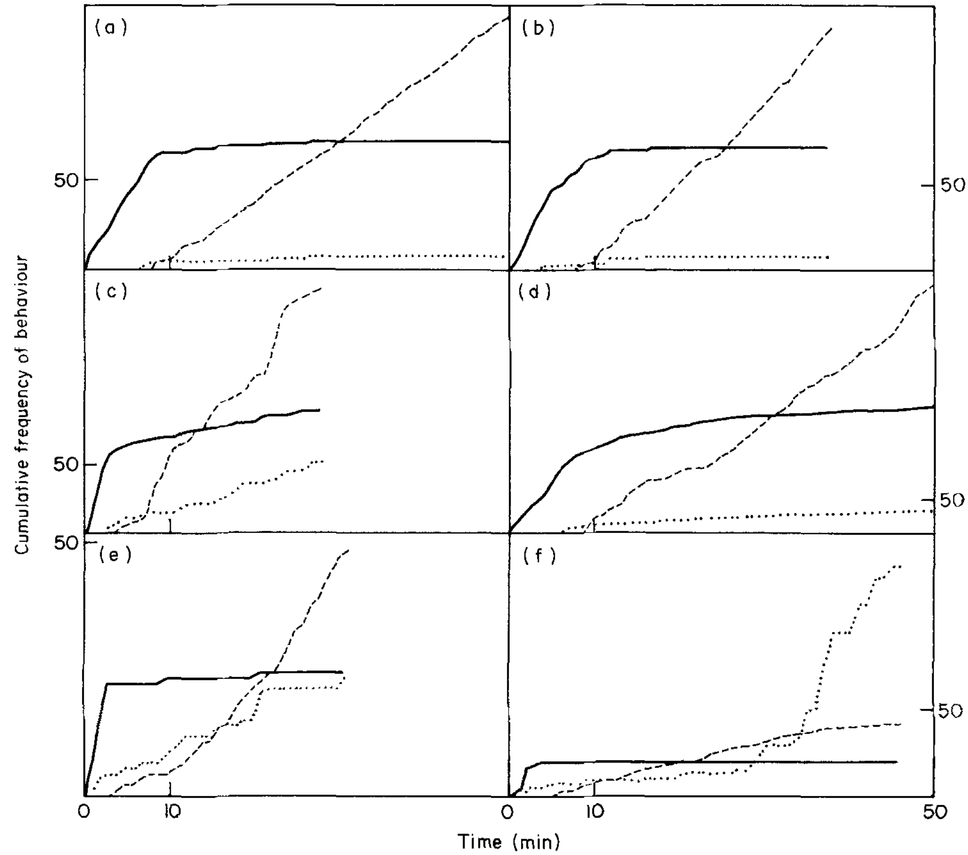

Figure 4. A sample of individual fights, showing cumulative frequency of tail beating (——) and biting (· · ·) and cumulative duration of mouth wrestling (– – –). The duration of mouth wrestling is measured in units of 5 s.

Results

Basic structure of a fight

According to prediction 2, fights should be divided into a number of phases, each characterized by the appearance of a particular behavioural element (only very long fights would contain all phases). *Nannacara anomala* fights have such a structure. Initially in a fight the fish change colour and approach each other with erected fins and usually orient laterally to each other. Apart from this they are rather inactive. This is followed by a period of intense tail beating (average time to first tail beat was 18 s). After a few minutes the first bites appear (average time to first bite was 97 s or 21 tail beats) and soon the first bout of mouth wrestling follows. In very long fights circling is also observed. This order of appearance of behavioural elements was very consistent, and only five exceptions occurred, when mouth wrestling appeared before any biting. Fights were observed to end in any of the described phases of fighting, and only five contests contained all behavioural elements.

