UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
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FACULTAD DE CIENCIAS
BIOLOGÍA EVOLUTIVA Y SISTEMÁTICA

DISMINUCIÓN DE LA PREFERENCIA FEMENINA Y SU RELACIÓN CON LOS COSTOS DEL ORNAMENTO EN *Xiphophorus montezumae* (PISCES: POECILIIDAE).

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTORA EN CIENCIAS

PRESENTA:

KARLA KRUESI CORTÉS

TUTOR(A) PRINCIPAL DE TESIS: DRA. GUILLERMINA ALCARAZ ZUBELDIA
FACULTAD DE CIENCIAS
COMITÉ TUTOR: DR. LUIS MEDRANO GONZÁLEZ
FACULTAD DE CIENCIAS
DR. LUIS ZAMBRANO GONZÁLEZ
INSTITUTO DE BIOLOGÍA
TUTOR(A) INVITADO: DR. GIL GUASTONI ROSENTHAL
TEXAS A&M UNIVERSITY

MÉXICO, D.F. JUNIO, 2013.

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VNIVERSDAD NACIONAL
AVTONOMA DE
MEXICO

POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
DIVISIÓN DE ESTUDIOS DE POSGRADO

OFICIO FCIE/DEP/272/13

ASUNTO: Oficio de Jurado

Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **4 de marzo de 2013**, se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** del (la) alumno (a) **KRUESI CORTES KARLA** con número de cuenta **98548897** con la tesis titulada: **"Disminución de la preferencia femenina y su relación con los costos del ornamento en *Xiphophorus montezumae* (Pisces: Poeciliidae)"**, realizada bajo la dirección del (la) **DRA. GUILLERMINA ALCARAZ ZUBELDIA:**

Presidente:	DRA. MARÍA DEL CARMEN URIBE ARANZABAL
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De acuerdo con lo anterior, el(a) alumno(a) se acogió a la nueva normatividad, con base en el artículo QUINTO TRANSITORIO en apegó a lo establecido en el Artículo 31 del Reglamento General de Estudios de Posgrado (9 octubre de 2006).

Sin otro particular, me es grato enviarle un cordial saludo.

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, D.F. a 28 de mayo de 2013.

Dra. María del Coro Arizmendi Arriaga
Coordinadora del Programa

FACULTAD DE CIENCIAS
DIVISION DE ESTUDIOS DE POSGRADO

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ÍNDICE

RESUMEN

La evolución de los caracteres sexuales secundarios (CSS) se debe a la selección sexual, que los favorece tanto en la competencia por el acceso a una pareja reproductiva como a través de la preferencia femenina. Los CSS pueden ser costosos de producir, de mantener, o generar desventajas para los portadores en el desempeño de actividades ecológicamente relevantes. Si además de ser costosos están relacionados con la viabilidad en los machos, y si la preferencia femenina los favorece, se puede suponer que son indicadores de la calidad de los individuos.

Uno de los grupos de peces dulceacuícolas más estudiados desde la perspectiva de la biología evolutiva de CSS es el grupo de los poecílidos. El género *Xiphophorus* presenta características que lo hacen particularmente interesante como la espada, un ornamento que desarrollan los machos de algunas especies al alargarse los rayos inferiores de la aleta caudal. Este carácter puede alcanzar una longitud mayor a la del cuerpo del pez. Tanto la preferencia de las hembras por esta estructura como la espada misma son caracteres ancestrales en el grupo, sin embargo la espada se ha perdido varias veces en la historia evolutiva de *Xiphophorus*. En este estudio se estimó la relación del desarrollo de la espada con la tasa de crecimiento corporal en *Xiphophorus montezumae* (especie con la espada más larga en el género) y sus costos en términos del desempeño de escape. Además, se estimó la preferencia de las hembras en relación a la longitud de la espada con el fin de determinar si en esta especie la relación de los costos con los beneficios reproductivos de la espada puede explicar su evolución como un carácter indicador de la calidad de los individuos.

Los resultados mostraron que bajo condiciones controladas los peces asignan mayores recursos al crecimiento corporal que al desarrollo de la espada. Al final de nuestro experimento los individuos de mayor talla presentaron espadas más cortas, sin embargo esta estructura aparentemente es un carácter que continúa su crecimiento a lo largo de la vida del pez. Adicionalmente, la espada, que es un ornamento conspicuo (riesgo de depredación), incrementa de manera significativa el tiempo en el que el pez completa la maniobra de escape al disminuir la propulsión del pez. Las hembras mostraron preferencia por la longitud de la espada, sin embargo este carácter no resulta atractivo independientemente de su longitud. Los resultados en este estudio sugieren que las hembras evalúan el desempeño de los machos durante el cortejo y que la espada, al ser un ornamento costoso podría comprometerlo resultando menos atractivo al llegar a cierto umbral en su expresión.

Para que un individuo sobreviva portando una espada en su medio natural, debe pagar los costos de esta estructura, que podrían incrementarse conforme la espada crece. Los resultados obtenidos en este estudio indican que la espada es un ornamento costoso que podría representar una desventaja para la supervivencia ya que disminuye la habilidad de escape. Con esta desventaja, y los costos que se han reportado para esta especie en términos energéticos y de desempeño de nado, sugerimos que la espada en la especie representa una desventaja de manera que sólo aquellos que tienen la calidad genética para pagar estos costos, tanto en el escape ante depredadores (selección natural) como en el cortejo en la competencia por el acceso a una hembra (selección inter-sexual), pueden ser exitosos en términos de adecuación. Adicionalmente, las hembras de *X. montezumae* muestran una preferencia por la espada con un valor inferior al de otras especies del género *Xiphophorus*, por lo que esta especie es un excelente modelo para explicar la evolución y el mantenimiento de ornamentos de expresión exagerada que son costosos en las especies animales, posiblemente debido a la evolución de mecanismos de compensación.

Palabras clave: caracteres sexuales secundarios, costos de ornamentos, preferencia femenina, pez cola de espada, *Xiphophorus montezumae*.

ABSTRACT

The evolution of secondary sexual traits is directed by sexual selection processes, favouring males with conspicuous characters in intrasexual competence or by female preference. Sexually selected traits (SST) might be costly to produce or maintain, or may generate disadvantages to the bearers while performing ecologically relevant activities. If besides being costly, the SST are correlated with male viability and favoured by female preference, they might indicate male quality as a reproductive mate.

From the perspective of the evolution of sexually selected traits, the poeciliids (livebearing fish) is one of the most studied groups of freshwater fish. Particularly, the genus *Xiphophorus* presents characteristics with scientific interest like the sword, which is an ornament that the males of some species develop when they reach sexual maturity. Their common name is swordtails. This trait consists of the enlargement and pigmentation of the inferior caudal fin rays, and in some species it may grow longer that the males bodies. Females in this genus prefer males with swords, even in species where males don't develop this traits. However, this character appears to have been lost independently several times in the history of *Xiphophorus*, probably due to its costs. In this study, we estimated the relationship of sword length with a life history trait like body growth and the costs it produces in terms of escape performance in *X. montezumae*, which is the species with the longest sword among swordtails. Aditionally, we measured female preference for sword length in order to estimate if this species shows a relationship between costs and the reproductive benefits that might explain its evolution as an indicator trait of male quality.

The results showed that under controlled laboratory conditions the fish allocate more resources to body growth. At the end of the experiment the fish which were bigger in size had shorter swords, however this character continues growing but at lower rates after the males reach their maximum adult body size. The sword, that is a conspicuous ornament (enhances predation risk) increased significantly the time of completion of the escape maneuver (C-start) because it reduces fish propulsion. Females showed preference for sword length, but there is a threshold in female response that suggests that this character is not attractive independent of its length. The results in this study suggest that Montezumae swordtail females assess male performance during courtship, which might be compromised by sword length making it less attractive to females.

That a male swordtail survives bearing a long sword in its natural environment involves paying the costs of this structure. Moreover, these could increase along with male age as the sword grows. This study suggests that the sword is a costly ornament that might be disadvantageous to male survival by decreasing its ability to escape from common predators. With this handicap and the energetic costs of the sword during courtship and steady swimming modes, we suggest that only the males with genetic quality might be capable of paying this costs in order to escape from predators (natural selecyion) and perform courtship displays that make them win the competence for resproductive mates (inter-sexual selection). Aditionally, the females of *X. montezumae* show lower preference for the sword than the females in other swordtail species. This makes Montezuma swordtails an excellent model to explain the evolution and maintenance of exaggerated ornaments, possibly due to the evolution of mechanisms of compensation.

Keywords: sexually selected traits, costs of ornaments, female preference, swordtails, *Xiphophorus montezumae*.

1. INTRODUCCIÓN GENERAL

“Los ornamentos: ¿Cuál es su función y significado?”

Karla Kruesi Cortés

Como un breve preámbulo, en estudios de conducta y evolución es reconocido el uso de términos de carácter subjetivo para calificar algunos atributos morfológicos y conductuales sobre los que tiene un efecto la selección sexual (caracteres honestos, exagerados, etc.), incluyendo algunos términos que se utilizan para calificar a los individuos que expresan estas características. La mayoría de estos conceptos fueron empleados por primera vez al plantearse las hipótesis para explicar los mecanismos con los que opera este proceso de evolución, señalado por Darwin en 1871. Aunque se reconoce que contienen un componente subjetivo, hoy en día siguen siendo aceptados y manejados comúnmente en documentos científicos, por lo que en este estudio se utilizarán de igual manera, no sin antes definir brevemente su significado estricto.

