A test of the sequential assessment game: the effect of increased cost of sampling

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The sequential assessment game describes a fight between two conspecifics as a statistical sampling process, allowing for specific predictions about fight duration and number of repetitions of a behavioral element depending on relative fighting ability. Fight duration and number of repetitions of a behavioral element correlate moderately to relative fighting ability. Variation in real contests depends on differences between the contestants in the ability to incur cost and the value of the contested resource. I hypothesized that an additional source of variation is differences between individuals in their perception of how dangerous it is to fight. To investigate this, I used the risk of predation to study the effect on the use of different agonistic behaviors in fights between males of the cichlid fish *Nannacara anomala*. In the group subjected to predation risk, the time until the most escalated behavior (mouth wrestling) was more variable and increased significantly on average. In addition, the duration of fights was significantly longer. In the predator treatment the use of visual assessment and tail beating varied more than in the control, giving a significant positive relationship between the use of low-intensity behaviors and time to mouth wrestling across the group. These relationships were less pronounced in the control group. The effect of predation risk on optimal information transfer is discussed based on the behavioral mechanism suggested by the sequential assessment game. Key words: cichlids, fighting behavior, *Nannacara anomala*, predation risk, sequential assessment. [Behav Ecol 10:726–732 (1999)]

The sequential assessment game (Enquist and Leimar, 1983, 1987; Enquist et al., 1990; Leimar, 1988; Leimar and Enquist, 1984) describes a fight between two contestants as an ongoing statistical sampling process, which makes it possible to predict fight duration and number of repetitions of a behavioral element depending on relative fighting ability (e.g., relative weight). A large asymmetry in relative fighting ability can be assessed using only low-intensity behaviors (Enquist et al., 1987). A small asymmetry between contestants is assessed either by using more repetition of a behavior or more costly and informative behaviors (Enquist and Jakobsson, 1986). The model has been supported qualitatively and quantitatively by empirical data (Hack, 1997; Keeley and Grant, 1993; Koops and Grant, 1993; Leimar et al., 1991), but some variation in contest behavior remains unexplained (Enquist et al., 1990; see also Koops and Grant, 1993; Turner and Huntingford, 1986).

Two factors have been shown to influence the variation found in real contests: differences between the contestants in the ability to impose cost on the opponent and the value of the contested resource (Austad, 1983; Enquist and Leimar, 1987; Grafen, 1987; Maynard Smith, 1982; Parker, 1974). Individuals may also differ in inherent aggressiveness, which may be a source of variation (Barlow et al., 1986). However, in this study I consider another potential source of variation—that individuals differ in their assessment of the risk associated with the fight. Fighting behavior can cause loss of time and energy and can inflict injuries, but there may also be other costs associated with fighting. The risk of predation has been suggested as a potential cost of intense fighting (Dow et al., 1976; Jakobsson, 1987). However, until recently no empirical studies existed to support this notion. Martel and Dill (1993) found that juvenile coho salmon significantly decreased their aggressive behavior toward their own mirror image when they could smell a bird predator in the water. Evidence has also been presented that escalated fighting behavior could increase predation risk due to decreased vigilance in the willow warbler *Phylloscopus trochilus* and in the South American cichlid fish *Nannacara anomala* (Jakobsson et al., 1995). Males of *N. anomala* also showed reluctance to reescalate to mouth wrestling, a high-intensity behavior, after a sudden introduction of a model predator and changed the performance of the mouth wrestling after the introduction of a model predator (Brick, 1998).

Based on these findings, I make two assumptions about the effect of predation risk. First, I assume that the risk of predation influences the overall cost of obtaining a sample of relative fighting ability. Second, I assume that the animal’s assessment of current risk of predation influences its choice of behavior during agonistic interactions. Even if the cost of predation has never been explicitly acknowledged by game theorists, Maynard Smith (1974: 215) wrote, “the cost of the contest is again measured by the expenditure of energy and any other risks that may be associated with a protracted contest.” Thus, the objective of this study was to determine what effect an increased risk of predation has on the sequential assessment of relative fighting ability between male *N. anomala*. By using the risk of predation to increase the cost of information acquisition, I was also able to test predictions from the sequential assessment game (Enquist and Leimar, 1987; Enquist et al., 1990; Leimar, 1988) of the use of different agonistic behaviors in relation to increased cost of sampling.

