

observed changes in dopamine levels are more likely to be consequence, rather than a cause, of the ovulatory process. The increase in dopamine levels may be caused by PMS-induced increase of estrogen secretion<sup>17</sup>, since estrogen in ovariectomized female rats has been shown to increase dopamine levels in the median eminence and the olfactory tubercle<sup>18</sup>.

- 1 This work was supported by a grant from the United States National Aeronautics and Space Administration (NSG 2183).
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0014-4754/83/020215-03\$1.50 0.20/0  
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## The aggressive behavior repertoire of an anophthalmic phreatic fish from Somalia<sup>1</sup>

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**Summary.** The authors complete the aggressive behavior repertoire of *Uegitglanis*, and refine the description of some patterns. The temporal sequence of various patterns is also shown. The biological significance of some patterns and of the persistence of a complex aggressive behavior in this highly regressed hypogean species is briefly discussed.

Until recently, aggressive behavior in blind fish dwelling in subterranean habitats (water-bearing layers and karstic systems) or in coastal anfractuosités, was known only in *Amblyopsis spelaea* De Kay<sup>2</sup>, *Typhlogobius californiensis* Steindachner<sup>3</sup> and *Caecobarbus geertsi* Boulenger<sup>4,5</sup>. Then similar behavior was recorded both in the laboratory and in the field in *Uegitglanis zammaranoi* Gianferrari (Clariidae, Siluriformes), an anophthalmic phreatic fish from Somalia<sup>6</sup>. In further laboratory experiments, 10 specimens of *Uegitglanis* raised for a long period in complete isolation were tested in pairs in a neutral aquarium (i.e., new to both fish) and then in the home aquarium of each partner. These tests revealed not only the complexity of their aggressive behavior, but also that it leads to the rapid – and evident – establishment of a dominance hierarchy between the 2 components of each pair<sup>7</sup>. Further analysis of our edited and unedited data (totalling 632 min of observation) has enabled us to refine and complete our catalogue of the aggressive behavior of *Uegitglanis*, and to pinpoint the

behavioral sequences leading up to each aggressive display. The present paper reports these latest findings.

**Behavioral repertoire.** Listed below are the behavioral patterns observed with varying frequency in all the fish pairs.

1. Bottom dive: swift dive at an angle of 45° to the bottom of the aquarium, instantly after release in the test aquarium.
2. Jerking: repeated short forward-and-backward jerks along the antero-posterior axis.
3. Zig-zagging: swift right-left oscillations on a horizontal plane of the anterior part of the body.
4. Pitching: swift forward movement along a sinusoidal path on a vertical plane.
5. Speed increase: abrupt increase in swimming speed prior to chases and attacks, or as part of exploratory activity.
6. Patrolling: tenacious inspection of the aquarium floor, usually along the perimeter, sometimes crossing the floor diagonally.
7. Bottom brushing: swift lateral movements of the anterior

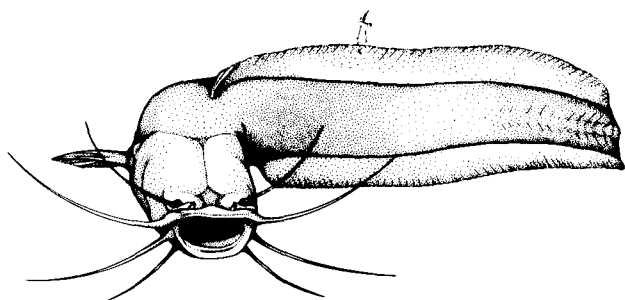


Figure 1. Gaping. Redrawn from a video-tape sequence.