Los caracteres sexuales secundarios (CSS) son atributos que expresan los organismos al alcanzar la madurez sexual, que no interactúan directamente con la fisiología de la reproducción pero que juegan un papel importante en la comunicación intraespecífica relacionada con la competencia por el acceso a una pareja reproductiva. En muchos casos, los CSS han evolucionado hacia formas elaboradas a través de los procesos de selección sexual y su evolución tiene que ver directamente con su función como señales ya que su expresión cambia el comportamiento del receptor beneficiándolo en un sentido adaptativo (Darwin 1871; Johnstone 1995; Maynard Smith y Harper 2003). La larga cola del pavo real y su cortejo, el cuerno de los escarabajos coprófagos, la coloración azul en las patas y la danza de cortejo del pájaro bobo, el tamaño y color rojo de las aletas del pez guppy, el canto en las aves y la cornamenta de algunos mamíferos son algunos ejemplos de estos caracteres a los que comúnmente se les llama caracteres ’exagerados‘ porque su expresión elaborada es fisiológicamente costosa de producir o de mantener (Pomiankowski et al. 1991).

El aspecto más importante de estos caracteres es que causan el apareamiento no azaroso entre los miembros de una población y que al ser elaborados pueden reducir la sobrevivencia de quien los porta (Darwin 1871). Los CSS presentan mayor variación fenotípica que aquéllos que sólo están sujetos a procesos de selección natural y de acuerdo con los principios fundamentales de la selección sexual, si existe variación entre los individuos (reproductivamente activos) de una población en su expresión, entonces aquéllos individuos que presentan los atributos más atractivos para el sexo opuesto (selección intersexual), las características que aseguren ganar la competencia por el acceso a una pareja o los individuos más eficientes como progenitores (selección intrasexual), tendrán mayor éxito reproductivo y como consecuencia una mayor adecuación (Darwin 1871; Andersson 1994).

La competencia por el acceso a parejas reproductivas ha producido CSS que pueden funcionar como armamentos u ornamentos en la selección inter e intrasexual. A diferencia de los armamentos, los ornamentos son caracteres fenotípicos que no tienen una función utilitaria pero que se explotan como señales en la comunicación entre individuos. Éstos pueden ser características morfológicas que se exhiben a los conespecíficos a través de despliegues conductuales, o pueden ser conductas de cortejo complejas que demuestren alguna cualidad del individuo (Ryan 1980; Brodsky, 1986; Ligon et al. 1990; Johnstone 1995). Varias décadas después de la propuesta de Darwin acerca de que los ornamentos tenían una función estética en el contexto de la selección de una pareja reproductiva, comenzaron a surgir diversas hipótesis para explicar su evolución y en los últimos años se ha producido un amplio marco teórico y empírico en estudios con diversos grupos animales, poniendo particular énfasis en aclarar los mecanismos por los que se genera la preferencia femenina y las consecuencias funcionales y ecológicas de desarrollar caracteres atractivos. Se reconoce que son posibles diferentes mecanismos evolutivos ya que no todos los caracteres sexuales han evolucionado dentro del mismo contexto y que la selección sexual es sin duda un proceso complejo que debe explicarse en muchos niveles (Irschick et al. 2007).

¿QUÉ BUSCAN ELLAS?: LA PREFERENCIA FEMENINA

Típicamente, en los diversos grupos de animales, el sexo femenino es el selectivo y de manera general puede elegir activamente una pareja reproductiva de entre los miembros del sexo masculino en competencia, puede controlar la paternidad de su progenie a través de la selección críptica- posterior al apareamiento- (Birkhead 1996) o de la inversión diferencial de recursos y el esfuerzo parental en relación con la calidad de la pareja reproductiva (De Lope y Møller 1993). El término ’calidad’ se utiliza para calificar a las parejas reproductivas que aportan beneficios para las hembras, incrementando su adecuación. Los modelos de evolución de caracteres por preferencia femenina están basados en su sentido adaptativo, que consiste en la adquisición de estos beneficios como consecuencia de su selectividad (Kirkpatrick 1996; Kirkpatrick y Ryan 1991).

Los beneficios directos son aquellos en los que la hembra adquiere algún recurso que le de ventajas en términos de adecuación, como obtener más o mejor alimento, mejor territorio, regalos nupciales más grandes o de mayor calidad, una pareja con mejores habilidades de cuidado parental o una elevada eficiencia de fertilización (Trivers 1972; ver Tazziman et al. 2011). Los beneficios indirectos son aquellos en los que la selección no da ventaja a ésta sino a su progenie por ejemplo al incrementar su éxito reproductivo, ya sea heredando los caracteres atractivos (hipótesis del hijo sexy; Fisher 1930) o alguna característica que esté asociada con su expresión como las que son dependientes de la calidad del alimento o la asimilación del mismo, o el adquirir calidad genética en términos de supervivencia, resistencia a enfermedades, etc. (teoría de buenos genes; Zahavi 1975; Kokko 1998), así como genes compatibles que incrementen la viabilidad de la progenie en este sentido (Tregenza y Wedel 2000). En las especies en las que las hembras no reciben beneficios directos, éstas pueden aportar a su progenie los beneficios genéticos de aparearse con machos atractivos. A través de estos mecanismos se mantiene la preferencia femenina por individuos con determinadas características (Kokko et al. 2002).

Aunque actualmente existe un gran número de publicaciones con ejemplos muy diversos que describen de manera específica cuáles son las preferencias femeninas en muchos grupos animales incluyendo la especie humana, los mecanismos por los que se originó la preferencia hacia determinadas formas de expresión de los caracteres sexuales secundarios aún no son completamente comprendidos (Cummings 2012). Las hembras utilizan sus capacidades de percepción sensorial y cognitivas en la evaluación y la selección de una pareja reproductiva (Ryan et al. 2009). Éstas pueden discriminar la intensidad y composición de las 'señales' de los machos a través de cualidades como la saturación y patrones de coloración, talla, forma, simetría corporal, olores, sonidos, así como pueden detectar aptitudes en el desempeño de las parejas potenciales en diferentes actividades como los despliegues de cortejo, la rapidez en la locomoción y la habilidad para evadir depredadores, entre muchas otras. Un ejemplo que está muy bien documentado es el canto de cortejo en las aves; los machos incrementan la intensidad del canto durante la etapa reproductiva y su máxima expresión ocurre apenas antes de la oviposición (Slagsvold 1977). Esta señal desencadena la actividad neuronal que está relacionada con la discriminación de sílabas 'sexys' y la ejecución de algunas conductas que señalan la receptividad en las hembras (Leitner y Catchpole 2002). La preferencia en las hembras puede ser muy específica hacia machos que tengan mayor repertorio de sonidos, que dichos sonidos sean más complejos, de mayor duración o incluso que en contenido sean familiares de acuerdo con su localidad (Nowicki y Searcy 2004).

En algunas especies, los mismos atributos que dan ventaja a los machos en la competencia con individuos del mismo sexo por el acceso a una pareja reproductiva son también favorecidos por la preferencia femenina. Por ejemplo, el berrendo (*Antilocapra americana*) desarrolla una cornamenta como carácter sexual secundario que es utilizada a manera de armamento en el combate con otros machos. Los individuos con una cornamenta de mayor tamaño suelen ganar los enfrentamientos y las hembras muestran preferencia por éstos, que además exhiben mayor vigor durante los combates (Byers et al. 1994). Sin embargo, esta convergencia no ocurre en todos los casos y existen también ejemplos en los que aquellos caracteres que dan ventaja a los machos en términos de competencia intrasexual no son favorecidos por preferencia femenina, como en la lagartija *Podarcis melise* en donde los machos presentan polimorfismo en su coloración ventral (anaranjado, amarillo y blanco). Mientras que los machos dominantes son de color anaranjado y de ellos los ganadores en encuentros agonísticos tienen cabeza grande y mayor fuerza de mordida, las hembras prefieren parejas que no señalen un peligro potencial para ellas (con coloración ventral amarilla o blanca) y generalmente evaden a los machos con coloración ventral anaranjada, posiblemente para evitar ser heridas en encuentros con los machos más fuertes. Se sugiere que esta divergencia podría ser responsable de mantener el polimorfismo en este carácter masculino (Huyghe et al. 2012).

