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Sequential Assessment in Contests among Common Freshwater Goby, *Rhinogobius brunneus* (Pisces, Gobiidae)

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The sequential assessment model describes a fight between two conspecific as an ongoing statistical sampling process, which makes it possible to predict fight length or repetition number of a behavioral element depending on relative RHP (resource holding potential; e.g. weight or fighting ability). We staged contests between males of common freshwater gobies to test some predictions of this model. Fights proceeded in a consistent sequence of phases. Most contests began with two contestants adopting lateral display, and then escalated to intense physical contacts. The length of contests was negatively correlated with weight difference between the contestants. The duration of complete phases was, however, independent of weight, and the prior information gained during complete phases did not appear to affect subsequent phases of the fight. Our results show that the contests of common freshwater gobies are well predicted by the sequential assessment model.

An animal in conflict with another animal over a valuable resource such as territory or mating opportunity may get sole access to the resource and try to displace the opponent. Animal fights are usually settled by relative RHP or the opponents' relative ability to inflict cost on one another (for a review, see Parker, 1974; Huntingford and Turner, 1987; Riechert, 1998). A fight is certainly costly due to high energetic demands and risk of injury or even death (Huntingford and Turner, 1987; Dugatkin and FitzGerald, 1997). Individuals that accurately assess the fighting ability of the opponents before engaging in the potentially costly fights should therefore be at a selective advantage (Maynard Smith and Parker, 1976). Early game theory models, which lacked realistic behavioral details and ignored the acquisition of information during contests, however, could not accurately predict the sequence of behavior seen in contests, or probability of winning or injury as a function of asymmetries.

The sequential assessment model (Enquist and Leimar, 1983, 1987; Leimar and Enquist, 1984; Leimar, 1988; Enquist et al., 1990; Brick, 1999) attempts to do this by introducing plausible behavioral mechanisms into the game theory models. This model describes a fight between conspecifics as an ongoing statistical sampling process, allowing for specific predictions about contest duration and number of repetitions of a behavioral element depending on relative fighting ability. Animals begin a contest with the behavior that provides the most information about the fighting ability at the lowest cost (Enquist et al., 1990). A particular behavior provides only a certain type of information about the asymmetry in fighting ability and a diminishing return of information with each repetition of the behavior. If the conflict cannot be resolved by the information provided by this behavior, it would escalate to the next most cost-effective behavior. Hence, fights should proceed in a consistent sequence of phases, with each phase composed of a particular behavior (or by one or more used at a constant frequency throughout the phase). Contest duration should be inversely related to the asymmetry in fighting ability of the opponents, whereas the duration (or number of repetition) of completed phases of behavior should be independent of the relative fighting ability.

The sequential assessment model has been supported both qualitatively and quantitatively by empirical data (Englund and Olsson, 1990; Leimar et al., 1991; Keeley and Grant, 1993a; Koops and Grant, 1993; Hack, 1997; Brick, 1999), but some variation in contest behavior remains unexplained (Turner and Huntington, 1986; Enquist et al., 1990; see also Koops and Grant, 1993). In fish, however, the novel predictions of the sequential assessment model have been tested only for cichlids (Enquist and Jakobsson, 1986; Enquist et al., 1990; Keeley and Grant, 1993a; Koops and Grant,

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1993; Brick, 1999). Here we investigate agonistic behavior in the common freshwater goby, *Rhinogobius brunneus*, a small and sexually dimorphic freshwater fish that occurs abundantly in rivers of East Asia (Kawanabe and Mizuno, 1989). Mature males establish territories for nesting or feeding and are exceedingly aggressive towards intruders. Similarly, in captivity, mature males readily establish territories and, if their ownership is disputed, a fight rapidly ensues, even when not breeding (personal observations). Fights consist of escalating encounters beginning with a short period of visual signaling (i.e. lateral display) followed by intense physical contacts (mainly composed of biting attempts).

In the present study, we staged contests between pairs of common freshwater goby males that varied in relative weight (larger/smaller) from 1.01 to 1.35 to test the following predictions from the sequential assessment model: (1) contests progress in a consistent sequence of behavioral phases, (2) the duration of contests will be inversely related to weight asymmetry, and (3) the duration of complete phases of behavior will be independent of weight asymmetry. We used body mass (weight ratio) as our estimate of fighting ability, because contests were usually won by the larger fish even when the difference is very small (personal observations).