When the fish reached a new phase they typically did not stop using behavioural elements used earlier in the fight, but the rate of using them decreased. This was most clearly seen at the onset of mouth wrestling, where the rate of tail beating decreased by about 90% on average (see Figs 4, 5). Between escalation events the rates of behaviour were rather constant (Fig. 5, compare prediction 2). However, as shown in Fig. 4, there was a lot of variation between fights. In some fights (e, f) very little tail beating occurred after the beginning of mouth wrestling, whereas in other fights (c, d) there was a small but rather constant rate of tail beating during the rest of the fight. Similarly, some fights contained a lot of biting and others hardly any. This variation seemed not to be explained by the weight asymmetry.

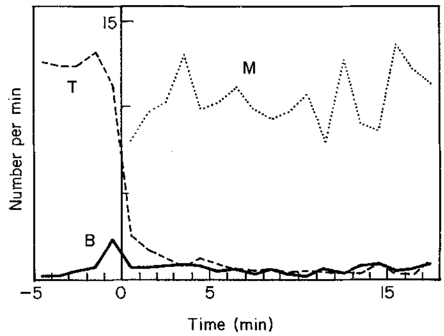

Figure 5. Average rates (per min) of tail beating (T), biting (B) and mouth wrestling (M) in fights with mouth wrestling (one unit of mouth wrestling is set to 2 s). The zero point in time is chosen as the start of mouth wrestling.

Duration of completed phases

To test the third prediction, i.e. that the duration of completed phases should be independent of relative fighting ability, we selected contests in which a certain behavioural element was used (tail beating, biting, or mouth wrestling) and looked for effects of contest weight asymmetry on the point of onset of the element. There were no significant correlations between duration until the beginning of the phase in question and contest weight asymmetry; measuring the number of repetitions prior to the phase instead of time gave the same result (Table II).

Giving up

The duration of fights varied a lot. Some fights ended at the first contact, and the longest fight observed lasted for 155 min. In accordance with prediction 4, some of this variation was explained by variation in weight asymmetry (one-tailed probabilities are given for the statistical analyses below testing predicted relationships with contest weight asymmetry; when a two-tailed probability is given this is noted). The fight duration tended to decrease when the contest weight asymmetry increased ($r_s = -0{\cdot}65$, $N = 102$, $P < 0{\cdot}001$; Fig. 6a). The level of escalation reached in a fight (0 = aggressive coloration and erected fins; 1 = tail beating; 2 = bites; 3 = mouth wrestling; 4 = circling) was also negatively correlated wih contest weight asymmery ($r_s = -0{\cdot}73$, $N = 102$, $P < 0{\cdot}001$). The probability of observing a particular behaviour pattern in a fight as a function of amount of weight asymmetry is plotted in Fig. 6b.

Measuring the frequency of various behaviour patterns in a fight instead of duration similarly yielded negative correlations with contest weight asymmetry: number of tail beats, $r_s = -0{\cdot}47$; number of bites, $r_s = -0{\cdot}58$; duration of mouth wrestling, $r_s = -0{\cdot}67$ ($N = 102$, $P < 0{\cdot}001$ in all cases). These relationships partly result from the lower probability of occurrence of behaviour patterns in contests with greater weight asymmetry (Fig. 6b), but there remains an effect of contest weight asymmetry when one looks only at contests in which a given behaviour pattern occurs: number of tail beats, $r_s = -0{\cdot}19$, $N = 85$, $P = 0{\cdot}039$; number of bites, $r_s = -0{\cdot}22$, $N = 73$, $P = 0{\cdot}033$; duration of mouth wrestling, $r_s = -0{\cdot}22$, $N = 69$, $P = 0{\cdot}035$.

As indicated by the rather small correlation coefficients and as seen in Fig. 6a, there was a great deal of variation in duration which was not explained by variation in weight asymmetry. The estimated spread in fight duration, measured by the standard deviation of each class, decreased when the difference in weight increased ($r_s = -0{\cdot}94$, $N = 6$, $P = 0{\cdot}008$; Fig. 6a).