Effects of increased risk of predation: predictions and mechanisms

The first prediction, which does not originate from the sequential assessment game per se, is that an increased risk of predation will lead to increased variation in behaviors used and in duration of contests (Table 1, case A). A hypothetical mechanism of increased variation in behaviors when predation risk increases is that animals differ in their assessment of how dangerous it is to fight and use different behaviors according to the assessed risk (Table 1, case A, prediction 1). Still, decreased vigilance during the most escalated behaviors (Brick, 1998; Jakobsson et al., 1995) would make the animals
hesitate to escalate, which leads to longer fighting times (Table 1, case A, prediction 2). The sequential assessment game contains two parameters that can be altered. The parameters are the cost of obtaining a sample of relative fighting ability and the accuracy of the information about relative fighting ability that is transferred during a fight. Increasing the cost of obtaining a sample of relative fighting ability gives two opposite predictions on behavior used and duration of fights: either shorter fights with high-intensity behaviors or longer fights with low-intensity behaviors. The hypothetical mechanism behind shorter fighting times facing an increased risk of predation is that the animals want to minimize the time exposed to predation risk and escalate to the most decisive behaviors to settle the fight as soon as possible (Table 1, case B, predictions 1 and 2).

The hypothetical mechanism of longer fighting times is that animals choose behavior so that the precision increases optimally for a given risk. Thus, to compensate for an increased risk of predation, the animals could decide to use more repetitions of a low-intensity behavior to accumulate more information at a relatively lower risk and thus avoid escalated behaviors. Because the information content in the low-intensity behaviors is limited, the animals have to escalate to settle the fight, but the entire fight would take more time, giving the opposite prediction on fighting times (Table 1, case C, prediction 1 and 2). Increased risk of predation would then push the evolutionary stable switching line toward longer fighting times (Figure 1, case C). From a biological point of view only case C should be considered plausible. Previous studies have shown seriously decreased vigilance during the most escalated behaviors, whereas animals that are engaged in low-intensity agonistic behaviors are able to maintain their vigilance (Brick, 1998; Jakobsson et al., 1995). It is therefore more likely that an increased risk of predation will lead to longer fighting times and an increased use of low-intensity behaviors, rather than fierce fighting.

The second parameter in the model is the accuracy of the information about relative fighting ability transferred during a fight. If the risk of predation decreases the accuracy of the information, the sequential assessment game predicts that additional repetitions of a behavioral element are needed to increase the accuracy, compared to a contest without predation risk. This would lead to longer fighting times (Table 1, case D, predictions 1 and 2). The hypothetical mechanism to a decreased accuracy is that animals may have to divide their attention between the opponent and a potential predator. In fact, this is a special case of optimization of information transfer because increasing the number of repetitions can compensate for less accurate sampling. It was not possible within this study to distinguish between case C and D (Table 1). They are not mutually exclusive.

### METHODS

All tests were carried out between 17 October 1995 and 2 April 1996 at Tovetorp Zoological Research Station in southwestern Sweden. I used males of the South American cichlid fish *P. anomala*. The animals came from a stock of originally 250 animals purchased from a local dealer. When males from the brood started to show secondary sexual characters (approximately 6 months after hatching), I isolated them in holding aquariums (30 × 30 × 30 cm) for at least 2 months before they were used in a test. I fed the fish twice daily on live midge larvae and dry fodder to keep fighting ability, resource value, and the value of the future equal for all contestants. All aquariums contained a substrate of gravel and a flower pot made of clay. The temperature was held constant at 26°C and a 12:12 h light:dark cycle was maintained. The fish weighed between 1 g and 2.5 g. I matched the fish in pairs of equal weight. In 20 out of 27 pairs, the difference