Materials and Methods

Subjects

The study was conducted from late April to late May, 1999-2000 in the laboratory at Seoul National University of Korea. A total of 108 males (54 pairs) were used in this experiment. They were collected using push-net from Gapyong Stream (North Han River; Gapyong-eup, Gyonggi-do, Republic of Korea; 37°55′N, 127°37′E). We kept them in stock aquaria (> 180 L). The stock aquaria and all laboratory setups had a natural dark:light cycle and daily water temperature was maintained at 21.1±3.21℃. The fish were fed frozen chironomid larvae twice daily. They were held in the laboratory at least for a month before being used in the experiment.

Rhinogobius brunneus is a species complex, which is currently represented by eight types but will be described as distinct species in the near future (Mizuno, 1976; Katoh and Nishida, 1994). The fish we used in our experiment were *R. brunneus* sp. OR, which occurs abundantly in the upstream rivers of Korea.

Observation

We staged contests using experimental aquaria and the procedure similar to the one described by Keeley and Grant (1993a) and Koops and Grant (1993). We divided the experimental aquaria measuring 64×30×45 cm into three compartments by two opaque Plexiglas partitions (A_3; Fig. 1). The two compartments on either end (A_2; home area) of the aquarium measured 24×30×45 cm and contained a ceramic tile (15×15×0.75 cm; A_4) available for shelter (Fig. 1). Individuals of a given pair were placed at home area and were allowed to become accustomed to being fed in their home area for 7 d. Food was delivered once daily at noon through a red plastic tube that was suspended above the aquarium. After the habituation period, the fish were trained for 7 d to feed individually from the central feeding area (A_1; Fig. 1). The partition was lifted for 20 min a day and the fish received all of its food there. The method of delivery was the same as in the home area. At the end of the feeding period we guided the fish back into its home area and repeated the procedure with the second fish in the pair.

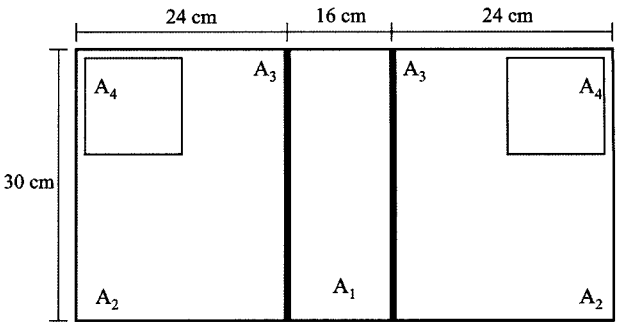

Fig. 1. Design of experimental aquaria used in this study. A_1, central feeding area; A_2, home area; A_3, an opaque Plexiglas partition; A_4, a ceramic tile.

After the training period, we raised both partitions simultaneously at the regular feeding time, and video-filmed the ensuing fight. Fights ended with one fish suddenly fleeing and making no further acts towards the opponent. The loser was also easily distinguished because he turned pale and folded his fins. We returned the contestants to their home areas immediately after one fish had lost the fight.

Four behavior patterns were observed and quantified. In a 'lateral display', the fish erect their fins with the mouth open widely. The two fish usually remain stationary in a parallel position in what appears to be an advertisement of size (Fig. 2). This posture was usually maintained for the entire duration of the contest, although varying in degree. We defined the duration of lateral display as the time from when the fish first interacted to the first biting. A 'bite' was defined as the act of rushing at the opponent with the mouth open and striking it with its mouth. In 'mouth wrestling', the contestants grip each other by the jaws and engage in a push-pull contest in what appears to be a test of strength. Mouth wrestling appears to be the most escalated form of fighting in this species. A 'mutual circling' occurred in just one contest when both individuals rapidly swim in a tight circle, trying to bite at the posterior part of their opponent.

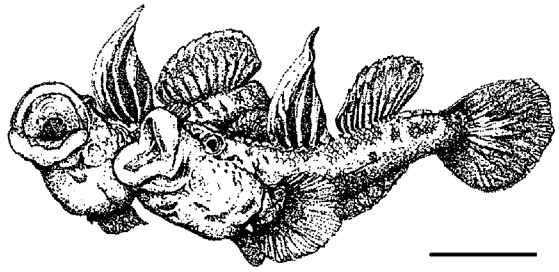

Fig. 2. A typical scene of lateral display in two common freshwater goby males. Scale bar = 2 cm.

Analysis

We used three measures of contest intensity: the cumulative duration of all displays (contest length); the level of escalation of the contest, i.e. the number of different behavioral patterns in the fight (the level of escalation; 0, 1, 2, or 3); and the total number of behavioral acts in the contest. The duration and frequency of all behavior patterns were $\log_e$-transformed. However, some data were significantly non-normal after transformation, so we used primarily nonparametric statistical tests. All tests are two-tailed.

