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Audience effect is context dependent in Siamese fighting fish, *Betta splendens*

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Investigations of communication networks in animals have focused primarily on determining whether animals extract information from peripheral contests (eavesdropping) or respond to the presence of bystanders (audience effect). The possibility that an animal's response to being watched might be context dependent, however, has been explored in far less detail. This study investigated the influence of two contexts, exposure to audiences of different sexes and presence or absence of a nest, on the aggressive behavior of interacting male Siamese fighting fish, *Betta splendens*. Males interacted in the presence (male, female) or absence of an audience in three different nest conditions (0, 1, or 2 nests). Audience sex and territorial status influenced aggressive behavior in the interacting males, but a strong audience × nest interaction also was uncovered. Males were more aggressive when neither male had a nest and a male audience was present than when a female or no audience was present. Males also were more aggressive when only one male had a nest and a male audience was present than when a female or no audience was present. When both males had nests and a male audience was present, however, males were less aggressive than when only one male or neither male had a nest. In sum, aggressive behavior was influenced by the interaction between audience and nest; neither nest nor audience alone was sufficient to explain the results. Male Siamese fighting fish alter their behavior based on both external cues, the sex of the audience, and internal cues, reproductive state and resource possession. Our results emphasize the importance of considering aspects of an animal's environment when examining audience effects and communication networks in general. *Key words:* aggression, audience effects, *Betta splendens*, communication networks. *[Behav Ecol 16:1025–1030 (2005)]*

There has been a growing trend to examine interactions in the context of communication networks that consist of many individuals rather than isolated pairs of signaling animals. Individuals outside of the interacting pair can either directly or indirectly influence another individual's behavior and are known as eavesdroppers or bystanders (McGregor and Dabelsteen, 1996). Information gained by eavesdropping can include the quality of a prospective mate or fighting ability of a future opponent and can be extracted without much risk or effort on the part of the eavesdropper (e.g., Johnsson and Akerman, 1998; McGregor, 1993; Mennill et al., 2003). Through this process, an audience can exert selective pressure on the evolution of communication signals. Signals could become more discrete to prevent eavesdropping. Alternatively, the presence of eavesdroppers might increase the prominence of behaviors that can be directed at both the intended receiver and any bystanders, thus serving a dual function. Because both female and male eavesdroppers use the information gained by observing male-male interactions (e.g., Doutrelant et al., 2001; Oliveira et al., 1998), the interactants themselves may benefit from altering their behavior when watched, a phenomenon known as an audience effect (Zajonc, 1965).

Audience effects have recently received much attention in a range of taxa (e.g., Dzieweczynski and Rowland, 2004; Evans and Marler, 1984; Striedter et al., 2003; Wich and Sterck, 2003; Zajonc, 1965). Because information can be conveyed to bystanders and used in later interactions, an audience could exert selective pressure on interaction dynamics by shaping the frequency and duration of certain behaviors (Matos and Schlupp, 2005). Special attention has been paid to how an audience affects male-male interactions in *Betta*. Doutrelant et al. (2001) found that opponents modify their behavior (e.g., increased tail beats and decreased bites) only in the presence of a female audience, while Matos and McGregor (2002) found that opponents respond to the presence of a male audience (e.g., increased bites).

Betta splendens is an ideal species in which to study audience effects because the aggressive behavior of males is both stereotypic and conspicuous and lends itself to eavesdropping by both male and female audiences (e.g., Bronstein, 1985; Doutrelant and McGregor, 2000; McGregor et al., 2001; Oliveira et al., 1998). Furthermore, aggressive interactions are honest indicators of male condition and motivation (Halperin et al., 1998). Studies reveal that the same behavior patterns, such as pelvic fin flickering and tail beating, are used in male-male interactions and male-female interactions but may differ in frequency and intensity (Simpson, 1968). Thus, it is not surprising that the sex of the onlooker alters the type and intensity of specific behaviors performed by the interactants.

During the breeding season, male Siamese fighting fish establish and defend territories centered around a bubble nest. The nest is built by the male and serves as a home for eggs and recently hatched fry and may be used to entice females to spawn (Simpson, 1968). Male *Betta* defend territories and may nest in close proximity to one another; thus, the nature of their interactions may depend on whether they possess nests and whether they are being watched. Doutrelant and McGregor (2000) recognized the possibility that the size of the male's bubble nest could influence a female bystander's mate choice decisions, but they did not examine whether males with nests behaved differently than males without nests.

