

# *Xiphophorus*: Carving a Niche Towards a Broader Understanding of Aggression and Dominance

RYAN L. EARLEY

## ABSTRACT

A review of some exciting new directions for *Xiphophorus* research in behavioral ecology and integrative animal behavior is presented. The primary objective of this review is to identify areas of research in this teleost genus that, if studied further, could yield insights into the manifold causes and consequences of dominance encounters that will have broad relevance in the behavioral biology community. First described is the phenomenon of social eavesdropping—the ability of animals to extract information from signaling interactions between others—as it applies to *Xiphophorus* systems, and how exploring the context-dependency of individual responses to watching fights will be of benefit. A brief discussion follows of the overwhelming tendency for research on *Xiphophorus* to focus on individual responses to visual cues available in their social environment, and to promote advancements towards a multimodal approach to understanding social dynamics. Lastly, historical studies on neuroendocrinology in this genus are reviewed, and recent advances in the molecular realm are highlighted that might serve as a springboard for integrative research addressing the behavioral impacts of direct (overt fighting) and indirect (eavesdropping) experiences in *Xiphophorus*.

## INTRODUCTION

For well over half a century, members of the genus *Xiphophorus* have captured the attention of behavioral ecologists. Much of the fame bestowed upon *Xiphophorus* has resulted from decades of rigorous studies in the area of intersexual selection, which have run the gamut from cues involved in mate recognition and the evolutionary history of female preferences to molecular genetic work underscoring the origins of elaborate traits such as the sword.<sup>1–4</sup> Another area of *Xiphophorus* research has focused on intrasexual competition in attempts to understand intersections among the many factors that contribute to success in dominance encounters and the consequences thereof. A number of benchmarks have been established by explorations of male–male contests in

*Xiphophorus*, including discoveries of maturational delays in subordinate individuals,<sup>5</sup> putative functions of facultative signals,<sup>6,7</sup> and sophisticated means through which fish assess the fighting ability of competitors.<sup>8</sup> Indeed, research in these areas over the past 30 years has demonstrated the power of the social environment in mediating numerous life history and behavioral parameters and has led to conceptual advances in many corners of behavioral ecology.

Despite the wealth of studies on aggression and dominance in *Xiphophorus*, the vast majority of research, some exceptions noted above, has centered on three related concepts: effects of prior fighting experience, social isolation, and asymmetries in residency or body size on contest dynamics and outcome. An exhaustive review of each parameter that influences or re-

---

Department of Biology, Georgia State University, and Center for Behavioral Neuroscience, Atlanta, Georgia.  
Support for this work was provided by a National Institutes of Health Ruth L. Kirschstein postdoctoral fellowship 1-F32-HD046240-02 to RLE.

T1,F1

sponds to contest outcome is outside the scope of this paper. Table 1 and Figure 1, however, provide a detailed survey of the literature with the express goal of highlighting areas that historically have gained significant attention. Importantly, the table reveals some exciting new paths that *Xiphophorus* research has traveled, and I will focus on three questions of this type. First, in what directions can we expand research on assessment of fighting ability to encompass the broader social and ecological milieu? Second, to what extent might information transfer during aggressive contests be multimodal in nature, and what do we stand to gain from examining multiple modes of sensory processing? And third, is it time to resurrect interest in the neuroendocrine bases for aggression and dominance in *Xiphophorus*?

### BROADER SOCIAL PERSPECTIVES ON ASSESSMENT OF FIGHTING ABILITY

#### Background

Our understanding of the behavioral mechanisms by which individuals assess the fighting ability of potential competitors is based on a long history of theoretical models.<sup>9–11</sup> A common assumption among these models is that animals can gauge the fighting ability of others only through direct interaction. Recent work on *Xiphophorus helleri*, however, indicates that fish are capable of extracting information about the fighting ability of future opponents via observation.<sup>8</sup> Male *X. helleri* bystanders typically avoid interactions with winners of an observed contest irrespective of its intensity. Bystander responses to losers, however, depend critically on the gradient of observed contest intensity, with avoidance responses being more prevalent towards losers that escalated in the observed conflict.<sup>8</sup> The behavioral changes exhibited by bystanders could not be attributed to general changes in motivational state (e.g., if watching fights primes individuals for combat or escape),<sup>12</sup> indicating that observation enables male *X. helleri* to estimate the competitive prowess of other individuals in the social environment by combining information about opponent identity, status, and persistence in a contest. This

phenomenon, dubbed social eavesdropping, has been unveiled in other fish species (e.g., *Betta splendens*<sup>13</sup>), and in contexts other than aggression (divorce in *Archocentrus nigrofasciatus*<sup>14</sup>), suggesting that eavesdropping might be an important component of the assessment repertoire of swordtails and other fish. A requisite of social eavesdropping is the ability of bystanders to distinguish particular individuals, and the capacity for individual recognition has indeed been demonstrated in *X. helleri*, *X. nigrensis*, and *X. multilineatus* (Table 1).

Few studies on dominance, individual recognition, or eavesdropping in *Xiphophorus* have been conducted in the field,<sup>15</sup> in part because of the inherent limitations that natural conditions pose for parsing out numerous subtle behavioral effects. This raises the question, however, as to whether these phenomena are artifacts of the laboratory or truly reflective of the social behavior of individuals under natural conditions. Several recent field observations provide telling evidence that *Xiphophorus* social systems are ripe with opportunities for direct (dominance interactions) and indirect (eavesdropping) assessment of fighting ability. Female *X. birchmanni* x *X. malinche* exhibit independent shoaling preferences for larger groups and like-sized individuals, underscoring their social nature<sup>16</sup> (but see contrast when shoal and individual size are pitted against one another). In *X. helleri* and *X. nigrensis*, males patrol overlapping home ranges and dominants actively exclude subordinates from access to females, while females typically migrate between home ranges to forage.<sup>15,17</sup> Aggressive interactions between males are common, and in some cases, dominance hierarchies among males of overlapping home ranges are established.<sup>18</sup> Males also are site faithful, occupying similar spatial domains for at least a couple of days at a time.<sup>19</sup> The fact that dominance interactions occur at a relatively high frequency in a social environment containing an ample constitution of bystanders sets the stage for social eavesdropping. Furthermore, site fidelity and overlapping home ranges favor repeated interactions between males, and this type of social system might place a premium on individual recognition as a means of stabilizing hierarchy structure, even if for only days at a time.<sup>20</sup>

*Future directions I: transitive inference*

Given the characteristics of *Xiphophorus* social systems described in the previous section, a fascinating question that emerges is whether individuals are capable of combining information from prior dominance interactions and eavesdropping to better evaluate their place in the social hierarchy. For instance, imagine a simple situation in which three unfamiliar males (A, B, and C) find themselves in the shallows of the Rio Atoyac, a river in the geographic range of *X. helleri* among other species. In attempts to establish and defend home ranges, individual A initially loses to B and then witnesses C defeat B. Individual A then opts out of an interaction with C because he is perceived by A (via eavesdropping) as an opponent of superior quality. There are three factors at work here—previous fighting experience (A vs. B), social eavesdropping (A watches B vs. C), and individual recognition (A distinguishes B from C). In the end, individual A combines all of this information to infer transitive dominance relationships:  $B > A$  and  $C > B$ , so A must be  $< C$ . Transitive inference thus enables the hierarchy to stabilize with the minimum number of direct confrontations. Can *Xiphophorus* species infer transitive social relations? At this point we do not know, but it is clear that they possess all of the behavioral ingredients. If it turns out that they can, *Xiphophorus* would join the company of some of the more adept social animals (e.g., pinyon jays<sup>21</sup>). This marks an intriguing direction for future research on the social behavior of *Xiphophorus* and would further an already expansive literature on the factors that govern dominance in this genus.