Es posible que la forma de expresión de los CSS que beneficia a los miembros de uno de los sexos no sea ventajosa para el sexo opuesto, generando un conflicto intersexual (Holland y Rice 1998; Arnqvist 2006). Aunque la evolución de los ornamentos por selección intersexual obedece a las ventajas reproductivas que adquieren hembras y machos, evaluar el contenido funcional y el significado de las señales es importante para explicarla. Es posible también que el origen y la evolución de los caracteres sexuales secundarios sea en algunos casos consecuencia de que son indicadores efectivos de la calidad del individuo que los expresa (Andersson 1994; Kokko et al 2003; Birkhead et al. 2006). El término 'calidad' generalmente se refiere al fondo estructural, funcional y fisiológico de los organismos, que los hace más viables en términos de adecuación. Algunos autores han propuesto que no todos los ornamentos son indicadores de la calidad de los portadores y que su evolución podría deberse a la explotación en la comunicación inter e intrasexual de sistemas sensoriales que evolucionaron por selección natural (Endler 1992). En este caso, los caracteres ornamentales son caracteres que evolucionaron maximizando la explotación de estos sesgos sensoriales de manera que únicamente sean consecuencia de ser percibidos (y de esta manera seleccionados) por la mayoría de las hembras (Basolo 1990; Ryan et al. 1990; Enquist and Arak 1993; Ryan 1998). Esta hipótesis se ha enfrentado a algunas críticas y en los últimos años se ha propuesto que los sesgos sensoriales podrían corresponder al origen de las preferencias más que a su dirección en la evolución, en la que ya están involucrados otros mecanismos.

¿LOS ORNAMENTOS SON SEÑALES HONESTAS?

Algunos autores asumen que cuando los ornamentos son indicadores de la calidad de los individuos que los expresan, entonces funcionan como señales 'honestas' de una cualidad que las hembras seleccionan (Kotiaho 1999; Payne y Pagel 2001). Aunque no todas las señales son honestas ya que algunas son utilizadas a modo de 'engaños', de manera general se piensa que el que un ornamento permanezca por un tiempo evolutivo es consecuencia de su función en la comunicación entre sexos advirtiendo cualidades del individuo que lo expresa, ya sea como un indicador o amplificador de esta cualidad y de la capacidad de superar las desventajas si el atributo que se exhibe es costoso (Zahavi 1975; Hasson 1990; Taylor et al. 2000; Husak y Swallow 2011).

La teoría de indicadores dice que el grado de expresión de los ornamentos está relacionado con los atributos que señala de manera que engañar es imposible. Por ejemplo algunas conductas hacen evidente el tamaño de estructuras corporales o la talla de los individuos que son seleccionados sexualmente como exhibir apéndices, estirar el cuerpo, o erguir las aletas en los peces. Algunas pueden ser conductas sencillas y de bajo costo de manera que la eficiencia de la señal dependa directamente de la dimensión de las estructuras que se exhiben. Otro tipo de señales son las ‘amplificadoras’ que por sí solas no son indicadoras de la calidad del emisor pero facilitan al receptor de la señal la evaluación de otro carácter importante en términos de selección sexual. Generalmente se trata de patrones de pigmentación contrastantes que no son costosos de producir o mantener, sin embargo la calidad de la señal amplificadora puede ser dependiente de condición al tratarse de pautas más complejas por lo que la eficiencia de expresión de la señal está positivamente correlacionado con la cualidad que se señala (Hasson 1991). Exhibir patrones de coloración u otro ornamento a través de ciertas conductas puede depender del estado de salud del individuo, de su condición, o de alguna cualidad metabólica (Iwasa y Pomiankowski 1999). Por ejemplo, el antílope acuático *Kobus ellipsiprymnus* presenta un patrón circular de pelaje de color blanco alrededor de su cola. Aunque este atributo se expresa tanto en hembras como machos, se ha estimado que las hembras utilizan este carácter para seleccionar una pareja reproductiva. Los machos con mayor éxito reproductivo son aquellos en los que este patrón es más redondo que elíptico y esto sólo es un efecto producido por la masa corporal de los individuos. Los machos que son reproductivamente exitosos son los que tienen una mejor condición, señalada por la redondez de la mancha en el pelaje (Taylor et al. 2000). El estado o condición de un individuo se entiende como el conjunto de recursos disponibles para asignarlos a aquellos caracteres que mejoran su adecuación (Kotiaho 1999). Cuando un carácter ornamental es dependiente de la condición, por definición existe una correlación directa entre ésta y el grado de expresión del carácter, entonces la señal revela la cualidad intrínseca de quien la emite y el carácter es honesto.

Muchos CSS elaborados como las vocalizaciones, ciertas pautas de conductas de cortejo y las estructuras de proporción exagerada que funcionan como ornamentos son atributos costosos (Darwin 1871). El grado en el que se expresan puede estar relacionado con la inversión fisiológica para producir y mantener la señal a costa de la inversión en otras características, ya sea porque comprometen al individuo a compensar las desventajas de expresar estos caracteres o lo afectan directamente en términos de supervivencia. Un organismo que debe pagar los costos asociados a la expresión de un ornamento puede limitar la inversión de recursos hacia otros procesos fisiológicos como alcanzar una talla adecuada en la etapa adulta o mantener la condición corporal (en función del peso), incluso puede limitar el desarrollo de otros caracteres morfológicos (Emlen 2001). Adicionalmente las estructuras de proporciones exageradas pueden producir una disminución del desempeño locomotor, ocasionando limitaciones en actividades relevantes como la búsqueda de alimento (Barbosa y Møller 1999), el cortejo (Basolo y Alcaraz 2003), el escape de los depredadores (Gwynne et al. 2007) e incluso pueden generar una disyuntiva de inversión energética que afecte seriamente la probabilidad de supervivencia de los individuos.

Aunque en muchos casos los costos de los ornamentos pueden no ser evidentes porque evolucionaron junto con mecanismos de compensación (McCullough et al. 2012), si se puede determinar que un ornamento es costoso, entonces se puede suponer que los individuos que superan estas desventajas son biológicamente más aptos en el desempeño de actividades ecológicamente relevantes y por lo tanto el CSS puede ser un indicador honesto de la viabilidad del portador. Zahavi (1975) afirmó que los ornamentos pueden indicar la calidad de los individuos que las expresan debido a que sus costos son relativamente más elevados para los individuos de menor calidad; de esta manera no todos los organismos de una población pueden explotar los ornamentos atractivos con éxito por ser una desventaja que afecta su supervivencia (‘handicap’ o principio de las desventajas). Por lo tanto, cuando las hembras seleccionan a los individuos con mejores atributos están discriminando hacia un individuo que ha ‘pasado una prueba’ a lo largo de su vida desde su maduración sexual, asegurando la selección de una pareja reproductiva con un genotipo viable en términos de adecuación. Para determinar que los caracteres sexuales evolucionan de acuerdo con este principio es necesario medir los costos que éstos generan (Grafen 1990).

Algunos científicos propusieron que los ornamentos deben, como requisito, ser costosos para que su función sea un indicador honesto de la calidad del individuo que lo señala (Johnstone 1995, Kotiaho et al. 1998). Sin embargo, comprobar los costos no es una tarea sencilla, ya que dependen de límites fisiológicos, morfológicos y conductuales que pueden presentar plasticidad fenotípica y ser interdependientes, además de que los mecanismos de compensación que los enmascaran pueden también ser complejos. Específicamente, se debe investigar en qué consisten estos costos, si es que están presentes. Por ejemplo, en algunas especies de reptiles y anfibios el éxito reproductivo depende de las vocalizaciones que son energéticamente costosas, de manera que pocos machos podrán efectuar vocalizaciones largas y de mejor calidad para atraer y ser seleccionados por las hembras (Sullivan y Kwiatkowski, 2007). Se han llevado a cabo numerosos estudios que pretenden conocer, a través de la estimación de diferentes parámetros biológicos, si dentro de una población los individuos con mayor expresión de un CSS elaborado son aquellos que deben pagar costos más altos y si existe o no una correlación entre éstos y la calidad genética de los individuos exitosos. Existe mucha información en este sentido y los trabajos teóricos y empíricos producidos hasta ahora han verificado que aunque no representaran costos, en la mayoría de los casos es necesario expresar alguna cualidad que respalde la señalización adecuada del potencial de un individuo como pareja reproductiva; es decir, que debe existir una correlación positiva entre la expresión de un carácter visible (un carácter sexual secundario) y una o varias cualidades que no se expresan de manera evidente (Számadó 2011).

EL GÉNERO Xiphophorus COMO MODELO DE EVOLUCIÓN DE ORNAMENTOS

Los peces dulceacuícolas de la familia Poeciliidae, se consideran excelentes modelos en biología experimental y evolutiva debido a su tamaño reducido, su disponibilidad, fácil manejo y bajo costo de mantenimiento. Este grupo presenta muchas especies endémicas que ocurren principalmente en México, Centroamérica y las Antillas (Hrbeck et al. 2007). Los poecílidos constituyen un grupo particularmente importante debido a que son uno de los cuatro grupos del orden Cyprinodontiformes que desarrollaron fertilización interna y uno de los tres que presentan viviparidad; lo cual tiene consecuencias estructurales, fisiológicas, conductuales y ecológicas en los organismos en estado reproductivo (Reznick et al. 1990; Plaut 2002). Particularmente, el género *Xiphophorus* (pez cola de espada) es un grupo monofilético de la familia Poeciliidae que habita en ríos poco profundos de las cuencas de agua dulce que son afluentes del Océano Atlántico en México y Centroamérica. Actualmente cuenta con 26 especies descritas. Los peces cola de espada y los platis (peces del mismo género cuyos machos no expresan la espada) son endémicos del continente americano y están ampliamente distribuidos en México, donde se encuentran 21 especies de las que comprenden este género (Rauchenberger et al. 1990; Espinoza 1993) y de las cuales 19 son endémicas. De acuerdo con el listado generado por la SEMARNAT (NOM-059-2010), una de ellas (*X. clemenciae*) es una especie amenazada y cuatro (*X. couchianus*, *X. gordoni*, *X. meyeri* y *X. milleri*) se encuentran registradas en peligro de extinción.