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The investment of male *Betta* in the nest-building process could have a considerable impact on a male's perception of the payoffs associated with aggressive interactions, particularly because only males with nests can successfully court females and spawn. The presence of a nest also likely indicates territorial status and, irrespective of the degree to which the male has invested, could alter aggressive motivation in male *Betta* (Bronstein, 1982). Often the dynamics of aggressive contests change considerably with the value of the contested resource or with asymmetries in ownership, whether the differences are actual or perceived (e.g., Austad, 1983; Dugatkin and Biederman, 1991; Parker and Rubenstein, 1981; Silbaugh and Ewald, 1987; but see Keeley and Grant, 1993). For instance, the duration of wrestling bouts in red-spotted newts, *Notophthalmus viridenscens*, varies linearly with the reproductive value of the contested female (Verrell, 1986). Despite the potential benefits to male nest owners (e.g., siring and protecting offspring) and the possibility that differences in investment or motivation, which arise from having a nest, could mediate changes in aggressive behavior by altering the perceived costs and benefits of fighting, the effect of nest presence on males' response to an audience has not yet been experimentally addressed.

The primary objective of this study was to determine how the presence or sex of an audience and territorial status interact to influence male-male contest dynamics in *B. splendens*. Numerous studies have shown that the context in which a signal is produced and the territorial or reproductive states of the individuals involved in an interaction have effects on communication in signaler-receiver dyads (e.g., Uetz and Roberts, 2002), but we are not aware of any studies that examine this prediction in a network setting. Males with nests potentially have incentive to transmit different information to receivers than males without nests. For example, they might want to direct more courtship-like behaviors to a female audience or increase their aggression toward another male who is both a potential territory usurper and courtship rival. Territorial status and audiences are both known to affect aggressive behavior in a wide variety of species (e.g., Leiser et al., 2004; Schuett, 1997). Such territory acquisition and status often elicits changes in circulating or brain hormone levels, many of which have been linked to aggression (e.g., Burmeister and Wilczynski, 2000; Davis and Fernald, 1990; Elofsson et al., 2000). Hormones, in turn, might influence a male's perception of the costs and benefits of aggressive encounters as well as alter his motivation (e.g., Cardwell and Liley, 1991). Being watched interact might elicit relevant neuroendocrine changes as well. Based on this body of literature, we predict that the highest levels of aggression will be found in males that are territorial holders and interact in the presence of a male audience. We expect the least aggression from males that have nests and interact in the presence of a female audience because these males may be in more of a reproductive rather than aggressive state. By examining the relative territorial status of the two opponents (neither, both, or one male possesses a nest) and the social context in which they interact (male, female, or no audience), we were able to investigate (1) whether the type of audience (male competitors or potential mates) elicits predictable changes in the aggressive behavior of males with similar territorial status and (2) whether territorial status, and asymmetries in territorial status, can explain variation in the aggressive behavior of males exposed to similar audience conditions.

MATERIALS AND METHODS

Subjects and setup

Male and female Siamese fighting fish were obtained from a commercial distributor in Indianapolis, Indiana, USA, in May 2003. Each fish was measured for standard length (distance between the mouth and the base of the tail) and weighed (g) before being placed into a small opaque container (500 ml) to prevent subjects from seeing each other when not being tested. Subjects were kept at 24.4°C on a 16:8 h photoperiod and were fed Tetra Min Betta Bits.

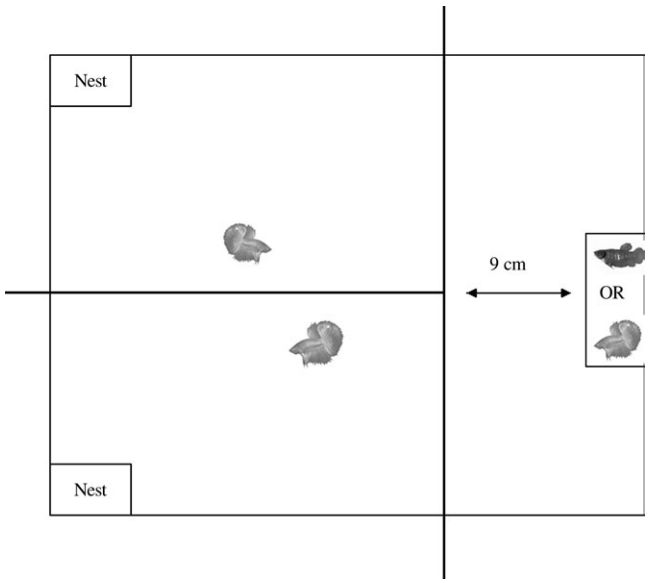

Figure 1
Diagram of experimental setup.