*Future directions II: context-dependent eavesdropping responses*

All studies on social eavesdropping in *Xiphophorus* to date have used males that differ only slightly in size, and have been conducted in a relatively sterile aquarium environment. This type of experimental design allows the investigator to target the effects of social eavesdropping without having to wade through masses of behavioral noise. Under natural circumstances, however, noisy environ-

ments prevail, with individuals of different size, dominance history, or sex comprising a social group, and with tremendous variation in habitat characteristics. Is it possible that eavesdropping responses change as a function of bystander type (e.g., dominant vs. subordinate; small vs. large) and environmental condition (e.g. turbidity; habitat heterogeneity)? Eavesdropping responses are likely to vary among individuals depending on their current state, and individuals should have some flexibility with respect to whether, when, and how eavesdropping is utilized as an assessment strategy. A few examples should illustrate these possibilities.

First, small/subordinate individuals might stand to gain more from eavesdropping (e.g., avoid highly competitive animals; facilitate increased rank by identifying and ousting weak animals). Thus, different size/status classes might be expected to utilize different strategies, or exhibit divergent responses to eavesdropping, as has been described for other aspects of aggressive contests (fight initiation<sup>22</sup>). Second, turbid waters might introduce significant errors in visual assessment of fighting ability even at close range, rendering information gained through observation suspect at best. Third, available refuge and predator presence might alter the benefit-cost ratio associated with eavesdropping and thus alter the strategies or responses of putative bystanders (see Johnson and Basolo<sup>23</sup> for these types of effects in the context of mate choice). Indeed, escalated fighting in cichlid fish (*Nannacara anomala*) increases predation risk presumably because fighters are less vigilant,<sup>24,25</sup> and opponents engage in less conspicuous agonistic displays in the presence of a predator.<sup>26</sup> It is reasonable to assume that eavesdropping also might reduce vigilance or increase predation risk by association with the fighters. Less complex habitats with fewer refuges may enhance this risk and offer limited opportunity for the bystander to escape predation. Although admittedly speculative, it therefore seems possible that bystanders might incur non-negligible predation costs and might be expected to alter their strategies in accordance with predation risk. This area of research in *Xiphophorus* currently is wide open, and the likelihood that eavesdrop-

TABLE 1. SURVEY OF XIPHOPHORUS RESEARCH ON THE CAUSES (A) AND CONSEQUENCES (B) OF VARIATION IN DOMINANCE SUCCESS

Factor type	Author(s) (Ref.)	Year	Species	Remarks
SOCIAL MILIEU Prior Contest Experience	Thines & Heuts (66) Wilhelmi (67)	1968 1975	X. helleri x X. maculatus X. helleri	<ul style="list-style-type: none"> <li>• Losers inhibited from initiating contests</li> <li>• Contests between prior subordinates more escalated than contests between prior dominants</li> </ul>
	Röhrs (68)	1977	X. helleri	<ul style="list-style-type: none"> <li>• Contests between prior subordinates more escalated than contests between prior dominants</li> </ul>
	Franck & Ribowski (69)	1987	X. helleri	<ul style="list-style-type: none"> <li>• Prior winners defeat prior losers; post-fight aggression towards mirror: winners &gt; losers</li> </ul>
	Franck & Ribowski (70) Ribowski & Franck (71)	1989 1993a	X. helleri X. helleri	<ul style="list-style-type: none"> <li>• Prior subordinates exhibit more displays in contests</li> <li>• Contests between prior subordinates more escalated than contests between prior dominants</li> </ul>
	Beaugrand et al. (72)	1991	X. helleri	<ul style="list-style-type: none"> <li>• Prior winners defeat prior losers; interaction of experience with size asymmetries</li> </ul>
	Beaugrand & Cotnoir (73)	1996	X. helleri	<ul style="list-style-type: none"> <li>• Prior contest experience trumped by size asymmetries in formation of triadic hierarchies</li> </ul>
	Beaugrand et al. (74)	1996	X. helleri	<ul style="list-style-type: none"> <li>• Prior winners defeat prior losers; interactions of experience with size and residency asymmetries</li> </ul>
	Beaugrand (75)	1997	X. helleri	<ul style="list-style-type: none"> <li>• Prior winners defeat prior losers; interactions with familiarity; see also Beaugrand &amp; Zayan 1985</li> </ul>
	Beaugrand & Goulet (76)	2000	X. helleri	<ul style="list-style-type: none"> <li>• Prior winners defeat prior losers; type of prior experience mediates aggressive response</li> </ul>
	Goulet & Beaugrand (77)	2001a	X. helleri	<ul style="list-style-type: none"> <li>• Aggression towards mirror stimulus: prior dominants &gt; prior subordinates; response of winners to mirror depends on prior contest intensity</li> </ul>
	Earley & Dugatkin (8)	2002	X. helleri	<ul style="list-style-type: none"> <li>• No significant effect of contest experience when winners/losers pitted against naive animals</li> </ul>
	Dugatkin & Druen (78)	2004	X. helleri	<ul style="list-style-type: none"> <li>• Order of triadic hierarchy: prior winners &gt; inexperienced &gt; prior losers</li> </ul>
	Individual Recognition & Opponent Familiarity	Zayan (20) Zayan (79) Wechkin (80)	1974 1975 1975	X. helleri x X. maculatus X. helleri x X. maculatus X. helleri x X. maculatus
Morris et al. (6) Beaugrand (75) Earley et al. (12)		1995 1997 2003	X. nigrensis & X. multiflineatus X. helleri X. helleri	<ul style="list-style-type: none"> <li>• Contest intensity: unfamiliar pair &gt; familiar pair</li> <li>• Contest intensity: unfamiliar pair &gt; familiar pair</li> <li>• Prior exposure to opponent visual cues reduces contest intensity</li> </ul>
Beaugrand & Cotnoir (73)		1996	X. helleri	<ul style="list-style-type: none"> <li>• Information gained through eavesdropping apparently trumped by size asymmetries</li> </ul>
Earley & Dugatkin (8)		2002	X. helleri	<ul style="list-style-type: none"> <li>• Watching fights alters bystander behavior towards observed winners and losers; no size asymmetries</li> </ul>
Earley & Dugatkin (81)		2005	X. helleri	<ul style="list-style-type: none"> <li>• Summary of social environment and aggression</li> </ul>
Eavesdropping				