Los peces de este grupo son especies relevantes en diversos campos de estudio de carácter científico y comercial. En el campo de investigación en medicina debido a que desde más de ocho décadas es utilizado en la investigación de cáncer, principalmente el de piel (formación de melanomas; Gordon, 1927; Kosswig, 1928). Comercialmente constituyen un grupo importante ya que algunas especies son consideradas peces de ornato (particularmente *X. helleri* y *X. variatus*). Sin embargo, los peces de este género son estudiados principalmente en una amplia gama de disciplinas de la Biología, siendo un excelente modelo en estudios de selección sexual.

Los peces del género *Xiphophorus* expresan caracteres sexuales secundarios que los han hecho particularmente interesantes para explicar, entre otros aspectos, los mecanismos de dirección sensorial, comunicación interespecifica, selección sexual y la evolución de ornamentos. Uno de los ornamentos más atractivos en términos científicos y que ha sustentado un gran número de estudios desde las observaciones de Darwin (1871) como parte de su teoría de Selección Sexual, consiste en la elongación y pigmentación de los rayos inferiores de la aleta caudal que forma una estructura que se denomina 'espada' (Basolo 1995). Este carácter es utilizado en la comunicación intraespecífica y se ha propuesto que ha tenido un papel importante en la evolución del grupo habiendo fuerzas selectivas que operan a su favor (selección sexual) y en contra (selección natural), pues al desarrollarse incrementa los costos de nado (energéticos) y el riesgo de depredación de los machos adultos (Rosenthal et al. 2001; Basolo y Wagner 2004, Hernández-Jiménez y Ríos-Cárdenas 2012).

Aunque la depredación actúa seleccionando contra los peces más conspicuos, las hembras de muchas especies, incluyendo aquellas en las que los machos no desarrollan espadas, muestran una preferencia hacia este carácter. La preferencia femenina en el grupo es un carácter ancestral y una de las propuestas de evolución de la espada dice que se debe a la explotación de un sesgo sensorial preexistente (Basolo 1990; Basolo 1995; Endler y Basolo 1998), como lo describió Endler (1992). Los análisis filogenéticos basados en una gran cantidad de caracteres morfológicos y conductuales (Rosen 1979) apoyaron la teoría de que las hembras en el grupo tenían una preferencia ancestral por la espada, la cual precedía a su origen. Sin embargo, esta teoría no fue del todo aceptada y de acuerdo con análisis moleculares filogenéticos posteriores utilizando secuencias de DNA nuclear y mitocondrial, los sesgos preexistentes parecen no explicar de manera adecuada la historia evolutiva del carácter en el grupo (Da Silva et al. 1991; Meyer et al. 1994). En cambio, se sugiere que la espada es un carácter ancestral que se ha perdido de manera secundaria en varios eventos independientes (Meyer et al. 2006; Cui et al. 2013). Con esta nueva hipótesis acerca de la historia evolutiva del grupo, Meyer y colaboradores (1994) propusieron que la presencia de la espada confiere costos en términos de selección natural que van en dirección contraria que cualquier beneficio que brinde la selección sexual, y que estos costos quizás dieron dirección en la evolución de algunas especies que perdieron la espada aún en la presencia de un sesgo 'retenido'.

Las hembras de este género muestran una consistencia en la preferencia por el carácter, lo que puede deberse a que la preferencia está muy relacionada con la percepción sensorial en las hembras del género, sugiriendo que este carácter puede ser heredable y plástico (Johnson y Basolo 2003; Basolo y Wagner 2004). Además de la comunicación química por vía hormonal (Fisher y Rosenthal 2006), la vía visual y el cortejo parecen ser componentes importantes en la comunicación intersexual en este grupo (Rosenthal et al. 1996), que en algunas especies puede estar constituido por un complejo compuesto de pautas de nado (Haas 1993). Aparentemente, existe un canal visual intraespecífico de comunicación (explotando la radiación UV) que no comparten con los depredadores acuáticos más comunes en su medio, como el pez tetra mexicano *Astyanax mexicanum* (Cummings et al. 2003). Se ha sugerido que en este canal de comunicación la línea lateral del pez se continúa con el patrón lineal de melanina (negro) de la espada, de manera que estos caracteres en conjunto pueden funcionar como una señal que incrementa la talla aparente de los machos (Rosenthal y Evans 1998) y que es exhibida durante el cortejo.

Existe una gran variación entre especies de *Xiphophorus* en la expresión de la espada, principalmente en su longitud, curvatura y en la composición de los patrones de pigmentación. Aunque los machos de los platys no expresan la espada, se conoce que los genes que codifican para la elongación de los rayos inferiores de la aleta caudal están presentes en muchas de las especies, pues su expresión puede ser inducida incluso entre las hembras por medio del tratamiento con testosterona (Zander y Dzwillo 1969). El desarrollo de la espada es iniciado con la expresión de los genes *msxC* (Zauner et al. 2003; Offen et al. 2009), sin embargo los límites de su longitud parecen estar asociados más bien con la variación ambiental. Los estudios que se han llevado a cabo al respecto indican que la disponibilidad de alimento determina la elongación de la espada, lo cual a su vez está asociado a una disyuntiva entre el desarrollo de este carácter y el incremento en la talla corporal; adicionalmente el riesgo de depredación también determina la longitud del ornamento en las poblaciones (Basolo 1998; Marcus y McCune 1999; Basolo y Wagner 2004). Existe evidencia empírica que sugiere que la espada se ha perdido en el grupo por efecto contrario de las presiones de selección natural sobre la selección sexual inducido por los costos de la depredación (Basolo y Wagner 2004; Hernández-Jimenez y Ríos-Cárdenas 2012) o porque la preferencia femenina por este carácter se ha debilitado (Rosenthal et al. 2002; Cui et al. 2013). En este estudio utilizamos la especie con la espada más larga del grupo (*Xiphophorus montezumae*) con el fin de estimar los costos asociados a este ornamento y determinar de qué manera están relacionados con la preferencia femenina.

¿QUÉ SABEMOS DEL PEZ COLA DE ESPADA DE MONTEZUMA?

Xiphophorus montezumae es una especie de pez cola de espada que fue descrita por Jordan y Snyder en 1900. Su nombre común es pez cola de espada de Montezuma y está distribuido en las cuencas de los ríos Tamesí y Pánuco en los estados de Tamaulipas y San Luis Potosí (Rauchenberger et al. 1990; Espinoza et al. 1993). Taxonómicamente pertenece al clado de los peces cola de espada del norte, que es un grupo monofilético compuesto por nueve especies actualmente reconocidas. Todas éstas convergen en el drenaje del Río Pánuco a lo largo del lado Este de la Sierra Madre Oriental. La localidad típica de *Xiphophorus montezumae* es Río

Verde (en San Luis Potosí) y es una especie tropical endémica del noreste mexicano. Principalmente habita en cuerpos someros de agua dulce, como arroyos de corriente moderada y manantiales en cuyas orillas crece vegetación abundante que utiliza como refugio.

Son omnívoros, se reproducen todo el año y sus depredadores pueden ser otros peces como el tetra *Astyanax mexicanum*, que cohabita con muchas especies de *Xiphophorus* en todo el país, algunos cíclidos como *Herichtys labridens* que puede ser un depredador ocasional (Rosenthal et al. 2001; Hernández-Jiménez y Ríos-Cárdenas 2012) y también reptiles acuáticos y algunas aves (Rosenthal y Jofre, comunicación personal). Tiene importancia comercial como pez de ornato. Entre acuaristas se le conoce como una especie esquiva, las trampas especiales para capturar peces no son efectivas con el pez cola de espada de Montezuma y el método más adecuado es cercar lentamente a los organismos con redes tipo jábega (observaciones personales).

Presentan dimorfismo sexual. El crecimiento corporal es determinado en los machos que pueden medir hasta 5.5 cm de largo y es indeterminado en las hembras que pueden rebasar los 6 cm de longitud patrón (Álvarez 1950). Al alcanzar la madurez sexual los machos desarrollan los caracteres sexuales secundarios que los hacen particularmente llamativos, principalmente la espada que comúnmente rebasa la longitud del cuerpo del pez (Fig. 1). La altura máxima del cuerpo es de 3 a 3.5 veces menor y la longitud cefálica de 4 a 4.3 veces menor que la longitud estándar. La aleta dorsal consta de 11 a 13 radios y la aleta anal de las hembras presenta de 6 a 8 radios. Los machos son generalmente de color amarillento con las escamas de la región dorsal marginadas en negro (Álvarez 1950). Las hembras se caracterizan por ser pálidas con aletas poco pigmentadas y su aleta caudal es redondeada y simétrica.