Prior to testing, we removed males from their isolation containers and placed them into individual 9.5-l tanks (15 × 31 × 21 cm). Each tank was equipped with a plastic plant for refuge and a 7.6 × 7.6 cm (58 cm^2) square of plastic bubble wrap placed on the surface of the water in one corner of the test tank; bubble wrap facilitates nest building (Granquist R, personal communication). The bubble wrap was always placed in the back left quadrant farthest away from the audience tank. Males were placed into adjacent tanks to form interacting pairs of matching color and size. We placed an opaque partition between the adjacent tanks to prevent the males from seeing each other before a trial began. These "interactant" tanks were placed beside another tank (15 × 31 × 21 cm) that held an audience (Figure 1). We confined the audience in a small transparent container (15 × 5 cm) within this tank, located 9 cm away from the interactants, to ensure that the distance between the subjects and the audience was constant both within and across trials. An opaque partition also prevented the interactants from viewing the audience before testing. Males resided in these test tanks for at least 24 h prior to testing for acclimation.

Testing procedure

To determine whether the presence of a nest influences the audience effect, we tested males under three different audience conditions: male, female, and no audience. Within these conditions, we created three subtreatments: neither male had a nest, one male had a nest, and both males had nests. We did not artificially manipulate the presence or absence of a nest but rather tested males based on their nesting status in relation to their partner's at the end of the 24-h period. We conducted 10 replicates (i.e., 10 pairs for each treatment) for each of these nine treatments for a total of 90 trials. A total of 180 males were used as subjects; an additional 30 females and 30 males were used as audience fish. Males that were used

as subjects were never used as audience fish and vice versa. All subjects were tested only once. The order of the treatments was randomized to prevent order effects.

Five minutes before a trial, the opaque partition that separated the subjects from the audience fish was removed, and they were allowed to see the audience tank or the empty (control) tank for 5 min. After this 5-min pre-exposure period, the partition between the two opponent tanks was removed, and the paired opponents were allowed to interact for 20 min. We chose 20 min rather than 10 min for interaction, as was used in prior studies, because oftentimes males did not immediately notice the presence of another male. Twenty minutes gave subjects ample time to interact but was not long enough for a loser to be determined. We recorded the trials by filming from above the tanks so that the behavior of all three fish could be observed simultaneously. Behaviors were scored using the Event Recorder software program designed by James Ha. This software program records both discrete events and durational measurements and stores them for later analysis. For each subject, four focal behaviors were measured: time spent within one body length of the opponent's tank (s), time spent flaring gills (s), number of tail beats directed toward opponent, and number of bites directed toward opponent. We also recorded the latency to the first aggressive behavior, time spent within one body length of the audience tank and any behavior directed at the audience (gill flaring, tail beats, and bites when oriented toward the audience), and the time spent at the nest. Gill flaring, tail beats, and bites were considered to be directed to the audience when the subject was within one body length of the audience and orienting head-on or broadside with respect to the audience.

Statistical analysis

To reduce the number of variables tested, we performed principal component analysis (PCA) on the following behaviors: time spent within one body length of opponent, time spent gill flaring at opponent, tail beats to opponent, bites to opponent, time spent within one body length of audience, time spent gill flaring at audience, tail beats to audience, bites to audience, and time spent at nest. We employed varimax rotation to obtain higher resolution. PCA compressed the behavioral data into three components (Table 1). The first principal component (PC1; eigenvalue = 2.78), with high loadings on opponent-directed behaviors, the second principal component (PC2; eigenvalue = 1.07), comprised predominately of time spent by audience, and the third component (PC3; eigenvalue = 1.47), comprised predominately of audience-directed behaviors, were retained for analysis and explained 76.68% of the total variation.