Prior Residency	Earley et al. (82)	2005	X. helleri	<ul style="list-style-type: none"> <li>• Watching fights does not elicit generalized aggressive response (e.g., no priming)</li> </ul>
	Braddock (83)	1949	X. maculatus	<ul style="list-style-type: none"> <li>• Residents dominate intruders in both sexes; interactions with size asymmetries</li> </ul>
	Zayan (84)	1976	X. helleri x X. maculatus	<ul style="list-style-type: none"> <li>• Residents dominate intruders in non-escalated but not escalated contests; interactions with isolation</li> </ul>
	Beaugrand & Beaugrand (72)	1991	X. helleri	<ul style="list-style-type: none"> <li>• Residents dominate intruders; persistent effect</li> </ul>
	Beaugrand et al. (74)	1996	X. helleri	<ul style="list-style-type: none"> <li>• Residents dominate intruders only in pairs of prior losers; interaction with experience, size asymmetry</li> </ul>
	Heuts & Nijman (85)	1998	X. helleri x X. maculatus	<ul style="list-style-type: none"> <li>• Residents dominate intruders; two color morphs</li> </ul>
	Nijman & Heuts (86)	2000	X. helleri x X. maculatus	<ul style="list-style-type: none"> <li>• Trend for residents to dominate intruders; depends on level of aquarium enrichment</li> </ul>
	Goulet & Beaugrand (77)	2001a	X. helleri	<ul style="list-style-type: none"> <li>• Residency asymmetries reduce contest intensity</li> </ul>
	Goulet & Beaugrand (87)	2001b	X. helleri	<ul style="list-style-type: none"> <li>• Changes in residency sufficient to reverse dominance relationships in familiar pairs</li> </ul>
	Social Isolation	Franck & Wilhelmi (88)	1973	X. helleri
Wilhelmi (67)		1975	X. helleri	<ul style="list-style-type: none"> <li>• Isolation → increased aggression towards opponent</li> </ul>
Zayan (84)		1976	X. helleri x X. maculatus	<ul style="list-style-type: none"> <li>• Residency advantage depends on prior isolation length</li> </ul>
Röhrs (68)		1977	X. helleri	<ul style="list-style-type: none"> <li>• Isolation alters courtship and aggressive behavior</li> </ul>
Goldenbogen (89)		1978	X. helleri	<ul style="list-style-type: none"> <li>• Isolation → increased aggression towards opponent</li> </ul>
Hannes & Franck (90)		1983a	X. helleri	<ul style="list-style-type: none"> <li>• Androgen and corticosteroid levels: non-isolated &gt; isolated</li> </ul>
Hannes (91)		1985	X. helleri	<ul style="list-style-type: none"> <li>• Isolation → depressed androgen and corticosteroid levels; restored with visual exposure to conspecific</li> </ul>
Franck et al. (92)		1985	X. helleri	<ul style="list-style-type: none"> <li>• Response to standard stimuli: non-isolated &gt; isolated</li> </ul>
Franck & Ribowski (69)		1987	X. helleri	<ul style="list-style-type: none"> <li>• Status-dependent changes in aggressive responses (pre vs. post isolation) towards mirror; dominants increase, subordinates decrease response after iso</li> </ul>
ENVIRONMENT				
	Nutrition/Growth			
Habitat Enrichment	Royle et al. (93)	2005	X. helleri	<ul style="list-style-type: none"> <li>• Early feeding regime and compensatory growth affects aggressive behavior and contest success</li> </ul>
	Nijman & Heuts (86)	2000	X. helleri & X. maculatus	<ul style="list-style-type: none"> <li>• Aquarium enrichment affects residency advantage in X. helleri, not X. maculatus</li> </ul>
INTRINSIC FACTORS				
	Genotype			
Size	Sohn (94)	1977	X. maculatus	<ul style="list-style-type: none"> <li>• <math>P^{pe} &gt; P^{pl}</math> until <math>&gt;</math> matures, then reversed</li> </ul>
	Zimmerer & Kallman (95)	1989	X. nigrensis	<ul style="list-style-type: none"> <li>• P-allele: <math>L &gt; S</math>, mating competition</li> </ul>
	Morris et al. (15)	1992	X. nigrensis	<ul style="list-style-type: none"> <li>• P-allele: <math>L &gt; I &gt; S</math>, mating competition</li> </ul>
	Braddock (83)	1949	X. maculatus	<ul style="list-style-type: none"> <li>• Large dominate small; affect residency situations</li> </ul>
	Beaugrand et al. (72)	1991	X. helleri	<ul style="list-style-type: none"> <li>• Equal experience: large dominate small; unequal experience: prior losers need to be much larger to dominate prior winners</li> </ul>
	Ribowski & Franck (96)	1993b	X. helleri	<ul style="list-style-type: none"> <li>• Heavier dominate lighter; effect more pronounced with greater size asymmetry</li> </ul>
	Morris et al. (6)	1995	X. nigrensis & X. multilineatus	<ul style="list-style-type: none"> <li>• Large dominate small; but small initiate fights</li> </ul>
INTRINSIC FACTORS				
	Size			
	Beaugrand et al. (74)	1996	X. helleri	<ul style="list-style-type: none"> <li>• Size trumps experience and residency with large asymmetries</li> </ul>
	Beaugrand & Cotnoir	1996	X. helleri	<ul style="list-style-type: none"> <li>• Size trumps experience in ordering triadic hierarchy</li> </ul>

(continued)

TABLE 1. SURVEY OF XIPHOPHORUS RESEARCH ON THE CAUSES (A) AND CONSEQUENCES (B) OF VARIATION IN DOMINANCE SUCCESS (CONT'D)