Table II. Test of independence between the behavioural sequence and weight asymmetry

Variable	r_s	N	P
Fights with tail beating			
Before start of tail beating:			
Duration*	0·08	52†	>0·5
Fights with bites			
Before start of biting:			
Duration	−0·05	73	>0·5
Tail beats	0·05	73	>0·5
Fights with mouth wrestling:			
Before start of mouth wrestling			
Duration	0·03	69	>0·5
Tail beats	0·02	69	>0·5
Bites	0·11	69	0·36
Frontal orientations	0·09	61	>0·5
Mouth wrestling attempts	0·03	67	>0·5

Variables are duration or frequency of a behaviour pattern prior to the onset of a particular phase. For each variable, the correlation with contest weight asymmetry is given.

*Duration from initial approach. Other durations are from the first tail beat.

†Tail beating occurred in 85 contests, but the initial approach was unclear in 33 of these.

Injuries

After a fight, we inspected the fish for injuries, which consisted of loss of scales on the body, torn

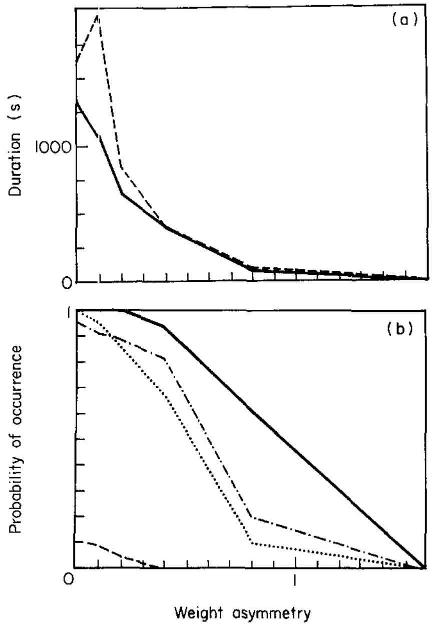

Figure 6. (a) Mean and SD (– – –) of fight duration as a function of contest weight asymmetry. (b) Probability of occurrence of various behavioural elements in a fight as a function of contest weight asymmetry. ——, tail beating; — · —, biting; · · ·, mouth wrestling; – – –, circling.

fins, or lip damage. All injuries observed were slight and seemed not to affect the ability of a fish to swim or eat. To get a measure of injury, five parts of a fish were identified: head, body, dorsal fin, caudal fin and other fins. Each part was classified as: not injured (0), slightly injured (1), or injured (2). The sum from all parts was then used as a semiquantitative measure of injury. The injury score depended strongly on weight asymmetry (Fig. 7).

In agreement with prediction 5, the sum of the injury scores in a fight was negatively correlated with contest weight asymmetry ($r_s = -0{\cdot}55$, $N = 102$, $P < 0{\cdot}001$). Considering fights with a given weight asymmetry and comparing all cases where the contestants got different scores of injury, we found that the smaller one was the more injured in 69% of these fights ($T = 105$, $N = 26$, $P < 0{\cdot}05$, Wilcoxon matched-pairs signed-ranks test), which is consistent with prediction 5.

Circling

Many bites were delivered during circling behaviour, potentially causing injuries. Two of the five fights showing this behaviour contained only little

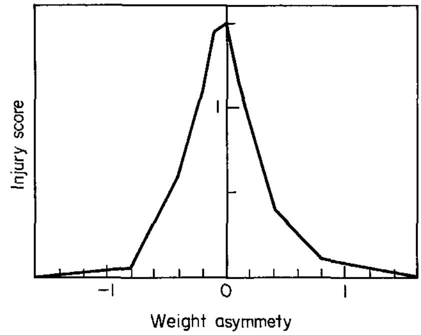

Figure 7. Average injury score in a fight as a function of weight asymmetry.

circling, causing no apparent damage. In the remaining three fights there were many bouts of circling, and the average injury score in this group was 3·8, compared with 1·5 for fights between matched opponents (see Fig. 7).