Table 1

Principal component matrices and percent variance explained for PCA on the contest behavioral scores

Behavior	Opponent (PC1)	Time by audience (PC2)	Audience-directed behaviors (PC3)
Time by opponent	0.666	0.574	0.020
Time gill flaring	0.534	0.489	−0.011
Tail beats	0.878	−0.053	0.184
Bites	0.844	0.136	0.113
Latency	−0.360	−0.086	−0.134
Time by audience	0.064	0.842	−0.016
Time at nest	0.052	0.478	0.360
Gill flaring to audience	0.145	−0.063	0.912
Tail beats to audience	0.275	0.043	0.816
Bites to audience	0.014	0.055	0.877
Percent variance explained	45.55	17.91	13.53

Because opponents represent nonindependent pairs and because the scores of the two opponents were significantly correlated (Pearson correlation: $r = .419$, $p < .001$, $N = 90$ pairs), we chose to average the behavior of the males in a pair and conduct statistical analyses on these averages. Analysis of variance was then used to assess the effects of different types of audience (female, male, none) and different nesting conditions (neither, one, both males have nests) on behavior (values for PC1, PC2, and PC3). Body size asymmetry between the contestants was also used as a variable in the analysis but had no effect on behavior (PC1: $F_{2,89} = 0.596$, $p = .992$; PC2: $F_{2,89} = 0.829$, $p = .811$; PC3: $F_{2,89} = 0.580$, $p = .994$). PCA scores were normally distributed, and variation across treatments was homogeneous. Post hoc Holm-Sidak tests were conducted for any significant treatment effects. All tests were performed using SPSS and SigmaStat.

RESULTS

Treatment effects on contest behavior

Male contest behavior (PC1) was influenced both by the type of audience present ($F_{2,89} = 5.382$, $p = .005$) and nesting condition ($F_{2,89} > 5.747$, $p = .004$). These factors cannot be interpreted separately, however, because a significant audience × nest interaction was found ($F_{4,89} = 3.474$, $p = .009$; Figure 2). With a male audience, contestants were less aggressive when both had nests than when only one male or neither male had a nest (Holm-Sidak: $t \geq 3.876$, $N = 10$, $p \leq .001$; Figure 2). However, when only one male had a nest, males were more aggressive in the presence of a male audience ($t = 3.617$, $N = 10$, $p < .001$) or a female audience ($t = 2.476$, $N = 10$, $p = .014$) than when no audience was present. Males were also more aggressive when neither male had a nest and a male audience was present compared to when a female audience

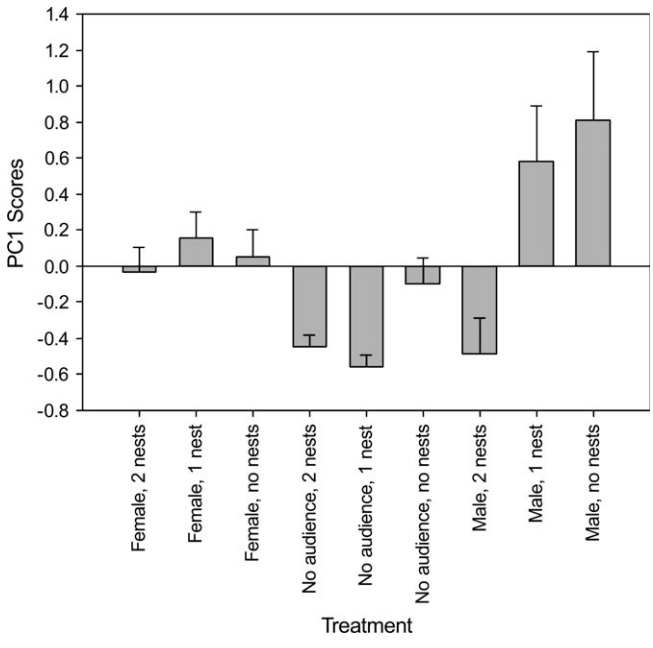

Figure 2
Differences between treatments with respect to PC1 score (aggressive behavior). Error bars are ±1 SEM.