Ethical note

We stopped fights as soon as the loser fish had made the decision to quit, thus preventing further attack from the winner. The degree of escalation observed in this confined laboratory condition was similar to fights observed under semi-natural conditions where the loser could escape and hide, suggesting that this study did not impose abnormally stressful conditions on the animals. None of the aggressive interactions resulted in bloodshed. Biting did not result in visible scale losses, although the males were sometimes slightly scratched. This minor injury did not appear to cause the fish stress and was healed within a week. Prior to the experiment we had decided to remove subordinate males from the stock aquarium if dominant males attacked the subordinates even if he was inactive.

Results

Contests could be divided into three phases, each characterized by the appearance of a particular behavioral element. Initially in a fight the fish changed in color and approached each other with erected dorsal fins. Most contests (50/53 contests) began with the two contestants adopting a lateral display (the first phase; mean duration $\pm$SD = 12.72 $\pm$ 6.30 s). Of the 50 contests 41 escalated to an intense biting period (the second phase; median duration = 109.42 s, range = 8.32 - 689.23 s), with either both males biting (N = 39) or one male biting (N = 2). Mouth wrestling (median duration = 93.32 s, range = 14.44 - 322.72 s) was observed in very long fights (> 142 s; 14/41 contests). The sequence of behavioral elements appeared consistent, and only one exception occurred, when mouth wrestling occurred before any biting.

Table 1. Relative weight (and contest outcome) in relation to the initiation of a behavioral element

Element	Winner*	Loser*	Binomial	Larger†	Smaller†	Binomial
First approach	27	26	NS	24	29	NS
First lateral display	21	29	NS	24	26	NS
First bite	17	24	NS	19	22	NS
Winner	-			46	7	P = 0.01

* The number of contests in which the winner (or loser) first attacks.
† The number of contests in which the larger contestant (or smaller contestant) first attacks.

Larger males defeated smaller males in 86.8% of contests (Table 1). In contests that did not escalate to physical contacts (N = 12), the larger contestant was always the winner. Relative weight did not influence the tendency to display first or to attack first (Table 1). In those contests that escalated to physical contacts, however, eventual winners (or larger males) attempted biting significantly more often than did losers (or smaller males; Table 2).

Contests took longer to resolve when the fish were closely matched for size. The contest duration tended to decrease when the weight asymmetry increased (Spearman's rank correlation: r_s = -0.702, N = 53, P < 0.001), even though it was highly variable when the asymmetry between the contestants was small (Fig. 3a). The level of escalation reached in a fight (0 = aggressive coloration and erected fins; 1 = the first phase; 2 = the second phase; 3 = the third phase) was also negatively correlated with the weight asymmetry (r_s = -0.408, P < 0.01). Similarly, measuring the frequency of biting (r_s = -0.745, P < 0.001; Fig. 3b) yielded negative correlation with the weight ratio.

The weight asymmetry was independent of the duration of complete phases or the number of repetition of behavior during complete phases. The duration of lateral display (the first phase) provided the most powerful test of this prediction, because it was a complete phase in 41 contests, which escalated at least to biting period. The weight ratio was not significantly correlated with the duration of lateral display (r_s = -0.082, P = 0.604). Considering those contests that escalated to mouth wrestling (N = 14), the weight ratio was not negatively correlated with either the duration

Table 2. The number of contests in which the winner (W > L; or larger male: Lg > Sm) performs biting more often than the loser (or smaller male)

Element	W > L	L > W	Binomial	Lg > Sm	Sm > Lg	Binomial
No. Bites	29	12	P < 0.05	32	9	P < 0.01