Circling is likely to be the most dangerous behavioural element in the repertoire of *N. anomala* (although not causing any serious injury), and in those fights where it appeared it was preceded by the other behavioural elements. It is tempting to identify circling with direct estimation of relative fighting ability; however, there is a discrepancy with the model in that some mouth wrestling was observed after the onset of circling.

Variation between individuals in choice of behaviour

According to the model, all fights should have the same time structure, the only variation in choice of behaviour being in how far a fight proceeds before one of the contestants gives up. However, the observed fights contained additional variation. First, the structure varied between pairs to a certain degree (Fig. 4).

Second, there were also some differences in choice of behaviour between the lighter and heavier fish of a pair. The total number of tail beats (Fig. 8a) was significantly greater for the smaller fish for the weight asymmetry classes 0·1 and 0·2 ($T = 52{\cdot}5$, $N = 21$, $P = 0{\cdot}027$, and $T = 31$, $N = 19$, $P = 0{\cdot}010$, respectively; Wilcoxon matched-pairs signed-ranks test, two-tailed). Similarly, in fights with mouth wrestling (see Fig. 9) the average number of tail beats prior to mouth wrestling was higher for the smaller fish in the same two classes ($T = 43{\cdot}5$, $N = 21$, $P = 0{\cdot}012$, and $T = 36{\cdot}5$, $N = 17$, $P = 0{\cdot}058$, respectively). There seemed to be no difference

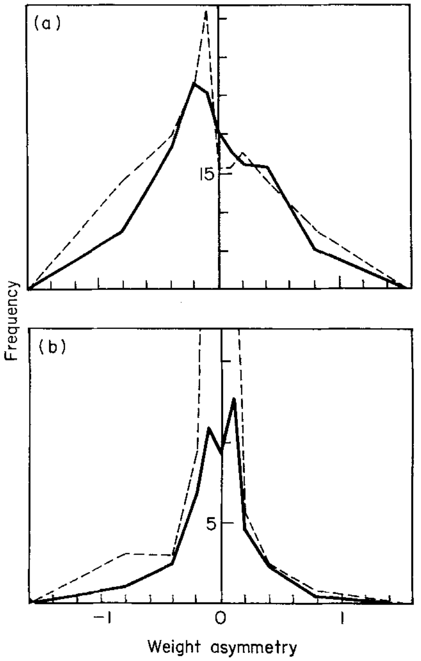

Figure 8. Mean and SD (broken line) of the total number of tail beats (a) and bites (b) in a fight as a function of weight asymmetry.

between the lighter and heavier fish in the total number of bites (Fig. 8b) or in the number of bites before the onset of mouth wrestling. However, in the last minute of a fight a winner bit twice as much as a loser ($P<0{\cdot}001$, Wilcoxon matched-pairs signed-ranks test, two-tailed).

There were attempts to start mouth wrestling that did not succeed. Such unsuccessful attempts might be due to conflicting interests between heavy and light individuals about which behaviour to perform. However, no significant rank correlation with weight asymmetry was found either with number of frontal orientations prior to the start of mouth wrestling or with the number of attempts (Table II).

Earlier studies of N. anomala

The fighting behaviour of *N. anomala* has previously been studied by Oehlert (1958), Jakobsson et al. (1979), Enquist & Jakobsson (1986) and Enquist et al. (1987). Apart from a few findings, there is good agreement between these studies and the present one. Enquist & Jakobsson, studying fights with weight asymmetry varying from 0·35 to 0·95, found that in fights without mouth wrestling the heavier fish performed more tail beats than the smaller one, whereas in the present study no differences were detected within this range. Similarly, in fights with mouth wrestling Enquist & Jakobsson found that the heavier fish bit more than the lighter one, whereas no such difference was found in the present study. Being based on only two heavy males, these particular results obtained by Enquist & Jakobsson might be less reliable than the current ones.