### Table 1

<table>
<thead>
<tr>
<th>Effect of increased predation risk</th>
<th>Predictions</th>
<th>Mechanism</th>
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<tbody>
<tr>
<td>A Increased cost of information acquisition</td>
<td>1. Increased variation in behaviors used</td>
<td>Individual animals differ in their assessment of how costly it is to fight</td>
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<td></td>
<td>2. Longer fights</td>
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<tr>
<td>B Increased cost of information acquisition</td>
<td>1. Faster escalation, less use of low-intensity behaviors</td>
<td>Minimize the time exposed to predation risk</td>
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<td>2. Shorter fights</td>
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<tr>
<td>C Increased cost of information acquisition</td>
<td>1. Increased use of low intensity behaviors</td>
<td>Optimize information acquisition</td>
</tr>
<tr>
<td></td>
<td>2. Longer fights</td>
<td></td>
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<tr>
<td>D Decreased accuracy of information acquisition</td>
<td>1. Increased repetition of low intensity behaviors</td>
<td>Maximize assessment accuracy (special case of optimization)</td>
</tr>
<tr>
<td></td>
<td>2. Longer fights</td>
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![Figure 1](image-url)

A contest lasting 10 steps. The trajectories illustrate how an individual’s estimate of relative fighting ability changes during the contest. When the trajectory crosses the switching line, the animal gives up. The solid line represents an evolutionarily stable switching line for a contest situation without predation risk; the hatched switching line, case C, represents a hypothetical switching line when predation risk increases. In case C the risk of predation is assumed to lead to longer fighting times—the fight continues beyond the tenth step. Elaborated from Enquist and Leimar (1985).
in weight was less than 1%. The weight difference in the remaining seven dyads were 6% in two dyads (1.5 g versus 1.6 g in both dyads), 7% in two dyads (1.4 g versus 1.5 g and 1.3 g versus 1.4 g), 8% in two dyads (1.2 g versus 1.3 g in both dyads), and 9% in one dyad (2.1 g versus 2.3 g). I used each fish only in a single contest.

Nine dyads were not exposed to any predator stimulus and were used as a control group, group 1. To find an appropriate predator stimulus, I used two treatment groups. One treatment group (n = 9) was subjected to a model predator with no facial features except the rude shape of a forepart of a fish. The other treatment group (n = 9) was subjected to a model predator with eyes and an open jaw. Both model predators were grayish and black and measured 15 × 7 × 6 cm (length × height × width) (Brick, 1998). However, the two treatment groups did not differ from each other in any of the investigated variables, and I pooled them in the analyses, group 2. There was no difference in weight asymmetry between the groups (Mann-Whitney U-test; n1 = 9, n2 = 18, U = 70, p = .59), nor was there a difference in absolute weight between the groups (Mann-Whitney U-test; n1 = 9, n2 = 18, U = 279.5, p = .42).

**Fighting behavior of Nannacara anomala**

Fights between males of *N. anomala* start with low-intensity behaviors which are gradually replaced by more dangerous and decisive behaviors (Baerends and Baerends-van Roon, 1950; Jakobsson et al., 1979). The fight is divided into three different phases, each characterized by the use of a new behavioral element: lateral display, tail beating, and mouth wrestling (Enquist and Jakobsson, 1986; Enquist et al., 1990). Bites often occur, and it has been suggested that one fish can bite to force the opponent to escalate (Enquist and Jakobsson, 1986). The fish can also temporarily reverse the fighting sequence throughout the fight (i.e., go from behavior of higher intensity to one of lower intensity). Observations from large tanks suggest that *N. anomala* males try to dominate a territory containing several females. However, males fight even if there are no females in the tank, which suggests that the contested resource is the alpha position (Enquist and Jakobsson, 1986; Enquist et al., 1990).

**Experimental procedure**

Twenty-four hours before a trial started, I moved two fish to the test aquarium (30 × 30 × 30 cm). The test aquarium was divided into two compartments of equal size by an opaque partition. Each compartment contained a box in which each fish could be enclosed 5 min before the test start-

<table>
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<td>Inspection behavior in the visual assessment phase</td>
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<td>Inspection behavior in the tail-beating phase</td>
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<td>Inspection behavior in the mouth-wrestling phase</td>
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**Statistical tests**

Due to the non-normal distribution of the variation in the samples, all tests used are nonparametric. I used the Mann-Whitney U test, Kolmogorov-Smirnov two-sample test, and Spearman rank order correlation. In addition, Gehan’s Wilcoxon test for censored time series data (Statistica 5.1) was used.