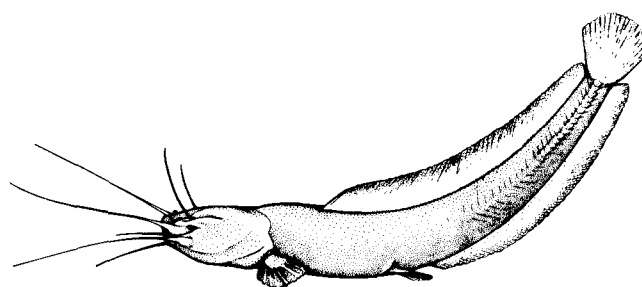


Figure 2. Back-bending. Redrawn from a video-tape sequence.

part of the body – usually inclined at an angle of about 45° to the bottom of the aquarium – rubbing the snout and whiskers along the floor. Recorded both during pauses between encounters and before the first contact between the fish.

8. Wall brushing: wide lateral movements of the anterior part of the body, held horizontally, rubbing the mouth and whiskers against the aquarium wall.

9. Snout shove: blow with the anterior part of the head, sometimes with the mouth open, usually on the side of the opponent's head.

10. Head shove: single or repeated blows with the lateral part of the head on the medio-anterior lateral part of the opponent's body, usually inflicted when the two fish are swimming side-by-side.

11. Lateral shove: thrust of varying strength and duration inflicted with the entire body when the fish are swimming side-by-side, sometimes reciprocal and often accompanied by head shoves.

12. Ventral shove: thrust from underneath the opponent's

abdomen, often inflicted with the head, which attempts to push the top fish away from the lower levels.

13. Nip: rapid, weak, often multiple bites over the entire body which do not cause any apparent damage to the recipient.

14. Bite: strong bite of varying duration, usually on the fins but elsewhere as well.

15. Reciprocal biting: the partners bite each other, often at length, on the fins and elsewhere.

16. Mouth-locking: prolonged (over 150 min) reciprocal bites on the mouth with one fish grasped by its mandible and the other by its maxillary, or else both fish grasped by the maxillary in which case one of the pair is rotated 180° along a longitudinal axis with respect to its partner.

One of the pair is often pushed backwards during this display.

17. Gaping: an opening of the mouth as wide as possible, usually after a fight or random contact but sometimes coupled with chasing and patrolling if the fish is particularly excited (fig. 1).

18. Gasping: rapid, pronounced, rhythmic opening of the mouth and operculum with the fish resting on the aquarium floor, usually after prolonged, intense fighting.

19. Chasing: rapid pursuit of one fish by the other, with the pursuing fish often attempting to bite the tail of the fleeing