DISCUSSION

There have been a few previous attempts to test particular game theory models of fighting behaviour (for example Parker & Thompson 1980; Austad 1983; Hammerstein & Riechert 1988). Although these studies tested models that lacked a behavioural mechanism allowing assessment of asymmetries, many observations were fairly consistent with predictions. The reason for such agreement would seem to be that there are certain robust properties of ESSs that to some extent are predicted by all game theory models of contests, e.g. a higher resource value usually results in a more persistent strategy (Enquist & Leimar 1987). There are, however, clear limitations to models which have no counterpart to the behavioural mechanisms that operate in real contests: predictions about sequences of behaviours cannot be made, nor can one make quantitative predictions of, for example, struggle durations and probabilities of winning, even if one can estimate relevant parameters such as resource value and rate of cost expenditure.

While it seems evident that assessment of asymmetries goes on and affects decisions throughout animal contests, the detailed nature of this process is not clear. As mentioned, several of the behaviour patterns shown by *N. anomala* during a fight make information available about the actor (Enquist & Jakobsson 1986), and the fact that a proportion of the observed variation in behaviour can be explained by variation in weight asymmetry shows that information is transmitted in one way or another. Enquist et al. (1987) demonstrated that *N. anomala* can assess weight asymmetry visually, although the precision was quite low (when the weight asymmetry was greater than 0·9, visual information was enough to cause the lighter fish to give up). The fact that we found an increase of, for example, duration after start of mouth wrestling with decreasing weight asymmetry indicates that

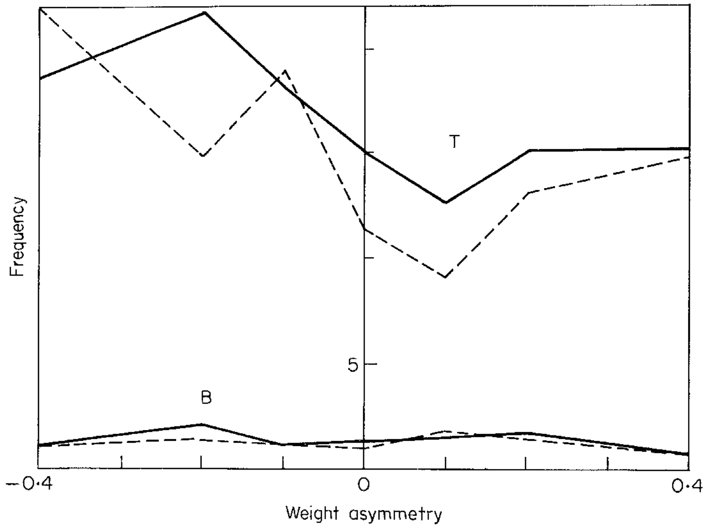

Figure 9. Mean and SD (broken lines) of number of tail beats (T) and number of bites (B) before the first bout of mouth wrestling as a function of weight asymmetry. Only fights with mouth wrestling are included.

assessment also takes place at later stages of a fight. However, these results provide no detailed information about the variables that are assessed during a fight or how different variables are combined in decisions about further actions.

In a sequential assessment game information is obtained in a way similar to statistical sampling and accumulates gradually during a fight. It is hard to substantiate this assumption directly but there is some indirect evidence in favour of it. Consider the alternative that information is gained in a very irregular manner. This alternative is not supported by the data: there is no tendency towards giving up being clumped, e.g. that most fights end after a given time of fighting or after a given sequence of behaviours.