W: winner, L: loser, Lg: larger male, Sm: smaller male

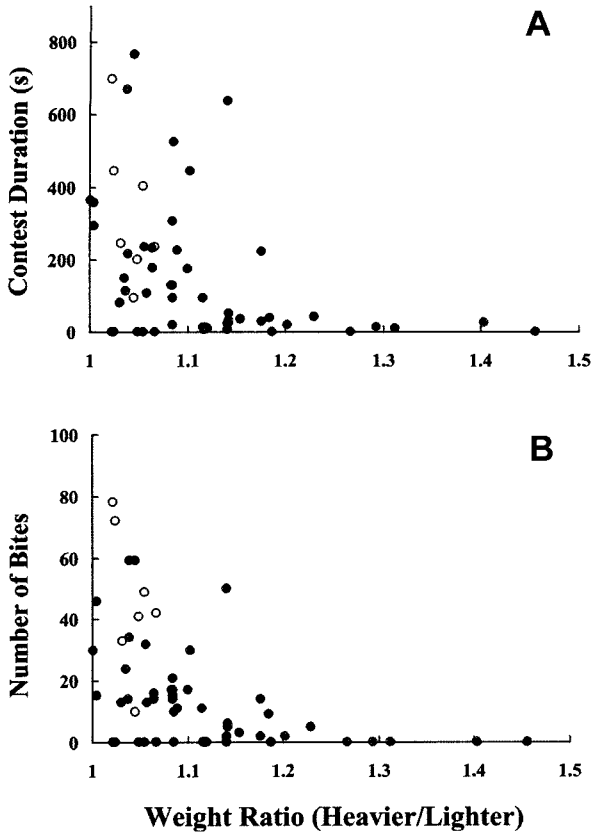

Fig. 3. Contest intensity in relation to weight ratio. A, Contest duration (cumulative duration of all behavior). B, Number of bites. Contests in which the smaller contestant was a winner are indicated by open circles.

of the second phase (r_s = -0.253, P = 0.362) or the number of biting (r_s = -0.194, P = 0.872).

Discussion

Our results are in accordance with several predictions of the sequential assessment model of conflicts. The behavioral sequence was organized into several phases, each characterized by the appearance of a new behavioral element, evenly matched pairs took longer to resolve their contests than unevenly matched pairs, and the duration of complete phases was independent of weight asymmetry. Concerning the probability of winning, the heavier individuals usually win, but in fights with small asymmetry (i.e. relatively long fights), the smaller fish had a chance of winning due to the random errors in the estimate of relative fighting ability.

In some cases the model failed to predict the results. For instance, the weight ratio was significantly and negatively correlated with the duration of contests, but there was still considerable variability between fights. Despite the variation observed between fights, the outcome was largely determined by weight asymmetry, suggesting that high precision of information for the opponent was reached differently in different fights. Instead of focusing on the number of repetitions or duration of a particular behavior, an animal might only be sensitive to the amount of information (Enquist et al., 1990). Some variation will also be due to differences between the contestants in their inherent aggressiveness (see Barlow et al., 1986), in their prior social experience (even though it was minimized during the 14-day training period; e.g. Beacham, 1988; Beaugrand et al., 1991) or in their physiological states, such as energy reserve (e.g. Chellapa and Huntingford, 1989; Neat et al., 1998a), body condition (e.g. Thornhill and Sauer, 1992), age (e.g. Choe, 1994) or reproductive state (Holder et al., 1991; Neat et al., 1998b). Differences in state may produce asymmetries between the contestants in the value of winning a contest (Enquist and Leimar, 1987; Keeley and Grant, 1993b).

Perhaps the most novel prediction of the sequential assessment model is that the duration (or the number of repetitions) of complete phases of behavior will be independent of relative RHP. The duration of lateral display in our study strongly supported this prediction. Nevertheless, the correlation coefficients were slightly negative, indicating that the estimates of relative fighting ability by contestants during visual interaction (e.g. lateral display) had some influence on the choice of next most cost-effective behavior. The posture of lateral display was usually maintained for the entire duration of all contests. In longer contests, more information from the lateral displays was accumulated, even after the fight had escalated to biting or mouth wrestling.

Whether or not information is available during a fight to allow the contestants to predict the eventual winner has generated controversy (see Barlow et al., 1986; Frank and Ribowski, 1989 for a review). A growing number of studies suggest that the winners either attack first or display at a higher rate than the losers (Dow et al., 1976; Clutton-Brock and Albon, 1979; Jakobsson et al., 1979; Figler and Einhorn, 1983; Barlow et al., 1986; Turner and Huntingford, 1986; Keeley and Grant, 1993a, b). In our study, however, many losers (smaller males) attacked first, even when the fights continued well beyond the first bite. The winners attempted biting more often than the losers. In other fishes, such as *Nanacara anomala* (Jakobsson et al., 1979), *Haplochromis burtoni* (Mosler, 1985) and *Xyphophorus helleri* (Franck and Ribowski, 1989), predicting the winner was possible only in late stages of the fight. In fact, since the first attack can be viewed as an indication of willingness to escalate but not of fighting ability, it may only predict the winners of fights between individuals of similar fighting ability (see Barlow et al., 1986) but not between unequal opponents (e.g. Dugatkin and Biederman, 1991; Dugatkin and Ohlsen, 1990). In fights with small asymmetry, the smaller fish with a perceived low RHP during the visual interactions had a chance to obtain more

information about asymmetry in other components during the more escalated phase. On the other hand, it could be that the contestants, assessing themselves being relatively weak or small during the visual interaction, tried to conceal this fact (see Franck and Ribowski, 1989 for a review).

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