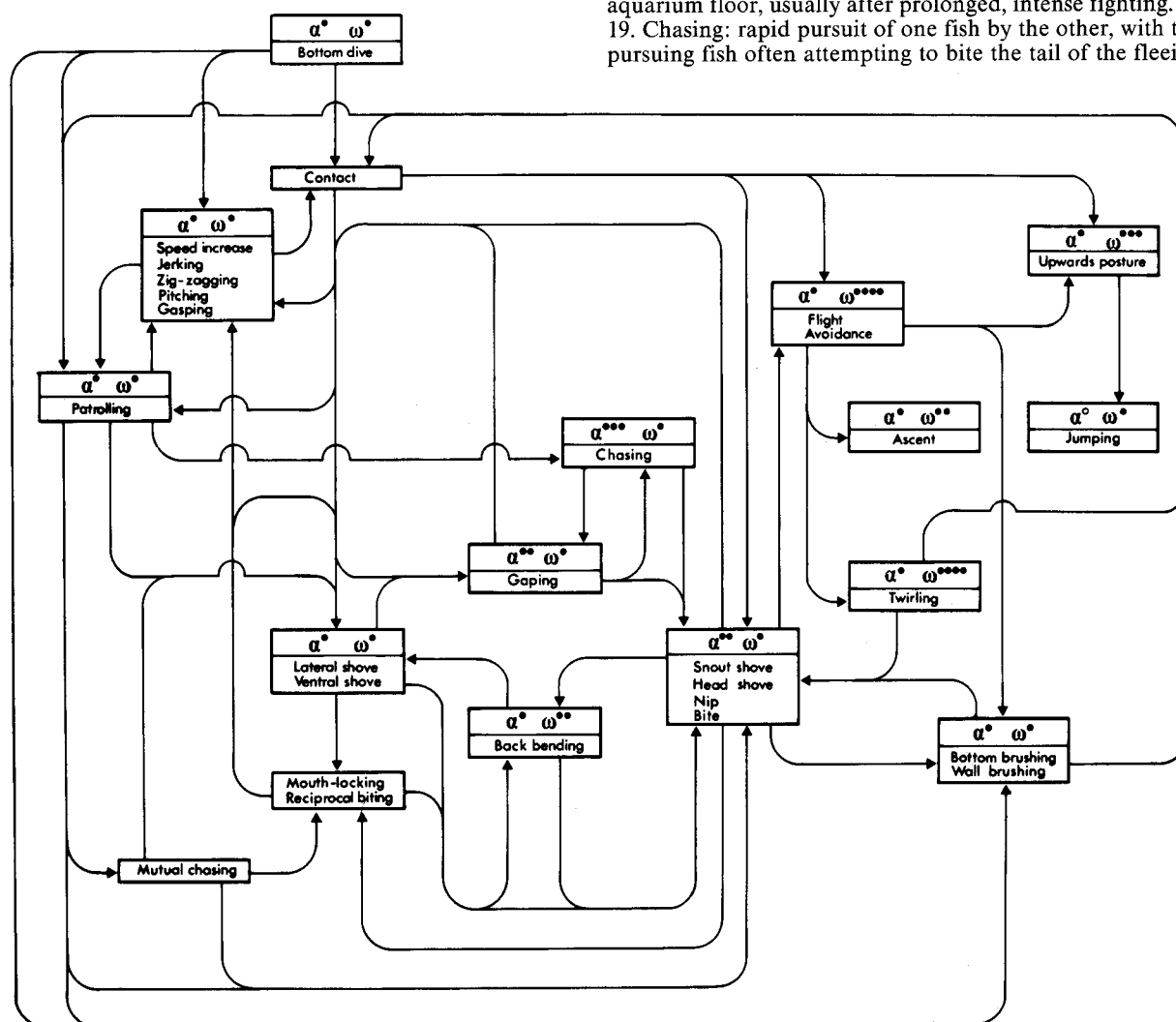


Figure 3. Diagram of the aggressive behavior. Shown are all the behavior patterns observed during testing. The ratio-value 'r' between the relative frequency of the patterns shown by both the dominant (a) and subordinate (ω) partner is indicated above the squares by black circles which have the following equivalents:

$(a, \omega)$  ●●●●●     $(\omega, a)$  ●     $1 \leq r < 2$      $(a, \omega)$  ●●●●●     $(\omega, a)$  ●●●●●     $5 \leq r < 10$   
 $(a, \omega)$  ●●●●●     $(\omega, a)$  ●●●●●     $2 \leq r < 5$      $(a, \omega)$  ●●●●●     $(\omega, a)$  ●●●●●     $10 \leq r$

The partner never showing the pattern mentioned is indicated by a white circle. Squares with no symbols refer to absolutely reciprocal patterns ( $r = 1$ ).

specimen. This behavior begins with a sudden increase in speed of the pursuant fish and appears after either aggressive or random contact, or when the presence of the opponent is clearly felt.

20. Mutual chasing: rapid revolutions on the aquarium floor with each fish trying to bite the other's tail fin.

21. Flight: retreat initiating with an abrupt increase in speed of the fleeing fish, after an attack or random contact.

22. Avoidance: displacement away from the opponent, varying from a swerve to a reversal of direction without pursuit by the other fish.

23. Twirling: the fish swims along a wall of the aquarium in an elliptical trajectory, with the major axis of the ellipse usually vertical. Contact with the wall is maintained with the belly during ascent and with the back during descent.

24. Ascent: rise from the bottom of the aquarium to the upper levels, usually in connection with flight and/or avoidance, less frequently with pursuit.