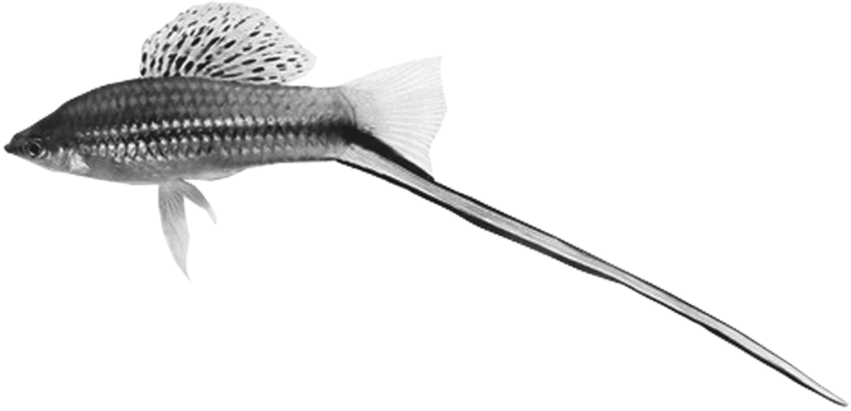

Fig. 1. Fotografía de *Xiphophorus montezumae* (Jordan y Snyder 1900) tomada por Greg Sage (Select Aquatics of Erie, CO, E.U.A). Macho adulto de la población de Tamasopo en San Luis Potosí (México) que ha desarrollado una espada que es 1.6 veces más larga que su cuerpo (longitud estándar).

ACERCA DE ESTE ESTUDIO

La presencia de un carácter sexual secundario como la espada modifica la forma de la aleta caudal y la hace asimétrica en comparación con la de las hembras. Esta asimetría resulta energéticamente costosa para los individuos tanto en el nado de rutina (de baja velocidad) como en las maniobras elaboradas de cortejo que *X. montezumae* utiliza en la competencia por una pareja reproductiva y disminuye la velocidad crítica de nado en un 20% (Basolo y Alcaraz 2003; Kruesi y Alcaraz 2007). Esta especie se ha utilizado para estimar los costos de la espada por expresar el carácter más largo en el grupo. Sin embargo, se ha publicado aun muy poca información acerca de la preferencia de las hembras, de las consecuencias de portar un ornamento que excede la longitud corporal y de cómo están relacionados los costos que los caracteres exagerados representan para los portadores con la preferencia en las hembras. Este estudio pretende relacionar la expresión de la espada con aspectos de historia de vida en los peces cola de espada de Montezuma. Se estima si existen límites en su expresión y si ésta disminuye la habilidad de maniobra durante el escape de los depredadores. Asimismo se pretende estimar si las hembras de esta especie seleccionan de manera consistente a los machos con espada larga.

La evaluación de la preferencia de las hembras de *X. montezumae* por este carácter y su relación con los costos que genera puede explicar los efectos de la selección sexual en la evolución de este carácter. Debido a que la expresión de este ornamento no es facultativa (es decir, es un carácter morfológico que se expresa de manera continua en los adultos) y a que los individuos que la desarrollan deben pagar los costos asociados de manera constante, nuestra hipótesis predice que si la espada en *X. montezumae* es costosa y las hembras muestran una preferencia por la longitud de este carácter, este ornamento puede ser un indicador de la calidad de los machos (en términos de su habilidad de sostener los costos en la locomoción).

2. CRECIMIENTO Y ORNAMENTACIÓN

K. Kruesi, G. G. Rosenthal y G. Alcaraz

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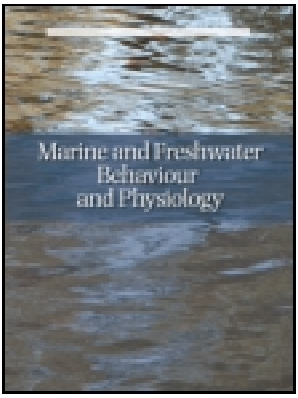

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Growth and male ornamentation in *Xiphophorus montezumae*

Karla Kruesi [a] , Gil G. Rosenthal [b] [c] & Guillermina Alcaraz [a]

[a] Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, México City, México

[b] Department of Biology, Texas A&M University, College Station, Texas, USA

[c] Centro de Investigaciones Científicas de las Huastecas "Aguazarca", Calnali, Hidalgo, México

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Growth and male ornamentation in *Xiphophorus montezumae*

Karla Kruesi[a], Gil G. Rosenthal[b,c] and Guillermina Alcaraz[a]*

[a]*Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, México City, México;* [b]*Department of Biology, Texas A&M University, College Station, Texas, USA;* [c]*Centro de Investigaciones Científicas de las Huastecas "Aguazarca", Calnali, Hidalgo, México*

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Juvenile growth rate is an important life-history trait that affects the size at maturity, and may influence the development of sexual ornamentation. The sword of several species of the genus *Xiphophorus* (Teleostei: Poeciliidae) is an elaborate secondary sexual trait that confers an advantage in terms of sexual selection, counterbalanced by locomotive and predatory costs. This study assesses differences in male juvenile growth, age, and size at maturation and their relationship with maximum body size and sword elongation in Montezuma swordtails (*Xiphophorus montezumae*). Fish size and sword length were measured over the course of 20 months. The size at which individual males initiated sword elongation varied considerably among individuals. Male maximum body size was correlated with early growth rate and age of maturation, and sword growth rate was positively correlated with male size at the onset of sword growth. Early growth in *X. montezumae* may provide valuable information about performance in subsequent stages and about probable future reproductive success.

Keywords: life-history traits; growth; poeciliids; swordtails; sexually selected traits; *Xiphophorus*

Introduction

Swordtails (Teleostei: Poeciliidae, genus *Xiphophorus*) are an important model to elucidate how male adult body size and ornamentation influences fitness. Females of several swordtail species prefer males with larger body size (Ryan and Wagner 1987; Rosenthal and Evans 1998; Fisher and Rosenthal 2007); males with larger body size are better fighters in intrasexual encounters (Benson and Basolo 2006), and also exhibit higher swimming endurance and velocity (Ryan 1988; Kruesi and Alcaraz 2007). In this sense, the greater the body size of an individual the higher its competitive ability. One important life-history trait that determines adult size is early growth; adult body size is a result of cumulative growth during an individual's lifetime. Male differences in growth may affect population structure by producing different dominance status between individuals due to variation in size (Aubin-Horth and Dodson 2004; Alcaraz 2005).

Male ornamentation also plays an important role in sexual selection. Female swordtails prefer to mate with males that display elaborate secondary sexual traits,

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*Corresponding author. Email: alcaraz@ciencias.unam.mx

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for example, ultraviolet coloration (Cummings et al. 2003), stereotyped courtship displays (Rosenthal et al. 1996), and melanophore pigment patterns (Morris et al. 1995; Fernandez and Morris 2008). Perhaps the most distinctive feature of swordtails (Darwin 1871) is the eponymous ornament: the sword, which is present in the males of some *Xiphophorus* species. The sword comprises an array of nine traits organized in four components: elongation of a specific set of caudal fin rays, a lower melanophore stripe, an upper melanophore stripe, and coloration between the upper and lower melanophore stripes which can be orange, yellow, and/or green (Basolo 1996). In some species, females prefer to mate with males bearing longer swords (Basolo 1990a); this appears to reflect a pre-existing perceptual bias, since the preference appears in species that diverged from a swordless common ancestor (Basolo 1990b). Nevertheless, the sword has been secondarily lost several times in the history of the swordtail lineage (Marcus and McCune 1999), and varies considerably in size and elaboration among species (Rauchenberger et al. 1990). Both predation risk (Rosenthal et al. 2001; Cummings et al. 2003) and changes in female preference (Rosenthal et al. 2002; Wong and Rosenthal 2006) are likely to drive the secondary loss of elaborate swords.

Little is known, however, about the mechanisms underlying variation in sword elongation among individuals of the same species. Interspecific crosses by Zander and Dzwillo (1969) estimated that the trait is largely associated with four genetic loci. Variation in sword length has also been attributed to environmental factors, such as food availability (Basolo 1998), predation risk (Basolo and Wagner 2004), and the population level of male ornamentation (Walling et al. 2007). A comparative analysis between species showed that differences in growth trajectories of both sword and body size were correlated with adult body size; sword growth is faster in swordtail species with larger adult size than in smaller species (Marcus and McCune 1999). An important question, then, is whether the pattern observed among species is also exhibited among individuals of the same population.

Sexual maturation in males activates the elongation of the sword, reduces body growth rate, and ultimately induces the cessation of body growth (Marcus and McCune 1999). The sword in the Montezuma swordtail (*Xiphophorus montezumae*) is the most exaggerated when comparing all swordtail species, it grows longer than the body of the bearer (Rauchenberger et al. 1990). Little is known about the intrinsic differences that determine sword elongation among individual males. The goal of this study was to test whether juvenile body growth rate and the age and size at sexual maturation explain the differences in sword growth rate among individuals, as well as variation in sword and body size among mature *X. montezumae* males.

Materials and methods

Maintenance and breeding

Juvenile *X. montezumae* were obtained from six breeding pairs originally collected from Capuchinas Spring, in San Luis Potosí, México. Each breeding pair was housed in a 40-L glass tank with a 16 : 8 hour light : dark schedule. Water conditions were held constant at a pH value of 7.0, salt content of $0.4\,\mathrm{g\,L^{-1}}$, and temperature of $25 \pm 1^{\circ}\mathrm{C}$. Fish were fed twice a day; their diet was alternated between live germ-free *Tubifex* worms and Tetramin flakes (36% protein), *ad libitum*. A third of the water content in all tanks was changed every 10 days.