Turning now to the specific predictions from the sequential assessment game listed above, the results show that the fighting behaviour of *N. anomala* is rather well predicted by the model. For instance, related to the fact that one on average has to sample more to detect a small difference than a large one, the model predicts that fights should on average be longer when the asymmetry in fighting ability decreases. This prediction has strong support when measuring both frequency of behaviour and time. The model also predicts that if several behavioural elements are available they should be used in roughly the same way in all fights, although fights end at different points along the behavioural sequence. Thus, short fights will contain only the initial type of behaviour, whereas long fights will contain all behavioural elements. Further, fights should be divided into phases with constant rates of behaviour within phases. These predictions also have support. The probability of observing a particular behavioural element in a fight increases when weight asymmetry decreases, behavioural elements occur in a strict order, and, in most fights, clear phases of fighting can be identified with constant rates of behaviour. The order in which the behaviour patterns occur also seems reasonable from what would be expected from the model. *Nannacara anomala* fights start with visual assessment, which is likely to be very cheap. Tail beating, the next behaviour, has at least some energy costs, whereas both biting and mouth wrestling can result in injuries. Finally, circling is likely to be the most dangerous behavioural element in the repertoire of *N. anomala*.

Another observation that is in accordance with the theory is that the fish cooperate in performing behaviours such as tail beating and mouth wrestling, i.e. they cooperate in assessing relative fighting ability. It is also worth noting that the behavioural elements used are likely to provide information about diverse aspects of relative fighting ability, which is to be expected of an efficient assessment procedure.

The analyses we performed used weight asymmetry as the independent variable. This was partly for practical reasons, but the fact that the heavier fish almost always won shows that weight asymmetry must be highly correlated with factors determining the outcome, so that, in the context of the model, weight asymmetry must be highly correlated with relative fighting ability. This interpretation is also consistent with our observations of injuries. The cost of fighting is predicted to be highest between fish of equal fighting ability, due to longer and more intense contests, and in asymmetrical contests the cost should be higher for the individual with lower fighting ability. Our injury score increased when weight asymmetry decreased and the lighter fish in a pair was usually the more injured.

The number of repetitions or duration of behaviour in a completed phase were predicted to be independent of fighting ability, and no significant correlation with weight asymmetry was detected. However, most rank correlation coefficients obtained were slightly positive (Table II). This may indicate that the estimate of relative fighting ability had some influence on choice of behaviour.

In some cases the model failed to predict the results. For instance, we observed differences in the rate of tail beating between the lighter and the heavier fish (Fig. 8a), and in the last minute of a fight there were clear differences in behaviour between the winner and the loser. A striking observation was the great variability between fights. Some of this variation is indeed predicted by the model. For instance, we expect a great deal of variation within weight classes in how far a fight proceeds before one of the contestants gives up. On the other hand, the model predicts that fights should not vary in their structure, i.e. in how different behavioural elements are used in relation to each other. It is clear from Fig. 4 that the structure varied between fights to a certain degree. The model predicts that the time between two phase changes should be independent of weight asymmetry and of given length. At first this prediction seems to have support, since no correlations with weight asymmetry were detected. However, there was a great deal of variation between fights within weight asymmetry classes (see Figs 4 and 9).

The above discrepancy between prediction and result may suggest that the behavioural mechanism assumed is too simple. Despite the variation in behavioural structure observed between fights, the outcome was highly determined by weight asymmetry, suggesting that high precision was reached differently in different fights. A tentative interpretation is that the behavioural mechanism controls the use of behavioural elements at a higher level, focusing more on amount of information than on number of repetitions or duration of behaviour. Instead of letting the number of times different behavioural elements have been used so far determine the choice of behaviour, an animal might also be sensitive to the variation in the observations. For instance, the animal could neglect some 'failed' observations and perform extra repetitions, or favour other behavioural elements that seem more informative (e.g. scatter less) in the particular fight. That animals can adjust their behaviour depending on the possibility of observing the outcome is shown in a study on fighting behaviour of the crayfish *Orconectes rusticus* under different light conditions (Bruski & Dunham 1987); the frequency of visually mediated behaviours decreased in the absence of light, while tactile behaviours were performed more frequently.

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