Factor type	Author(s) (Ref.)	Year	Species	Remarks
Endocrine State	Heuts & Nijman (85)	1998	X. helleri x X. maculatus	<ul style="list-style-type: none"> <li>• Large dominate small</li> <li>• When size asymmetry perceived, small animals initiate</li> <li>• Large dominate small; but small initiate fights</li> <li>• Pre-fight cortisol levels predict contest outcome; individuals with higher cortisol tend to lose</li> <li>• Bites towards mirror do not predict outcome</li> <li>• Pre-fight aggression scores towards mirror positively related to contest success</li> <li>• Mention of vertical bars as agonistic signal</li> <li>• Vertical bars deter competitors</li> <li>• Species-specific aggressive response to vertical bars</li> </ul>
	Early et al. (12)	2003	X. helleri	
	Moretz (22)	2003	X. cortezi	
	Netherton et al. (52)	2004	X. helleri	
Aggression Levels	Franck & Ribowski (69)	1987	X. helleri	<ul style="list-style-type: none"> <li>• Bites towards mirror do not predict outcome</li> <li>• Pre-fight aggression scores towards mirror positively related to contest success</li> </ul>
	Goulet & Beaugrand (77)	2001a	X. helleri	
Heritable Signals (Vertical bars)	Zimmerer & Kallman (95)	1988	X. nigrensis	<ul style="list-style-type: none"> <li>• Differences between barred and barrless morphs in aggression levels during contest and dominance success</li> </ul>
	Morris et al. (6)	1995	X. multilineatus	
	Moretz & Morris (77)	2003	X. birchmanni, X. cortezi	
	Moretz (27)	2005	X. nigrensis, X. multilineatus	
<b>B. Consequences of Variation in Contest Success</b>				
Factor type	Author (s) (Ref.)	Year	Species	Remarks
Maturation	Borowsky (5)	1973	X. variatus	<ul style="list-style-type: none"> <li>• Dominants inhibit sexual maturation in subordinates</li> <li>• Dominants inhibit sexual maturation in subordinates</li> </ul>
	Sohn (94)	1977	X. maculatus	
Endocrine State	Borowsky (98)	1978	X. variatus	<ul style="list-style-type: none"> <li>• Field evidence for social inhibition of maturation</li> <li>• Maturational delay depends on subordination magnitude</li> <li>• Social rank affects adrenocortical activity</li> <li>• Winners and losers show elevated corticosteroids after fight, but winners recovery faster; elevation/depression in androgen levels of winners/losers</li> <li>• Winners and losers show elevated corticosteroids after fight, but winners recovery faster</li> </ul>
	Borowsky (99)	1987	X. maculatus & X. variatus	
	Scott & Currie (100)	1980	X. helleri	
	Hannes et al. (101)	1984	X. helleri	
Reproductive Success	Netherton et al. (52)	2004	X. helleri	<ul style="list-style-type: none"> <li>• Dominants exclude subordinates from female access (lab and field)</li> </ul>
	Morris et al. (15)	1992	X. nigrensis	
Dominance Hierarchies	Luo et al. (102)	2005	X. multilineatus	<ul style="list-style-type: none"> <li>• Large, dominants sire more offspring; skewed reproduction inferred from offspring genotype</li> <li>• laboratory</li> <li>• field</li> <li>• field; overlapping home ranges of males</li> </ul>
	Beaugrand et al. (103)	1984	X. helleri	
	Franck & Ribowski (18)	1993	X. helleri	
	Franck et al. (17)	1998	X. helleri	

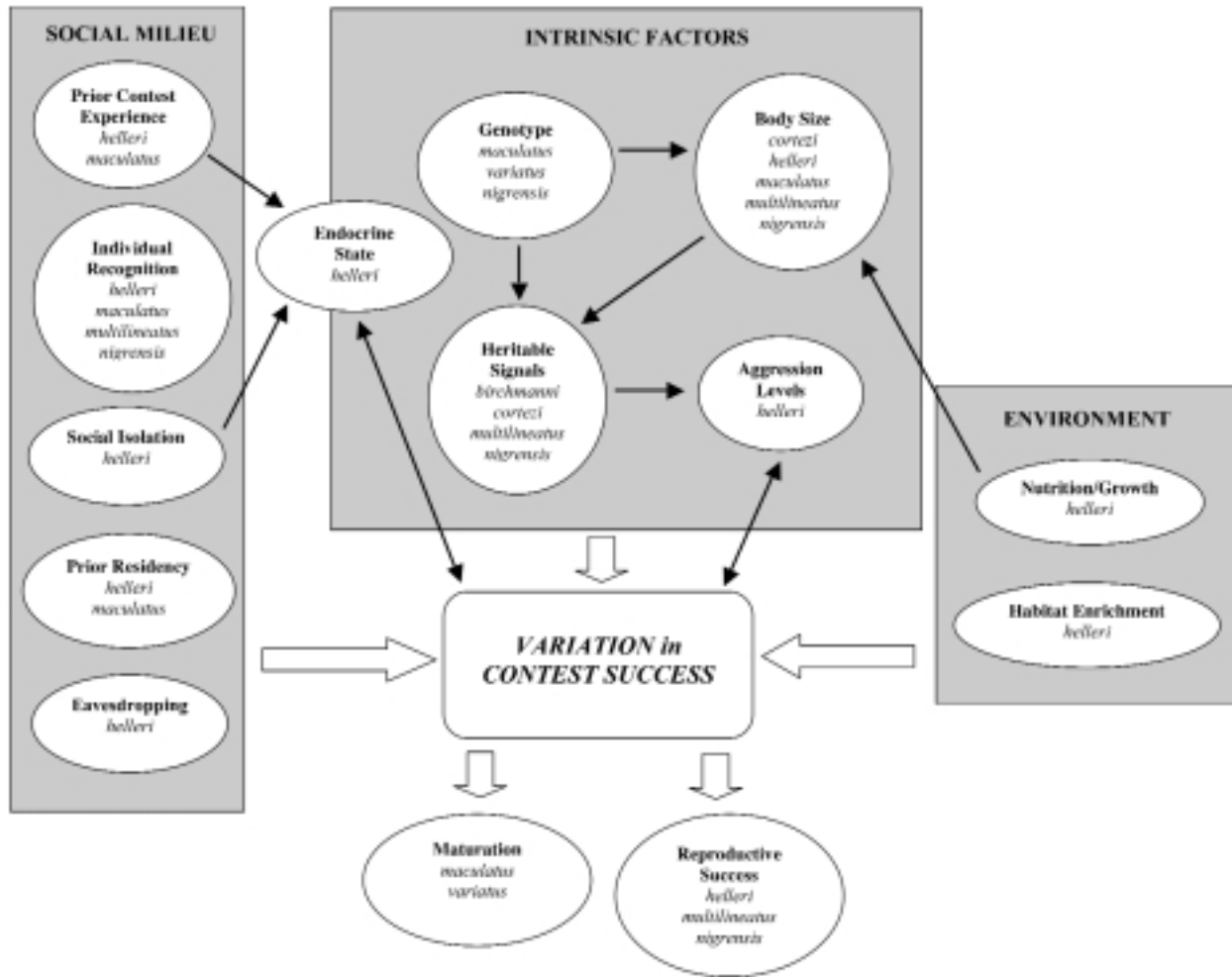


FIG. 1. Graphical representation of the factors that both influence and are influenced by variation in contest behavior and outcome in members of the genus *Xiphophorus*; if the parameter of interest has been studied in a particular species, it is noted with the species name.

ping responses are modulated under variable social and/or ecological contexts warrants further exploration.