The juveniles used for this study were born in the laboratory. Broods from each breeding pair were placed in individual 60-L communal tanks with water conditions set as described above. Seven days after birth, five fish were randomly selected from each communal tank and set apart in isolation, until the onset of the development of secondary sexual traits. Each was assigned randomly to one of two compartments of a 25-L tank divided by an opaque plastic screen. In this way, fish were maintained in physical and visual isolation. Olfactory communication might have occurred between the two fish that shared a tank; however, its effect on individual growth rate was minimized by randomly rotating the fish between the tanks each time they were measured (approximately every 30 days).

We checked for the initial stages of external secondary sexual traits, which are highly recognizable in males of Montezuma swordtails and other poeciliids (Marcus and McCune 1999; Dries et al. 2001), and consist primarily of the fusion of anal fin rays into a gonopodium, the appearance of dorsal fin pigmentation and the development of a sword primordium. The onset of gonopodium differentiation is an indicator of male maturation (Snelson 1989). As soon as any incipient male traits were observed, males were housed individually in a new 25-L glass tank for the rest of the experiment. We reared a total of 28 juveniles (17 males, 11 females) but gathered data only on the males.

Morphometrics

Standard length (SL; snout to hypural plate; ±0.5 mm) was measured for all fish approximately every 30 days (measurement date was registered), starting the seventh day after birth, and until growth rates plateaued to near zero (approximately after 20 months from birth). To minimize handling stress, we used a photo tank (150 mm length; 100 mm width; and 15 mm deep) marked with a scale in millimeters. We took a picture of one fish at a time with a CANON® Ultra video recorder (set in picture mode), and used image analysis software (NIH Image; Rasband 1997) for morphometrics. We measured sword length (distance from the inferior proximal margin of the caudal fin to the distal farthest limit of the sword) in all males from the onset of the sword primordium until the end of the experimental period. Body mass (M; ±0.01 g) was measured twice in the experiment using a plate balance: at the onset of sword elongation and at the end of the experiment. This measurement was not taken periodically or during the juvenile stages to avoid stress produced by handling without the use of anesthesia or by the use of it; previous studies report long-term effects of anesthesia in body growth in teleost fish (Fabrizio and Pessutti 2007).

Growth parameters

We modeled body growth using the standard von Bertalanffy (1968) equation:

$$L(t) = L_{\infty}(1 - e^{-k}\exp\{t + t_0\}) \tag{1}$$

where $L(t)$ is the SL at time (t); L_{∞} the asymptotic maximum SL; t_0 the hypothetical time when SL equals zero; t the time; and k the growth rate constant.

Growth in sword length was fitted to a logistic model:

$$\text{Sword length} = \ln[(1/x_t) - (1/u)] \tag{2}$$

where u is the upper bound parameter for the sword length ($u =$ mean sword length at the end of the experiment [final sword length]).

We also calculated key parameters describing male body and sword growth at different life-history stages. Juvenile growth rate was estimated considering size data during the juvenile stage (using measurements of SL from the age of 7 days to the onset of gonopodium differentiation). As a measure of male condition at the onset of sword elongation, the Fulton condition factor was estimated for each individual male according to Chellappa et al. (1995), using the following equation:

$$\text{Condition factor} = (100 \times M)\text{SL}^{-3} \tag{3}$$

The age at the onset of sword elongation was identified as the earliest recognizable stage of extension of the inferior fin rays that constitute the sword (primordium shorter than 4 mm in length).

The maximum growth rate of the sword was identified for each individual male as the linear slope of the logarithmic phase of the logistic growth curve when the data were ln-transformed; that is, excluding the lag phase of the curve and the steady state or decreasing growth phase (Wareing and Philips 1981; Sibley and Calow 1987). Finally, sword index (SI; Rauchenberger et al. 1990) was calculated for males at the end of the experiment.

Statistical analysis

The von Bertalanffy and logistic growth functions describing male body and sword growth, respectively, were fitted to the observed data (mean values of all males used for this study) to nonlinear regression analysis using SPSS version 13.0 for Windows (SPSS Inc. 2004).

To estimate if growth during the juvenile stage in *X. montezumae* has an effect on adult size and sword length, we conducted two multiple regressions: the first using juvenile growth rate, male condition, and age at the onset of sword elongation as independent variables against the standard length at the end of the experiment (dependent variable). The second multiple regression was conducted to test the relationship between the same set of independent variables describing male juvenile growth and the sword length at the end of the experiment as the dependent variable. To test for the effects of juvenile growth on the development of the sword, a third multiple regression was used to estimate whether juvenile growth rate and male age and/or size (SL) achieved at the onset of sword elongation can explain the maximal growth rate of the sword. Finally, a simple linear regression was conducted to estimate the relationship between male body size and sword length at the end of the experiment.

Results

Male growth trajectories

The von Bertalanffy growth function described growth trajectory of the male *X. montezumae* (nonlinear regression; $r^2 = 0.98$; $F_{(1,\ 0.05)} = 734.14$; $P < 0.01$) in the following equation: $\text{SL}(t) = 50.9\ (1 - e^{-0.2\ \exp[t+3.4]})$. Mean sword growth of all males

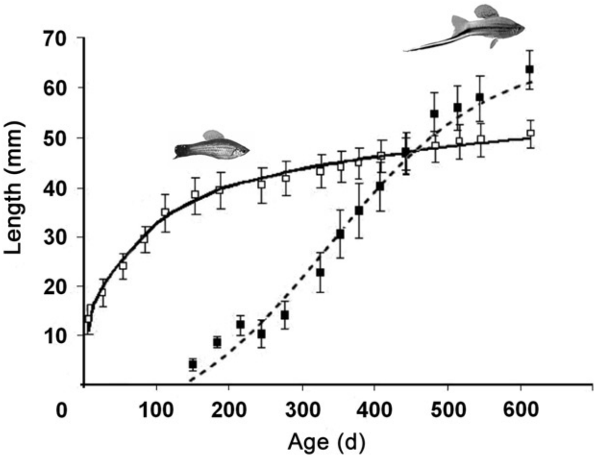

Figure 1. Von Bertalanffy body growth model (solid line) of the pooled SL data (clear squares, mean ± SD) in *X. montezumae* males. Sword growth is described by the logistic model (dashed line) of the pooled sword length data (filled squares, mean ± SD).

showed a sigmoid trajectory (nonlinear regression; $r^2 = 0.95$; $F_{(1,\ 0.05)} = 179.78$; $P < 0.01$), described in the following logistic equation: $L(t) = \ln([1/x_t] - [1/64])$. Both models are shown in Figure 1.

Mean body size (SL) of male 7-day-old juveniles was 12.1 ± 3.1 mm (SD). During the period of juvenile growth, male size increased at a rate of $0.09 \pm 0.04\,\text{mm day}^{-1}$ (SD). Gonopodium differentiation was observed at a mean age of 164 ± 52 days (SD), which coincided with the onset of sword elongation. Male size at sword onset showed a mean SL of 40.0 ± 3.5 mm (SD). The maximum sword growth rate of all males was $0.20 \pm 0.04\,\text{mm day}^{-1}$; this fast-increasing period of sword length lasted a mean time of 207 ± 47 days. Males reached a sword length at the end of the experiment (after 20 months since birth) of 64.4 ± 7.2 mm, and body size (SL) of 50.8 ± 2.6 mm (Figure 1); mean SI was 1.3 ± 0.1.

Relationship between body and sword growth parameters

Both juvenile growth rate and the age at the onset of sword elongation predicted male size at the end of the experiment (Panel A of Table 1). The largest males at the end of the experiment had higher juvenile growth rates and developed the sword at later age (Figure 2).

Neither juvenile growth rate, nor age or condition at sword onset predicted sword length at the end of the experiment (Panel B of Table 1). The maximum sword growth rate, however, was positively related to male SL at the onset of sword elongation, but not to juvenile growth rate or the age at sword onset (Panel C of Table 1). Thus, males that were larger at the onset of sword growth were the ones developing a sword at higher rates (Panel C of Table 1). However, male size at the end of our experiment was negatively related to final sword length (linear regression; $r^2 = 0.36$; $P = 0.03$).

Table 1. Multiple regression results comparing the effect of juvenile growth rate, age, and male condition at sword onset on male size (SL; Panel A); and on sword length at the end of the experiment (Panel B). A third multiple regression (Panel C) shows the effect of male juvenile growth rate, and the age and male size (SL) at sword onset on sword growth rate (ranged left above table).

Dependent variable	Independent variables	β	B	t-Value	P-Value	r^2 (model)	P-Value (model)
Panel A							
Body size (SL at the end of the experiment)	Intercept		−68.85	−1.61	0.14	0.66	0.01
	Juvenile growth rate	3.34	390.34	2.87	0.02		
	Sword onset	3.71	0.35	3.18	0.01		
	Condition at sword onset	0.12	976.37	0.42	0.68		
Panel B							
Sword length (at the end of the experiment)	Intercept		−153.04	−0.80	0.44	0.28	0.33
	Juvenile growth rate	1.92	679.44	1.12	0.29		
	Sword onset	1.57	0.46	0.93	0.38		
	Condition at sword onset	0.64	16,650	1.61	0.14		
Panel C							
Sword growth rate	Intercept		−0.09	−1.07	0.31	0.70	0.01
	Juvenile growth rate	0.04	0.05	0.20	0.85		
	Sword onset	−0.12	<0.00	−0.67	0.52		
	Size at sword onset	0.83	0.01	4.12	<0.01		

Note: β, error probability and B, regression coefficient (ranged left under table).