25. Back-bending: the fish lies immobile with the antero-ventral part of its body in contact with the aquarium floor and the remainder arched so that the caudal axis is often vertical. This is usually seen during pauses between particularly prolonged and violent encounters (fig. 2).

26. Upwards posture: prolonged pause in a vertical position, with the head towards the water surface and the belly touching the aquarium wall. The fish maintains this position by slow movements of its tail, occasionally sinking passively to the floor where it remains briefly immobile with the tip of its tail touching the bottom.

27. Jumping: repeated attempts to jump out of the aquarium, sometimes as a sequel to upwards posture.

Of the above patterns all but three (23, 26 and 27) were shown – with varying frequency – by both the  $\alpha$  and  $\omega$  of each pair, and thus can be defined as 'common' displays whose appearance could be related to the onset of aggressivity rather than to the attainment of a dominant or subordinate status. Instead, twirling (23), upwards posture (26) and jumping (27) were shown almost exclusively (23, 26) or exclusively (27) by the  $\omega$ . This, plus the fact that they were the sequel to avoidance or flight rather than to strictly aggressive events, probably indicates that these are typical of a subordinate status.

Of particular interest are the patterns of gaping (17) and back-bending (25). In fact, their role in the aggressive behavior of *Uegitglanis* is not completely clear. One hypothesis – which we deem worthy of thorough investigation in any case – is that these might be related to the emission of

mechanical (gaping) and chemical (back-bending) signals. If confirmed, the biological and behavioral significance of the 2 patterns would be explained. Otherwise, these may have been inherited unmodified, as behavioral rudiments, from the epigeal ancestor, in which the 2 patterns probably operated as visual displays.

The temporal sequence of the various patterns and their relative frequency in each partner is shown in figure 3.

**Conclusions and discussion.** The complexity and extreme variety of the aggressive behavior patterns used by *Uegitglanis* is obvious both from their description and from a careful study of figure 3. The behavioral repertoire of this species includes all the patterns observed in the epigeal siluriforms *Ictalurus natalis* Lesueur and *I. nebulosus* Lesueur<sup>8</sup>. In contrast to other species which show a similar adaptation to the hypogean biotope but have a reduced behavioral repertoire<sup>9-12</sup>, the pronounced morpho-physiological regression of *Uegitglanis* – so clearly adapted to the hypogean environment<sup>3</sup> – has not been paralleled by a regression in behavior. This, in fact, seems to have conserved all the aggressive behavior patterns of the epigeal Siluriformes. A probable explanation of this phenomenon is that, during the process of regressive evolution undergone by *Uegitglanis*, the biological significance and adaptive value of their aggressive behavior has remained unaltered.

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0014-4754/83/020217-03\$1.50 + 0.20/0  
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## Sting alarm pheromone of the honeybee: the recruiting effect of an artificial blend of volatile compounds of the worker sting (*Apis mellifica* L., Hymenoptera, Apidae)<sup>1</sup>

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**Summary.** Eight volatile compounds present in the sting of the honeybee worker were incorporated in different hexane solutions and their recruiting effect was evaluated by a bioassay at beehive entrances. The efficiency of the whole blend was higher than that of pure isoamyl acetate.

Sting alarm pheromone of the honeybee worker, released from the setaceous membrane of disturbed bees during alarm behavior<sup>2</sup> provokes the recruitment of the other workers ready to attack the intruder. The effect can be readily induced by freshly excised stings crushed at beehive entrances<sup>2</sup>. Isoamyl acetate has been identified as a major and active compound of the worker bee sting secretion<sup>3</sup>,

but its efficiency at hive entrances is lower than that of the whole sting extracts<sup>4</sup>, indicating the presence of other compounds in the sting alarm pheromone.

Recently, other volatile compounds have been identified in the worker sting<sup>5</sup>, but neither their presence on the setaceous membrane nor their role in the elicitation of the alarm response has been reported.