**RESULTS**

**General observations**

Twenty-six of 27 dyads started the agonistic interaction with visual assessment and one dyad in group 1 began with tail beating. In group 1 all nine dyads escalated to mouth wrestling within the experimental period (60 min). In group 2, 12 of 18 dyads escalated to mouth wrestling. Three dyads escalated only to tail beating. In two of them, the reciprocal tail beating continued throughout the experimental period. In the remaining dyad, there was only one sequence of tail beat-
Table 3
Time to first agonistic interaction, time to mouth wrestling, and the duration of low-intensity behaviors before mouth wrestling in group 1 and group 2 (s)

<table>
<thead>
<tr>
<th></th>
<th>Group 1</th>
<th></th>
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<th>Group 2</th>
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<th>Mann-Whitney U-test, 1 vs. 2</th>
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<tr>
<td></td>
<td>Median</td>
<td>Range</td>
<td>n</td>
<td>Median</td>
<td>Range</td>
<td>n</td>
<td>U</td>
</tr>
<tr>
<td>First agonistic interaction</td>
<td>29</td>
<td>13–1165</td>
<td>9</td>
<td>75</td>
<td>15–538</td>
<td>18</td>
<td>59</td>
</tr>
<tr>
<td>Time to mouth wrestling</td>
<td>195</td>
<td>67–971</td>
<td>9</td>
<td>1928.5</td>
<td>69–3585</td>
<td>18</td>
<td>28</td>
</tr>
<tr>
<td>Visual assessment</td>
<td>81</td>
<td>0–246</td>
<td>9</td>
<td>72</td>
<td>9–528</td>
<td>18</td>
<td>69.5</td>
</tr>
<tr>
<td>Number of tail beats</td>
<td>35</td>
<td>10–122</td>
<td>9</td>
<td>46</td>
<td>5–173</td>
<td>15</td>
<td>44</td>
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Escalation

A comparison between the groups shows that there was no difference in time until the start of the fight (i.e., until the first reciprocal agonistic behavior; Table 3). However, escalation to mouth wrestling was slower in group 2 (Figure 2). Thus, it took significantly longer for the dyads in group 2 to reach mouth wrestling (Table 3). There was also a significant difference in the distribution of time until mouth wrestling in the two samples (Kolmogorov-Smirnov two-sample test: $n_1 = 9$, $n_2 = 18$, $p < .025$, Figure 3). All the dyads in group 1 had reached mouth wrestling before 30 min, in comparison with only half of the dyads in group 2 (Figure 3). The duration of fights was significantly longer in group 2 compared with group 1 (Gehan’s generalized Wilcoxon test for censored time series: $n_1 = 9$, median = 566 s, range = 295–2542 s, $n_2 = 18$, median = 3329.5 s, range = 194–3585 s, $p = .013$).

Behaviors used

Despite the significant difference between the two groups in time until mouth wrestling and the significant difference in the duration of fights, the duration of active visual and the number of tail beats before the onset of mouth wrestling did not differ significantly between the two groups (Mann-Whitney U-test: $U_{1,2} = 333.5$ for active visual, $U_{1,2} = 309.5$ for number of tail beats, $p > .05$).
Figure 3
Histogram of number of trials reaching mouth wrestling in group 1 (open bars; \(n = 9\)) and in group 2 (filled bars; \(n = 18\)); \(>3600 = \text{censored data}\).

Figure 4
The relationship between the duration of visual assessment and time until mouth wrestling in group 1 (open circles; \(r_s = .52, p = .15, n = 9\)) and in group 2 (filled circles; \(r_s = .75, p = .005, n = 12\)). Note that only complete phases are used in the analysis.

Figure 5
The relationship between the number of tail beats and time until mouth wrestling in group 1 (open circles; \(r_s = .72, p = .03, n = 9\)) and in group 2 (filled circles; \(r_s = .83, p = .00083, n = 12\)). Note that only complete phases are used in the analysis.

not differ between the groups (Table 3). However, the power of these tests was low. There was only a 32% chance of rejecting the null hypothesis at \(\alpha = 0.05\) for the use of visual assessment and a 8% chance to statistically detect a difference between the groups in the use of tail beating. In both groups 1 and 2, there were positive relationships between the use of low-intensity behaviors and time until the initiation of mouth wrestling. However, in group 2 these relationships were more strongly pronounced. This is because several dyads in group 2 used more low-intensity behaviors before the onset of mouth wrestling (Figures 4 and 5).