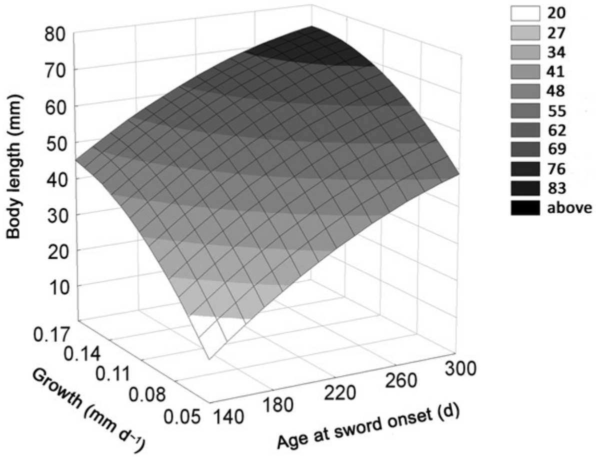

Figure 2. Relationship of juvenile growth rate, the age at the onset of sword elongation, and SL at the end of the experiment (length in mm is represented as intervals in the legend by a grayscale color gradient).

Discussion

As with reports on other *Xiphophorus* species (Marcus and McCune 1999), males grew rapidly until the onset of sexual maturity; growth then slowed, coinciding with the start of sword elongation. The decrease in male body growth rate when approaching sexual maturity can be explained by the change in energy allocation from somatic growth to the development of reproductive traits (Sibley and Calow 1987; Alexander 1999). The diversion of energy allocated from somatic growth to sexual maturation in male *X. montezumae* may involve testicular maturation, gonopodial differentiation, increase of the dorsal fin area, and/or the elongation of the lower caudal fin rays (Kallman and Schreibman 1973; Kallman 1983; Marcus and McCune 1999). The development of the sword is also accompanied by the increasing energetic costs of routine swimming activities (Basolo and Alcaraz 2003).

Both growth rate and the size at which males initiate sexual maturation varied considerably among individuals in this study. The juvenile males that displayed higher growth rates developed a sword later than those males which grew at a lower rate. Early sexual maturation can be an advantage since it may reduce a male's risk of dying without reproducing (Stearns 1992). However, maturation in this species, as in other swordtails (*Xiphophorus nigrensis*, Ryan et al. 1992; *Xiphophorus helleri*, Basolo 2008), may be costly in terms of the decrease in both growth rate and size at maturity. Additionally, in swordtails, maturation is also accompanied by increasing fitness costs associated with the sword: energetic costs of swimming (Basolo and Alcaraz 2003), reduced swimming velocity (Kruesi and Alcaraz 2007), and increased predation risk (Rosenthal et al. 2001). Several lines of evidence suggest that sexual selection favoring sword elongation is counterbalanced by natural selection. The loss of the sword and the preference for the sword in several lineages of *Xiphophorus* (Rosenthal et al. 2002; Wong and Rosenthal 2006) may reflect direct selection against the expression of a sword.

Juvenile males who grew at a higher rate and started maturation later also reached a larger adult size. Later-maturing males could have a long-term advantage by reaching a greater adult size. Lagarde et al. (2001) found a similar result in the steppe tortoise (*Testudo horsfieldi*) in which both age at maturity and the elaboration of sexually selected ornaments were correlated with growth rate. Although juvenile growth and the onset of sexual maturation explained adult size in male swordtails, neither juvenile growth rate, condition nor age at maturity explained maximum sword elongation. However, at the end of the experiment, sword length was negatively correlated with SL. The smaller size of the males bearing longer swords suggests resource partitioning between body size and sword elongation. Increases in both body size and sword elongation are energetically demanding in terms of somatic growth; but sword elongation comes also with an increasing energetic cost associated with swimming activity (Basolo and Alcaraz 2003). Basolo (1998) proposed that, under restricted food conditions, *X. helleri* divert energy from body growth to sword elongation, as seems to occur in Montezuma swordtails during sword elongation.

Our results contrast with the data reported by Basolo and Wagner (2004) in *X. helleri*, in which SL and sword length were positively correlated. However, the results reported were taken from a wild population in which the abiotic and social environment, not to mention differential survival and sublethal predation on swords, could play an important role structuring the covariation between body size and sword length. Further, swords are substantially smaller in *X. helleri* (SI of 0.6–0.8) than in *X. montezumae* (0.7–1.3; Rauchenberger et al. 1990). Moreover, our analysis focused on males that had reached their maximum body size under controlled conditions, while Basolo and Wagner (2004) were likely to have collected males of different ages in the wild.

Additionally, males in this experiment reached 51 mm SL and 64 mm sword length, corresponding to a mean SI of 1.3. Field-caught males (Capuchinas spring, San Luis Potosí) had similar size ($\mathrm{SL} = 50.5 \pm 8.6\,\mathrm{mm}$; $n = 97$) but had considerably shorter swords ($54.9 \pm 18.6\,\mathrm{mm}$) and consecutively a lower SI (1.1; Kruesi and Alcaraz unpublished data) than the males reared in this study. Thus, it seems that under laboratory conditions the sword can reach a larger size than under natural conditions. The relatively shorter sword of males captured in the field may suggest that the wild population is composed mainly of younger males than the ones reared in this study. Our results show that the sword continues growing with age, which is accompanied by the increasing energetic cost of swimming (Basolo and Alcaraz 2003), and possibly higher predation risk (Rosenthal et al. 2001). Thus, the increase in sword length through life may play an important role in male survival, making it costly for males in the wild to have long swords.

Variation in growth can be explained through differences in foraging efficiency, food assimilation efficiency, energetic food conversion and its allocation to different activities, and overall metabolism (Peck et al. 2004). The data reported here do not account for the particular individual functional responses playing a role in growth differences; instead, this study, conducted under controlled conditions, reveals intrinsic inter-individual differences in life-history traits and their relation with male ornamentation. Our data support the notion that early life-history traits may provide valuable information about an individual's role in a population. Our results show that variation among individuals in life-history traits, such as growth rate, adult size, and the timing of maturation, plays an important role in adult size and male ornamentation that might strongly affect performance in subsequent stages and ultimately individual reproductive success and survival.

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3. LA ESPADA Y SUS COSTOS

K. Kruesi, G. Alcaraz, C. Stern y R. Zenit

(manuscrito enviado)

The sword does decrease the escape performance in swordtails

Short title: The cost of the sword on fast starts

K. Kruesi [a], G. Alcaraz *, [a] , C. Stern [b], and R. Zenit [b]

[1]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, C. P. 04510, Distrito Federal, México

[2]Departamento de Física, Laboratorio de Acústica, Facultad de Ciencias, Universidad Nacional Autónoma de México, C. P. 04510, Distrito Federal, México

[3]Instituto de Investigaciones en Materiales, Universidad Nacional Autónoma de México, C. P. 04510, Distrito Federal, México

Corresponding author: alcaraz@ciencias.unam.mx

Summary

1. Male swordtail fish of the genus *Xiphophorus* develop a sword-like caudal fin extension, that evolved by sexual selection through female choice.
2. The female swordtails prefer males possessing longer swords, likely increasing males reproductive success. However, the sword also increases the energetic cost of routine and courtship swimming, and decreases male performance in steady swimming modes.
3. However, the maximum performance of unsteady swimming compromise different fish morphology compared to steady swimming.
4. We propose that the sword could improve the male´s ability to escape faster. The increase of the area due to the sword may favor the ability of accelerate the surrounding fluid through increase the added mass force.
5. Here we evaluated evaluated the hydrodynamic effects of the exaggerated sexually selected trait of the swordtail *Xiphophorus montezumae* on the C-start performance.
6. We recorded the kinematics of the C-start as the first stage of escape maneuver, the speed and acceleration of the head turning, and the added mass force associated to the C-start maneuver in males with their intact sword and after the sword excision.
7. The excision of the sword does not increase C-start performance despite increase the body area. Instead, the sword increases the duration of the escape maneuver and decreases the velocity and acceleration of the head turning achieved during a C-start, and the added mass force of the males with the sword excised was six-times larger than that with an intact sword.
8. The force generated by the sword during the C-start maneuver was smaller than that generated by the body in males either with the sword or with the sword excised.
9. In summary the sword represents a burden for the escape performance in Montezuma swordtails.

Key-words: Unsteady swimming, C-start, sexually selected traits, added mass force, escape maneuver.

Introduction

Sexually selected traits can have extremely exaggerated forms, recognized as adaptive because they advertise mates about themselves as potential reproductive partners (Endler 1986). Male swordtails of the genus *Xiphophorus* are distinguished among poeciliids by the elongated and pigmented lower caudal fin rays that males develop when they become sexually mature and form a trait called a sword. The female *Xiphophorus* spends more time attending courtship behavior from males possessing longer swords, likely increasing male reproductive success (Basolo 1995). However, this ornament produces a variety of costs to the bearers, such as increased predatory risk (Rosenthal *et al*. 2001) and energetic expenditure during routine swimming (Basolo & Alcaraz 2003), and decrease of the steady swimming speed (Kruesi & Alcaraz 2007). After the excision of the sword, swordtails increase their maximum swimming speed and spend less energy to sustain routine and courtship swimming, which suggests that the costs produced by this ornament can be explained through the drag forces caused by the increased surface area due to the caudal fin elongation.