### MULTIMODAL SIGNALS/CUES ASSOCIATED WITH DOMINANCE INTERACTIONS

The vast majority of research on communication in *Xiphophorus*—aggressive or otherwise—has targeted visual cues/signals that are available to a receiver. For example, the intensity of vertical bars located on the flank of many *Xiphophorus* species can be modulated in a facultative manner, and can have either deterrent or excitatory effects on the aggressive response

of an opponent depending on the species in which the bars are manifest.<sup>6,7</sup> In addition, barred and barless males within a species (*X. cortezii*) differ both in their aggression levels and dominance ability.<sup>27</sup> Recent evidence also indicates that some northern swordtails (*X. nigrensis*; *X. malinche*) exploit ultraviolet ranges of the spectrum for communication in a private domain (i.e., exploiting wavelengths that predators are unable to decipher.<sup>28</sup>) These examples, and many others in the realm of intersexual selection,<sup>29</sup> demonstrate that members of the genus *Xiphophorus* rely heavily on visual input. Given the spectacular morphological ornamentations (sword) and signals (vertical bars) possessed by many *Xiphophorus* species, it is not surprising that a majority of research on

communication in these fish has focused on the visual sense. This, in turn, has left open a niche likely to bear many empirical fruits. Namely, the possibility that *Xiphophorus* integrates visual information with information contained in olfactory/chemical and possibly auditory stimuli, and that the full cocktail of stimuli guides behavior during and after aggressive contests. Indeed, at least five species of swordtail (*X. birchmanni*, *X. cortezi*, *X. helleri*, *X. nigrensis*, and *X. pygmaeus*) utilize olfactory/chemical cues as a means of distinguishing conspecifics from heterospecifics or of assessing predation risk.<sup>4,30–33</sup> Despite the fact that agonistic behavior in other fish species is guided by various cues (acoustic<sup>34</sup> and chemical<sup>35</sup>), the multimodal approach has yet to catch on in studies of dominance in *Xiphophorus*. If employed, however, this approach has great potential to yield insights into communication dynamics during aggressive disputes and possibly the identification of additional cues available to attentive bystanders.

#### NEUROENDOCRINE SYSTEMS: REGULATORS AND RESPONDERS TO SOCIAL INTERACTIONS

Mechanistic investigations using *Xiphophorus* have targeted two areas related to life history transitions during development and behavior. Genetic determinants of sexual maturity and size have been identified in this genus, centering primarily on a pituitary locus (P-allele) involved in regulating differentiation of the gonadotropic zone in the adenohypophysis.<sup>36–38</sup> Preceding the identification and further characterization the P-allele and its downstream effects, many researchers implicated components of the hypothalamic–pituitary–gonadal (HPG) axis, including gonadotropins and androgens, in the regulation of sexual differentiation and maturity (e.g., gonopodium and secondary sex character development).<sup>39–42</sup> More recent neuroendocrine work has continued to focus on the HPG axis, primarily in *X. maculatus* and *X. helleri*, and has been successful in localizing various forms of gonadotropin-releasing hormone and gonadotropins in the brain and pituitary,<sup>43,44</sup> and

in ascertaining further the roles of steroid hormones and their metabolism in sexual differentiation and reproduction.<sup>45,46</sup>

These studies all have contributed neuroendocrine groundwork for exploring how the HPG axis both mediates dominance ability and responds to status acquisition. Indeed, cross-talk between the HPG axis and social behavior has gained significant attention in other fish. For instance, a burgeoning literature on cichlid fish has demonstrated a critical role for the HPG axis in mediating social inhibition of reproduction and responding to social dynamics.<sup>47</sup> If extended to *Xiphophorus*, the HPG axis and its many components might act as a neuroendocrine intermediary between dominance status and maturational delay or status-dependent behavioral modifications.<sup>48,49</sup>

The 1980s saw *X. helleri* emerge as a model candidate for investigating endocrine responses to social isolation, winning, or losing aggressive contests. In particular, this species was used to assess whether dominant and subordinate animals exhibited differential cortisol and androgen release following a fight (Table 1; Refs. 50 and 51). Due to a sharp decline of such studies in *Xiphophorus* towards the turn of the century, however, most of the existing literature and the techniques described therein (e.g., whole body hormone analysis and nuclear diameter of interrenal cells as a proxy for adrenocortical activity), although still informative, are necessarily dated. Netherton, Grober, and Earley<sup>52</sup> resumed behavioral neuroendocrinological investigations in *Xiphophorus* with their study on the time course of cortisol release following agonistic bouts in *X. helleri*. With the advent of noninvasive techniques for hormone collection in fish (water-borne steroids<sup>53</sup>), which has been modified for applications in small fish, *Xiphophorus* systems hold much promise for understanding the independent influences or interactions among hormone systems that might be activated during agonistic interactions and subsequently feed back on the brain and peripheral systems to influence behavior.

Although there has been comparatively little neurobiology conducted in *Xiphophorus*, several recent studies have focused on the characterization and localization of novel

neurotrophins or enzymes (e.g., NADPH-diaphorase/nitric oxide synthase).<sup>54–59</sup> Neurotrophins and nitric oxide synthase play an important role in neurogenesis, axon guidance, learning, and memory<sup>60,61</sup> in many vertebrates, but the precise function of these molecules in fish has not yet been identified. If these molecules mediate learning and memory processes in *Xiphophorus*, then a potential link between molecular neurobiology and experience-dependent behavioral change (e.g., responses to eavesdropping, winning, or losing) would be established. I anticipate that research elaborating on existing neuroanatomical and genetic work in *Xiphophorus* to pursue questions in the realm of integrative animal behavior will be met with lucrative returns. Hopefully, this will include identification of brain regions or nuclei involved in social behavior (e.g., nucleus preopticus<sup>62</sup>), which certainly will be facilitated through consultation of the detailed *Xiphophorus* brain atlas developed by Anken and Rahmann.<sup>63</sup> In addition, integrative pursuits will help to resurrect interest in other neuroendocrine factors that could mediate social behavior in this genus (e.g., arginine vasotocin<sup>64</sup> and steroid receptors<sup>65</sup>) using the advanced techniques of today's neuroendocrine climate.

### CONCLUSION

This review started by describing intriguing behavioral phenomena in *Xiphophorus* and has concluded with insights into the molecular mechanisms that might guide these phenomena. Important investigations are being conducted on both ends of the spectrum, and there is some indication that collaborative research endeavors are being established between ecologists, behaviorists, geneticists, and neuroendocrinologists who study *Xiphophorus*. With species of this genus emerging as model organisms to address an arsenal of valuable questions at the fundamental and applied levels, I expect that interdisciplinary pursuits among *Xiphophorus* researchers will lay the groundwork for numerous exciting discoveries into how and why these remarkable fish behave the way that they do.

### ACKNOWLEDGMENTS

The author would like to extend my sincere thanks to Steven Kazianis for organizing this special *Xiphophorus* issue, and to Molly Cummings and an anonymous reviewer for insightful suggestions on the original version of this manuscript.