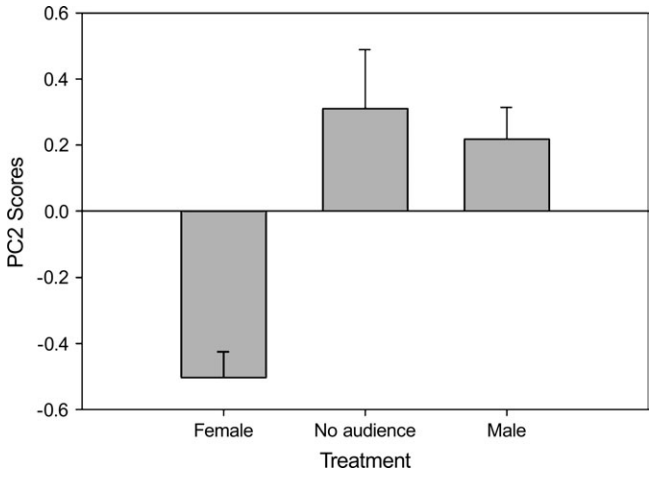

Figure 3
Differences between treatments with respect to PC2 score (time by audience). Error bars are ±1 SEM.

was present ($t = 1.953$, $N = 10$, $p = .025$) or no audience was present ($t = 2.322$, $N = 10$, $p = .021$). Within the two-nest condition, males were more aggressive when a female audience was present than when a male audience was present ($t = 2.137$, $N = 10$, $p = .034$).

Treatment effects on audience-directed behavior

The time that males spent near the audience (PC2) was influenced by the type of audience that was present ($F_{2,89} = 14.167$, $p = .001$; Figure 3) but not by nesting condition ($F_{2,89} = 0.644$, $p = .526$) or an audience × nest interaction ($F_{4,89} = 0.437$, $p = .782$). Males spent more time near a male audience or no audience than when there was a female audience present (Holm-Sidak: $t \geq 3.840$, $p \leq .001$), regardless of nesting condition (Figure 3). The aggressive behavior subjects directed toward the audience (PC3) was not influenced by the sex of the audience ($F_{1,89} = 0.790$, $p = .221$), nesting condition ($F_{2,89} = 0.762$, $p = .058$), or an interaction between the two factors ($F_{2,89} = 0.537$, $p = .053$). It is important to note that a male directed behaviors toward the audience only after the opponent had been unresponsive for a number of minutes, indicating that the male may switch receivers when the initial receiver ceases to react. Lack of interaction with the audience during the beginning phases of the focal contest also ensures that changes in opponent behavior across treatments can be attributed to the effects of audience presence, rather than direct interactions with the audience.

DISCUSSION

The results of this study add a new dimension to communication networks by examining the effects of audience and territorial status on aggressive behavior during contests. The data show that audience effects are context dependent in *B. splendens*. It is not the presence or absence of a nest or the sex of the audience alone but rather the interaction between these two factors that causes males to differ in aggression during male-male interactions.

When both males in a pair have nests, we see a reduction in aggression. The presence of a male's nest has already been determined to serve as an indicator of territory and may even reflect dominance (Bronstein, 1982). A nest, therefore, may reflect a male's territory-holding status as well as his motivation. Many investigations have isolated the effects of territorial status, opponent identity, or audience sex on the aggressive behavior of *Betta* males (e.g., Jaroensutasinee M and Jaroensutasinee K, 2003; Matos and McGregor, 2002). In most cases, males modulate their behavior in a context-dependent fashion, suggesting that aggression in this species is sensitive to a range of changes in individual and/or social milieu. These changes in the motivation to fight may be linked to changes in breeding condition, and similar changes have been found in Siamese fighting fish. For instance, *Betta* males exhibit varying degrees of aggression depending on whether an intruder is another male or a female; aggression is also influenced by the presence of eggs or newly hatched fry (Jaroensutasinee M and Jaroensutasinee K, 2003) and depending on territorial status (Bronstein, 1982). Our study provides further support for aggression in *Betta* males being strongly context dependent and revealed, perhaps not surprisingly, that interactions between the sex of an audience and the territorial status of the focal males uniquely modify aggressive behavior.