DISCUSSION
In agreement with case A, prediction 1, increasing the risk of predation significantly increased the variability in the use of different agonistic behaviors. Some dyads in the predation risk treatment used visual assessment and tail beating instead of escalating to mouth wrestling, while other dyads escalated to mouth wrestling like the dyads in the control group. The presentation of the model predator also significantly increased the time it took for the contestants to reach the mouth-wrestling phase and the duration of fights, supporting case A, prediction 2. After 30 min, all the dyads in the control group had reached mouth wrestling, while only half of the dyads had done so in the group subjected to increased risk of predation. A contributing factor to the slower escalation in the predation risk treatment was inspection behavior that occurred mostly during the low-intensity phases.

Because of the increased use of visual assessment and tail beating in some of the dyads in the predator treatment, there was a significant relationship between the use of low-intensity behaviors and time to mouth wrestling across the group. In
the control group, the relationship was less pronounced. As hypothesized in case A, a possible mechanism behind the increased variation in the group subjected to an increased risk of predation may be that individual animals differ in their assessment of how dangerous it is to fight. If both animals assess the danger to be high, they would agree to use only low-intensity behaviors such as visual assessment or tail beating so that they can maintain their vigilance. If the contestants differ in this respect and one of the contestants starts to escalate, it is likely that the other individual must also escalate to avoid getting bitten (Enquist and Jakobsson, 1986). Still, it would probably take a little longer before escalation occurred compared to a dyad were both animals were likely to escalate quickly (Leimar, 1988). If both animals assess the danger to be low, they would agree to escalate in a way similar to the dyads in a control group. If the animal’s boldness (Wilson, 1994) is known in advance and the dyads are put together accordingly, the variation might decrease within a group subjected to an increased risk of predation. This prediction could easily be tested. However, the present study does not make it possible to decide whether the variation indeed originates from differences between individuals in boldness. It could also originate from differences between the animals in their stress tolerance or from some other unknown reason.

As already pointed out in the Introduction, the data do not give any support to case B, predictions 1 and 2, that an increased risk of predation would lead to less use of low-intensity behavior, faster escalation, and shorter fights in order to minimize the time exposed to predation risk. The explanation may be that even though animals may differ in their response to an increased risk of predation, the price for lost mating opportunities in the future would outweigh a smaller gain in fitness due to shorter fights and a minimized time exposed to predation risk. However, there are circumstances when fierce fighting could be expected (Grafen, 1987).

A number of the dyads in the predator treatment group preferred to use low-intensity behaviors, which ultimately led to longer fighting times on average. There are two possible explanations for this. As suggested in case C, animals may optimize information acquisition by the increased use of low-intensity behaviors. Using low-intensity behaviors allows the contestants to monitor the environment. However, the alternative, case D, is also possible. Predation risk could degrade the accuracy of the information, and the contestants could repeat the behaviors to increase the accuracy. However, it is not possible from this experiment to uncover the mechanism. Indeed, the suggested mechanisms are not mutually exclusive, and all the dyads in the group subjected to an increased risk of predation may pay a cost in terms of less accurate information being transferred during the fight. The information available from visual assessment and tail beating is quickly depleted (Enquist et al., 1987), and “sloppy” mouth wrestling may result in decreased accuracy in the information that is transferred. This could ultimately lead to wrong decisions (i.e., the slightly lighter fish winning the contest more often than expected during increased risk of predation). This question deserves further attention.

To conclude, this study shows that an increased risk of predation leads to an increased variability in behaviors used and time until the initiation of the most decisive and dangerous behaviors in fights between male N. anomala. Increased predation risk also leads to longer fighting times on average. In addition, in some of the dyads, increasing the external acquisition costs changed the optimal sequence of information transfer in a way that can be interpreted in terms of the behavioral mechanism suggested by the sequential assessment game. The results indicate that individual differences in boldness contribute to the observed variation in real contests. A more accurate treatment and design of the experimental groups, taking into account individual differences in boldness, may lead to an even better fit between theoretical predictions and empirical data.

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