### REFERENCES

1. Rosenthal GG, Evans CS. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proc Natl Acad Sci USA* 1998;95:4431–4436.
2. Morris MR, Nicoletto PF, Hesselman E. A polymorphism in female preference for a polymorphic male trait in the swordtail fish *Xiphophorus helleri*. *Anim Behav* 2003;65:45–52.
3. Zauner H, Begemann G, Mari-Beffa M, Meyer A. Differential regulation of *msx* genes in the development of the gonopodium, and intromittent organ, and the “sword”, a sexually selected trait in swordtail fish (*Xiphophorus*). *Evol Devel* 2003;5:466–477.
4. Wong BBM, Fisher HS, Rosenthal GG. Species recognition by male swordtails via chemical cues. *Behav Ecol* 2005;16:818–822.
5. Borowsky RL. Social control of adult size in males of *Xiphophorus variatus*. *Nature* 1973;245:332–335.
6. Morris MR, Mussel M, Ryan MJ. Vertical bars on male *Xiphophorus multilineatus*: a signal that deters rival males and attracts females. *Behav Ecol* 1995;6:274–279.
7. Moretz JA, Morris MR. Evolutionarily labile responses to a signal of aggressive intent. *Proc R Soc Lond B* 2003;270:2271–2277.
8. Earley RL, Dugatkin LA. Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking. *Proc R Soc Lond B* 2002;269:943–952.
9. Parker GA. Assessment strategy and the evolution of fighting behaviour. *J Theor Biol* 1974;47:223–243.
10. Enquist M, Leimar O. Evolution of fighting behaviour: decision rules and assessment of relative strength. *J Theor Biol* 1983;102:387–410.
11. Payne R. Gradually escalating fights and displays: the cumulative assessment model. *Anim Behav* 1998;56:651–662.
12. Earley RL, Tinsley M, Dugatkin LA. To see or not to see: does previewing a future opponent affect the contest behavior of green swordtail males (*Xiphophorus helleri*)? *Naturwissenschaften* 2003;90:226–230.
13. Oliveira RF, McGregor PK, Latruffe C. Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc R Soc Lond B* 1998;265:1045–1049.
14. Van Breukelen NA, Draud M. The roles of male size

- and female eavesdropping in divorce in the monogamous convict cichlid (*Archocentrus nigrofasciatus*, Cichlidae). *Behaviour* 2005;142:1023–1035.
15. Morris MR, Batra P, Ryan MJ. Male–male competition and access to females in the swordtail *Xiphophorus nigrensis*. *Copeia* 1992;1992:980–986.
  16. Wong BBM, Rosenthal GG. Shoal choice in swordtails when preferences conflict. *Ethology* 2005;111:179–186.
  17. Franck D, Klamroth B, Taebel-Hellwig A, Manfred Schartl. Home range and satellite tactics of male green swordtails (*Xiphophorus helleri*) in nature. *Behav Proc* 1998;43:115–123.
  18. Franck D, Ribowski A. Dominance hierarchies of male green swordtail (*Xiphophorus helleri*) in nature. *J Fish Biol* 1993;43:497–499.
  19. Morris MR, Gass L, Ryan MJ. Assessment and individual recognition of opponents in the pygmy swordtails *Xiphophorus nigrensis* and *X. multilineatus*. *Behav Ecol Sociobiol* 1995;37:303–310.
  20. Zayan RC. Le rôle de la reconnaissance individuelle dans la stabilité des relations hiérarchiques chez *Xiphophorus* (Pisces, Poeciliidae). *Behaviour* 1974;49:268–312.
  21. Paz-Y-Miño CG, Bond AB, Kamil AC, Balda RP. Pinyon jays use transitive inference to predict social dominance. *Nature* 2004;430:778–781.
  22. Moretz JA. Aggression and RHP in the northern swordtail fish, *Xiphophorus cortezi*: the relationship between size and contest dynamics in male–male competition. *Ethology* 2003;109:995–1008.
  23. Johnson JB, Basolo AL. Predator exposure alters female mate choice in the green swordtail. *Behav Ecol* 2003;14:619–625.
  24. Jakobsson S, Brick O, Kullberg C. Escalated fighting behavior incurs increased predation risk. *Anim Behav* 1995;49:235–239.
  25. Brick O. Fighting behaviour, vigilance and predation risk in the cichlid fish *Nannacara anomala*. *Anim Behav* 1998;56:309–317.
  26. Brick O. A test of the sequential assessment game: the effect of increased cost of sampling. *Behav Ecol* 1999;10:726–732.
  27. Moretz JA. Aggression and fighting ability are correlated in the swordtail fish *Xiphophorus cortezi*: the advantage of being barless. *Behav Ecol Sociobiol* 2005;59:51–57.
  28. Cummings ME, Rosenthal GG, Ryan MJ. A private ultraviolet channel in visual communication. *Proc R Soc Lond* 2003;270:897–904.
  29. Basolo AL. Congruence between the sexes in preexisting receiver responses. *Behav Ecol* 2002;13:832–837.
  30. Crapon de Caprona MD, Ryan MJ. Conspecific mate recognition in swordtails, *Xiphophorus nigrensis* and *X. pygmaeus* (Poeciliidae): olfactory and visual cues. *Anim Behav* 1990;39:290–296.
  31. McLennan DA, Ryan MJ. Responses to conspecific and heterospecific olfactory cues in the swordtail *Xiphophorus cortezi*. *Anim Behav* 1997;54:1077–1088.
  32. Mirza RS, Scott JJ, Chivers DP. Differential responses of male and female swordtails to chemical alarm cues. *J Fish Biol* 2001;59:716–728.
  33. Hankison SJ, Morris MR. Avoiding a compromise between sexual selection and species recognition: female swordtail fish assess multiple species-specific cues. *Behav Ecol* 2003;14:282–287.
  34. Amorim M, Hawkins A. Growling for food: acoustic emissions during competitive feeding of the streaked gurnard. *J Fish Biol* 2000;57:895–907.
  35. Gainquinto PC, Volpato GL. Chemical communication, aggression, and conspecific recognition in the fish *Nile tilapia*. *Physiol Behav* 1997;62:1333–1338.
  36. Kallman KD. Evidence for the existence of transformer genes for sex in the teleost *Xiphophorus maculatus*. *Genetics* 1968;60:811–828.
  37. Kallman KD, Schreibman MP, Borkoski V. Genetic control of gonadotrop differentiation in a platyfish, *Xiphophorus maculatus* (Poeciliidae). *Science* 1973;181:678–680.
  38. Kallman KD, Borkoski V. A sex-linked gene controlling the onset of sexual maturity in female and male platyfish (*Xiphophorus maculatus*), fecundity in females and adult size in males. *Genetics* 1978;89:79–119.
  39. Van Oordt GJ. The relation between the development of secondary sex characters and the structure of the testis in the teleost *Xiphophorus helleri* Heckel. *J Exp Biol* 1925;3:43–59.
  40. Baldwin FM, Goldin HS. Effects of testosterone propionate on the female viviparous teleost, *Xiphophorus helleri* Heckel. *Proc Soc Exp Biol Med* 1939;42:813–819.
  41. Grobstein C. Effect of testosterone propionate on regenerating anal fin of adult *Platypoecilus maculatus* females. *Proc Soc Exp Biol Med* 1940;45:484–486.
  42. Baldwin FM, Li MH. Effects of gonadotropic hormone in the fish, *Xiphophorus helleri* Heckel. *Proc Soc Exp Biol Med* 1942;49:601–604.
  43. Magiulo-Cepriano L, Schreibman MP, Blüm V. Distribution of variant forms of immunoreactive gonadotropin-releasing hormone and  $\beta$ -gonadotropins I and II in the platyfish, *Xiphophorus maculatus*, from birth to sexual maturity. *Gen Comp Endocrinol* 1994;94:135–150.
  44. Somoza GM, Lescheid DW, Miranda LA, Lo Nostro FL, Magliulo-Cepriano L, Montaner AD, et al. Expression of pejerrey gonadotropin-releasing hormone in three orders of fish. *Biol Reprod* 2002;67:1864–1871.
  45. Paris F, Kaminski C, Loose C, Saidapur SK, Blüm V. Gonadal steroid metabolism *in vitro* and localization of  $3\beta$ -hydroxysteroid dehydrogenase activity in *Xiphophorus helleri* (Pisces, Teleostei, and Poeciliidae). *Ann NY Acad Sci* 1998;839:578–580.
  46. Kinnberg K, Lorsgaard B, Bjerregaard P, Jespersen A. Effects of nonyphenol and  $17\beta$ -estradiol on vitellogenin synthesis and testis morphology in male platyfish *Xiphophorus maculatus*. *J Exp Biol* 2000;203:171–181.