We found the strongest effect of audience presence when the audience is male. Males were most aggressive toward their opponent in the presence of a male audience when neither or only one male had a nest. This result is in general agreement with that of Matos and McGregor (2002) who showed increased biting frequency and decreased latency to bite in the presence of a male audience relative to female or no audience, but contrary to Doutrelant et al. (2001) who showed no effect of male audience. Proximity to the male audience appears to have a substantial influence on the aggressive behavior of the contestants. In our study, the male audience was placed at an intermediate distance (9 cm) relative to previous studies (Doutrelant et al., 2001: 12.5 cm; Matos and McGregor, 2002: 7 cm). As the distance between two interacting male Siamese fighting fish increases the interactants become less responsive (Bronstein, 1983), which may account for different responses to the male audience in the two studies. Thus, there appears to be a threshold distance (>9 cm) above which contestants fail to respond to the male audience. Although very little is known about the spacing of male *Betta* territories in nature, this threshold distance could reflect nearest-neighbor distances or a zone of increased nest defense.

Interestingly, the presence or absence of a nest had a lesser effect on males' behavior in the presence of a female audience. Perhaps a trade-off between being aggressive and being successful at attracting a female exists. If this is true, the pressure imposed by female audiences (e.g., be less aggressive so as to not deter mates; Ophir and Galef, 2003) may be so strong that, regardless of nesting condition, males fail to respond aggressively. Males in our two-nest condition, however, were most aggressive in the presence of a female audience, which may indicate that this is not the case. One explanation for the increase in aggression in the presence of a female audience is that both nest holders are capable of mating and thus act increasingly aggressively in order to expel the rival from the area and gain an uninterrupted mating opportunity with the available female.

The type of effect an audience had was associated with territorial status. When neither male in a pair had a nest, the presence of a male audience had the strongest effect. When only one male had a nest, both types of audiences elicited similar effects. Finally, when both males had nests, the presence of the female audience seemed to have the biggest impact. We found that contestants are less aggressive in the presence of a male audience when both opponents have nests compared to when neither or only one opponent has a nest. The concealment hypothesis, proposed by Grinnell and McComb (2001), states that individuals may choose to conceal

their presence from male bystanders when it is beneficial. Territorial male three-spined stickleback, a species in which males build nests and tend fry like *Betta*, conceal their courtship of a dummy female when a rival is present (Dzieweczynski and Rowland, 2004). By reducing aggression toward neighboring nest owners, male *Betta* might avoid the risk of attracting nearby intruding males who could pose a threat to their territory or nest.

Our findings, however, do not support the hypothesis that males in the two-nest condition reduce their aggression as a means of concealing their presence or status from the observer male. Instead, because aggression levels exhibited by males in the two-nest, male audience condition are similar to those exhibited in the two-nest, no-audience condition, this might reflect baseline levels of contest aggression. Thus, a more parsimonious explanation is that males increase their aggression in the no-nest and one-nest conditions. When there are two males (an intruder and a bystander) present and a male does not have a territory, he must compete with both these males to establish a territory. Therefore, contestants might be more willing to escalate rapidly so as to deter both the rival and the audience. Although male *Betta* eavesdroppers are more likely to challenge an observed loser (Oliveira et al., 1998), the likelihood of them doing so might be influenced by the intensity of the watched contest. For example, if eavesdroppers avoid losers that escalated the observed contest, as is the case in green swordtail fish (Earley and Dugatkin, 2002), then increasing aggression in the presence of a male audience when males are competing for territories could be a beneficial strategy.

Recent work on communication networks has made a strong case for examining social interactions in the context of a broader social environment. This social environment includes eavesdroppers that may have substantial effects on immediate behavior, as was demonstrated in this study, or even signaler-receiver evolution (McGregor and Dabelsteen, 1996). Selection should favor plasticity in behavioral responsiveness in individuals, especially in social interactions. This plasticity allows an individual to alter its behavior based on the costs and benefits of a particular situation, such as a predator adjusting its attack behavior to maximize prey capture. Audiences may constitute a major factor that causes signalers and receivers to adjust the perceived costs and benefits of an aggressive interaction and thus their behavior during the interaction. Therefore, selection would favor individuals that are attentive to their social environment and are capable of altering their behavioral responses in a way that maximizes the cost-benefit ratio for an interaction. Our study expands on the current literature by integrating influences from the social environment, the audience, with an additional factor, defendable resources, known to influence aggressive motivation (Elwood et al., 1998).

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