47. Fernald RD. How does behavior change the brain? Multiple methods to answer old questions. *Int Comp Biol* 2003;43:771–779.
48. Schreibman MP, Margolisnunno H, Halpernsebold LR, Goos HJT, Perlman PW. The influence of androgen administration on the structure and function of the brain–pituitary–gonad axis of sexually immature platyfish, *Xiphophorus maculatus*. *Cell Tissue Res* 1986;245:519–524.
49. Breuckmann A, Paris F, Schreibman MP, Blüm V. Immunoreactive gonadotropin-releasing hormone GnRH in the brain and pituitary of adult and juvenile swordtails (*Xiphophorus helleri*, Teleostei, Poeciliidae). *J Morphol* 1996;230:55–67.
50. Hannes R-P, Franck D. Diurnal variation of blood androgen and corticoid levels in male swordtails (*Xiphophorus helleri*). *Zool J Physiol* 1983;87:337–341.
51. Hannes R-P. Blood and whole-body androgen levels of male swordtails correlated with aggression measures in a standard-opponents test. *Aggressive Behav* 1986;12:249–254.
52. Netherton JD, Grober MS, Earley RL. Temporal decay of cortisol in green swordtail fish (*Xiphophorus helleri*) following aggressive encounters: differences between winners and losers? *Horm Behav* 2004;46:117–118.
53. Scott AP, Pinillos M, Ellis T. Why measure fish steroids in plasma when you can measure them in water? In: *Perspectives in Comparative Endocrinology: Unity and Diversity*. Goos HJT, Rastogi RK, Vaudry H, Pierantoni R (eds.), pp. 1291–1295. Mod-uzzi Editore, Bologna.
54. Götz R, Raulf F, Scharl M. Brain-derived neurotrophic factor is more highly conserved in structure and function than nerve growth-factor during vertebrate evolution. *J Neurochem* 1992;59:432–442.
55. Götz R, Koster R, Winkler C, Raulf F, Lottspeich F, Scharl M, et al. Neurotrophin-6 is a new member of the nerve growth factor family. *Nature* 1994;372:266–269.
56. Anken RH, Rahmann H. An atlas of the distribution of NADPH-diaphorase in the brain of the highly derived swordtail fish *Xiphophorus helleri* (Antheriniformes: Teleostei). *J Brain Res* 1996;37:421–449.
57. Anken RH, Sorger I, Bremen D, Rahmann H. NADPH-diaphorase reactivity in the Mauthner cells of the swordtail fish, *Xiphophorus helleri*. *Neurosci Lett* 1996;206:49–52.
58. Koster R, Götz R, Altschmied J, Sendtner M, Scharl R. Comparison of monocistronic and bicistronic constructs for neurotrophin transgene and reporter gene expression in fish cells. *Mol Mar Biol Biotechnol* 1996;5:1–8.
59. Li X, Franz J, Lottspeich F, Götz R. Recombinant fish neurotrophin-6 is a heparin-binding glycoprotein: implications for a role in axonal guidance. *Biochem J* 1997;324:461–466.
60. Rickard NS, Gibbs ME, Ng KT. Inhibition of the endothelial isoform of nitric oxide synthase impairs long-term memory formation in the chick. *Learning & Memory* 1999;6:458–466.
61. Branchi I, Fracia N, Alleva E. Epigenetic control of neurobehavioural plasticity: the role of neurotrophins. *Behav Pharmacol* 2004;15:353–362.
62. Jasinski A. Nucleus preopticus in hypothalamus of platyfish *Xiphophorus helleri*. *Gen Comp Endocrinol* 1966;6:386–387.
63. Anken RH, Rahmann H. Brain atlas of the adult swordtail fish *Xiphophorus helleri* and of certain developmental stages. G. Fisher, Stuttgart, 1994.
64. Schreibman MP, Halpern LR. Demonstration of neuropeptin and arginine vasotocin by immunocytochemical methods in the brain and pituitary gland of the platyfish, *Xiphophorus maculatus*. *Gen Comp Endocrinol* 1980;40:1–7.
65. Kim YS, Stumpf WE, Sar M. Topographical distribution of estrogen target-cells in the forebrain of platyfish, *Xiphophorus maculatus*, studied by autoradiography. *Brain Res* 1979;1709:43–59.
66. Thines G, Heuts B. The effect of submissive experience on dominance and aggressive behaviour of *Xiphophorus* (Pisces, Poeciliidae). *Z Tierpsychol* 1968;25:139–154.
67. Wilhelmi U. Über den Einfluß sozialer Isolation auf die Rangordnungskämpfe männlicher Schwertträger (*Xiphophorus helleri*). *Z Tierpsychol* 1975;38:482–504.
68. Röhrs WH. Veränderungen der sexuellen und aggressiven Handlungsbereitschaft des Schwertträgers *Xiphophorus helleri* (Pisces, Poeciliidae) unter dem Einfluß sozialer Isolation. *Z Tierpsychol* 1977;44:402–422.
69. Franck D, Ribowski A. Influences of prior agonistic experience on aggression measure in the male swordtail (*Xiphophorus helleri*). *Behaviour* 1987;103:217–240.
70. Franck D, Ribowski A. Escalating fights for rank-order position between male swordtail (*Xiphophorus helleri*): effects of prior rank-order experience and information transfer. *Behav Ecol Sociobiol* 1989;24:133–143.
71. Ribowski A, Franck D. Subordinate swordtail males escalate faster than dominants: a failure of the social conditioning principle. *Aggressive Behav* 1993;19:223–229.
72. Beaugrand JP, Beaugrand M. Prior residency and the stability of dominance relationships in pairs of green swordtail fish *Xiphophorus helleri* (Pisces, Poeciliidae). *Behav Proc* 1991;24:169–175.
73. Beaugrand JP, Cotnoir P-A. The role of individual differences in the formation of triadic dominance orders of male green swordtail fish (*Xiphophorus helleri*). *Behav Proc* 1996;38:287–296.
74. Beaugrand JP, Payette D, Goulet C. Conflict outcome in male green swordtail fish dyads (*Xiphophorus helleri*): interaction of body size, prior dominance/subordination experience, and prior residency. *Behaviour* 1996;133:303–319.
75. Beaugrand JP. Erratum to “Resolution of agonistic conflicts in dyads of acquainted green swordtails (*Xiphophorus helleri*): a game with perfect informa-

tion" [Behav Proc 1997;41:79–96]. Behav Proc 1997; 41:293–310.

76. Beaugrand JP, Goulet C. Distinguishing kinds of prior dominance and subordination experiences in males of green swordtail fish (*Xiphophorus helleri*). Behav Proc 2000; 50:131–142.
- AU3** → 77. Goulet C, Beaugrand JP. Relation between dominance rank, prior agonistic intensity and subsequent aggressive levels in winners and losers of dyads of male green swordtail fish (*Xiphophorus helleri*). Unpublished 2001a; available at <http://cogprints.org>.
78. Dugatkin LA, Druen M. The social implications of winner and loser effects. Proc R Soc Lond B (Suppl) 2004;271:S488–S489.
79. Zayan RC. Défense du territoire et reconnaissance individuelle chez *Xiphophorus* (Pisces, Poeciliidae). Behaviour 1975;52:266–312.
80. Wechkin S. Social familiarity and nip dominance in male swordtails (*Xiphophorus helleri*) and platys (*Xiphophorus maculatus*). Psychol Reports 1975;37: 435–438.
81. Earley RL, Dugatkin LA. Fighting, mating and networking: pillars of poeciliid sociality. In: Animal Communication Networks. McGregor PK (ed), pp. 84–113. Cambridge University Press, Cambridge, 2005.
82. Earley RL, Druen M, Dugatkin LA. Watching fights does not alter a bystander's response towards naïve conspecifics in male green swordtail fish, *Xiphophorus helleri*. Anim Behav 2005;69:1139–1145.
83. Braddock JC. The effect of prior residence upon dominance in the fish *Platypleurodon maculatus*. Physiol Zool 1949;22:161–169.
84. Zayan RC. Modification des effets liés à la priorité de résidence chez *Xiphophorus* (Pisces, Poeciliidae): le rôle de l'isolement et des différences de taille. Z Tierpsychol 1976;41:142–190.
85. Heuts BA, Nijman V. Aggressive behaviour of two swordtail colour breeds (*Xiphophorus*, Poeciliidae) in a prior residence situation. Behav Proc 1998;43:251–255.
86. Nijman V, Heuts BA. Effects of environmental enrichment upon resource holding power in fish in prior residence situations. Behav Proc 2000;49:77–83.
87. Goulet C, Beaugrand JP. Inversion of initial dominance relationships following the interchange of roles of resident and intruder within pairs of male swordtail fish (*Xiphophorus helleri*). Unpublished 2001b; available at <http://cogprints.org>.
- AU4** → 88. Franck D, Wilhelmi U. Changes of aggressive attack readiness of male swordfish, *Xiphophorus helleri*, after social isolation (Pisces, Poeciliidae). Experientia 1973;29:896–897.
89. Goldenbogen I. Influence of social isolation on attack readiness of *Xiphophorus helleri* and *Haplochromis burtoni*. Z Tierpsychol 1977;44:25–44.
90. Hannes R-P, Franck D. The effect of social isolation on androgen and corticosteroid levels in a cichlid fish (*Haplochromis burtoni*) and in swordtails (*Xiphophorus helleri*). Horm Behav 1983;17:292–301.

91. Hannes R-P. The influence of standard-opponent tests on blood androgen and corticoid levels of high- and low-ranking swordtail males (*Xiphophorus helleri*) before and after social isolation. Aggressive Behav 1985;11:9–15.
92. Franck D, Hannes R-P, Lanffermann H, Ribowski A. Effects of social isolation on aggressiveness in fish with special reference to the swordtail (*Xiphophorus helleri*). Behav Proc 1985;10:415–427.
93. Royle NJ, Lindström, Metcalfe NB. A poor start in life negatively affects dominance status in adulthood independent of body size in green swordtails *Xiphophorus helleri*. Proc R Soc Lond B 2005;272:1917–1922.
94. Sohn JJ. Socially induced inhibition of genetically determined maturation in the platyfish, *Xiphophorus maculatus*. Science 1977;195:199–201.
95. Zimmerer EJ, Kallman KD. Genetic basis for alternative reproductive tactics in the pygmy swordtail, *Xiphophorus nigrensis*. Evolution 1989;43:1298–1307.
96. Ribowski A, Franck D. Demonstration of strength and concealment of weakness in escalating fights of male swordtails (*Xiphophorus helleri*). Ethology 1993;93:265–274.
97. Zimmerer EJ, Kallman KD. The inheritance of vertical barring (aggression and appeasement signals) in the pygmy swordtail, *Xiphophorus nigrensis* (Poeciliidae, Teleostei). Copeia 1988;1988:299–307.
98. Borowsky RL. Social inhibition of maturation in natural populations of *Xiphophorus variatus* (Pisces: Poeciliidae). Science 1978;201:933–935.
99. Borowsky RL. Agonistic behavior and social inhibition of maturation in fish of the genus *Xiphophorus* (Poeciliidae). Copeia 1987;1987:792–796.
100. Scott DBC, Currie CE. Social hierarchy in relation to adrenocortical activity in *Xiphophorus helleri* Heckel. J Fish Biol 1980;16:265–277.
101. Hannes R-P, Franck D, Liemann F. Effects of rank-order fights on whole-body and blood concentrations of androgens and corticosteroids in the male swordtail (*Xiphophorus helleri*). Z Tierpsychol 1984;65:53–65.
102. Luo J, Sanetra M, Schartl M, Meyer A. Strong reproductive skew among males in the multiply mated swordtail *Xiphophorus multilineatus* (Teleostei). J Heredity 2005;96:346–355.
103. Beaugrand JP, Caron J, Comeau L. Social organization of small heterosexual groups of green swordtails (*Xiphophorus helleri*, Pisces, Poeciliidae) under conditions of captivity. Behaviour 1984;91:24–60.

Address reprint requests to:

Ryan L. Earley  
 Department of Biology  
 Georgia State University & Center for  
 Behavioral Neuroscience  
 24 Peachtree Center Avenue NE  
 Atlanta, GA 30303

E-mail: biorle@langate.gsu.edu

## **EARLEY**

### **AU1**

**Reference style for journal is to cite authors in text using a superscript Arabic number, with the reference list in numeric order as cited in the text. These instructions are provided at the back of the Zebrafish journal, and on the liebertpub.com website. In your article, because the authors were listed in alphabetical order with year of publication, there were many inconsistencies found upon correction of style. For example, year of publication cited in text did not always agree with year in reference list. Several references could not be validated on PubMed.com. Please check every reference for correction. The following references were not cited in the text:**

**Beaugrand JP, Zayan R. An experimental model of aggressive dominance in *Xiphophorus helleri* (Pisces, Poeciliidae). Behav Proc 1985;10:1–52.**

**Beaugrand JP, Goulet C, Payette D. Outcome of dyadic conflict in male green swordtail fish, *Xiphophorus helleri*: effects of body size and prior dominance. Anim Behav 41: 417: 424.**

### **AU2**

**Reference 53. Please provide year of publication.**

### **AU3**

**Reference 77. Please give date of last accession to site.**

### **AU4**

**Reference 87. Please give date of last accession to site.**

### **QU1**

**Which is correct; “fishes” or “fish”? msp. shows “fishes” and file shows “fish”**