The hypothesis based on the hydrodynamic cost of the sword has not been directly tested. However, the increased tail area may have important hydrodynamic consequences during swimming (Webb & Corolla 1981; Boisclair & Tang 1993). Interspecies comparisons show that larger caudal fin areas among fish species are linked to higher tail-beat frequencies and a greater power required for swimming (Hunter & Zweifel 1971). Thus, it could be expected that the gain in caudal fin surface area associated with the sword elongation could increase the drag forces during steady swimming. However, a different hypothesis could be conceived about the role of the sword during unsteady swimming (fast-starts and turns), considering the trade-off between steady and unsteady locomotion associated with body form (Langerhans 2009). The thrust in steady swimming is enhanced by a stiff, streamlined body form and a high aspect-ratio caudal fin that minimizes drag and reduces energy losses (Webb 1994; Long & Nipper 1996;

Langerhans 2008), whereas high performance in unsteady swimming is favored by having a flexible body, a smaller anterior body head (relatively small head), large caudal peduncle, and a low aspect-ratio caudal fin (Walker 1997; Webb 1983; Blake 2004). Because the sword in *Xiphophorus* increases the caudal fin area it is possible that the negative hydrodynamic effect of the sword extension during steady swimming could be reversed for unsteady swimming modes.

In fast-starts, fish bend its body into a C-shape (first stage of the movement) and by producing a sudden propulsion stroke the fish achieves an accelerated swimming burst to complete the maneuver (Domenici & Blake 1997). To bend into a C-shape fish require to gain a high angular velocity, with the accelerating and deflecting of the anterior part of the fish body moving some volume of the surrounding fluid. The driving force of this motion is inertial (added mass) rather than viscous (Weihs 1971). The added mass of a body being accelerated in a liquid depends on the area exposed to the flow (Brennen 1982) as $m_{AM} \propto \rho h^2 L$, where ρ is the liquid density, h is the height and L is the length of that body. Then, one can argue that the magnitude of the sudden propulsion should be increased by having a greater caudal fin area. We can expect a swordtail fish to attain a large value of the added mass caused by the increased body area compared to the same fish that does not have the sword e.g. eliminated by surgery. As a consequence, sworded males should achieve larger speed (angular velocity) and acceleration of the head turning, improving the propulsive stroke during the first stage of escape maneuver (C-start; Domenici, Lefrançois & Shingles 2007). It is the main purpose of our study to test if the long sword that develop male *Xiphophorus montezumae* has an effect on the added mass forces throughout the body (and sword) improving the efficiency of the C-start maneuver.

In contrast to the displacement of the center of mass that describes the overall performance of the escape maneuver, the first stage of the C-start maneuver can be described through the motion of the head (Domenici *et al*. 2007). In this study, we used the angular velocity and acceleration of the head turning because our goal was to test the role of the increased caudal fin area of male sword on the motion of the anterior part of the fish body during C-starts. The angular velocity or turning rate has been measured as an indicator of the strength of muscular contraction that determines the ultimate performance of the escape maneuver (Domenici *et al*. 2007). However since the sword should not affect the strength of the muscular contraction, differences between males with and without the sword should be attributed to hydrodynamic effects, but not to differences in muscular performance.

Males of *X. montezumae* are ornamented with the longest sword within the swordtail group and it may exceed the males' body length (Fig. 1A; Rauchenberger, Kallman & Morizot 1990). The contribution of drag forces are commonly studied, however the role of the added mass on the C-start is few studied despite its importance in the first stage of the escape (Chang & Kang 2011). Additionally, although caudal fins have an important role on fast-start in fishes a measurement of the forces contributing to C-starts are rarely reported (Zhao *et al*. 2006; Epps & Techet 2007).

Materials and methods

Male swordtails (*Xiphophorus montezumae* Jordan and Snyder) were collected by seining from the Rio Capuchinas, San Luis Potosi, Mexico (21°46′30.5″N; 99°18′13.2″W) in April 2006. The fish were transported to the Laboratory of Ecophysiology, Facultad de Ciencias (UNAM) at Mexico City, where they were maintained. Males were acclimated to laboratory conditions in individual tanks (20 litres) 15 days before the escape trials, by using filtered and aerated water with the temperature set similar to the water temperature at the collection site (25 ± 1 °C). Fish were fed Tetramin flakes.

Each fish was measured for total length *L* (mm), defined as the distance from the tip of the mouth to the end of the caudal fin, not including the sword. The sword length *S* (mm) was measured from beyond the distal edge of the inferior rays of the caudal fin to the tip end of the sword (Fig. 1A). The cross-section height *h* (mm), which varies along the length of the body, was measured all along the fish. Males were weighed and measured 10 days before testing.

The experiments were made in a rectangular tank 26 cm x 29 cm, filled with water to a height of 10 cm in order to induce the escape response occurred in a plane with no important vertical motion; this was confirmed by the fact that the size of the males did not change relative to the grid. The floor of the experimental tank was provided with a grid with 1-cm squares to set the software calibration. The temperature of water in the experimental tank was similar to the one of the acclimation period. The array was illuminated from above with diffuse light.

Individual males were placed in the experimental tank and were allowed to swim without restraint for 30 min. We caused an escape maneuver by tapping the bottom of the tank just behind the male at 60-95 cm from the caudal fin (± 1.3 body length; Marras *et al*. 2011). This was repeated for each fish up to five times to ensure to obtain the maximum performance of each individual (Baumgartner, Coleman & Swanson 2011). The escape trials were separated by twenty-minute intervals, this period is enough to avoid the decline on performance over time due to muscle fatigue (Marras *et al*. 2011). The fish motion during each trial was recorded with a REDLAKE MOTION SCOPE® PCI8000S (IDTVISION, Tallahassee, Florida, USA) high speed camera (12.5-7.5 mm lens; 1.7 m above the object) at a rate of 500 frames s^{-1}.

After the escape trials, fish were exposed to a simple surgery in which the sword extension was excised from its origin at the edge of the caudal fin. Previous to the surgery males were anaesthetized with MS-222, Stresscoat was applied to the point of the excision. Then, they were kept in recovery tanks for at least 8 days (Basolo 1995). The same procedure was done to all the individuals, so the escape maneuver of each specimen was studied with and without the sword. As reported in different studies when evaluating swimming in swordtails (routine, courtship, and steady swimming), males do recover from the surgical procedure without affecting swimming modes (Basolo & Alcaraz 2003; Kruesi & Alcaraz 2007). Hence, we did not make a sham surgery. Data from 17 specimens with an intact sword and after sword excision were obtained.

IMAGE ANALYSIS

Speed and acceleration of the head turning

A series of still images were extracted from the videos. The fish position was tracked over successive frames to obtain its progression over time. The images were treated with image processing software MATLAB® R2010a (The Mathworks Inc., Natick, Massachusetts, USA). The head was tracked in time with a semiautomatic code in order to calculate the angular velocity (turning rate) and acceleration of the head turning. The speed and acceleration of the head turning were obtained by using a central-difference scheme. With these measurements the kinematics of fish motion during C-start maneuver was determined. The normalized values of speed and acceleration were computed considering $\sqrt{gL}$ for speed and g for acceleration. In our study we used dimensionless values to describe the fish motion during the first stage of the C-start.

The C-start maneuver was defined as the rapid fish motion that began when the fish started to bend its body into a C-shape by contracting lateral muscles on one side (first stage of the fast-start, Domenici & Blake 1997) and ended when the fish returned to its linear position after contracting the muscles on the other side producing a tailbeat that unfolds its body from the C-shape and causes propulsion. The evolution of the speed and acceleration of the head turning during the escape maneuver was calculated in each of the five recordings obtained for each fish with and without the sword. We compared the maximum values of the achieved speed and acceleration and the time elapsed to achieve the C-shape by each fish with and without the sword by making a paired test of comparison of distributions for nonparametric data (Wilcoxon signed-rank test). For this analysis we used the normalized values of the speed *V*, and acceleration A, of the fastest trial among all five attempts for each individual (Peterson & Husak 2006). Two multiple regressions were made to estimate the effects of body length L, maximum height (h_{max}, mm; Fig. 1A), and sword size S on a) the normalized maximum speed V and b) the maximum acceleration A of the fastest escape trial of all males, first before and then after sword excision (SPSS® 13.0 for Windows; IBM, Armonk, New York, USA).

Added-mass force

The added-mass force was obtained from the digital image of one specimen (L= 56 mm; h_{max}= 13 mm; S = 49 mm) using the procedure proposed by Weihs (1971). A line was fitted running from the center of the head along the backbone of the fish until the proximal end of the caudal fin and then segmented into 40 equal-length segments. This was done at each frame of the complete recorded C-start. First, a coordinate system was defined (shown schematically in Fig. 1B).The motion of the fish was assumed to occur only in a horizontal (x,z) plane. Hence, the fish motion can be both a function of displacement length l and time t. The force during the C-start maneuver and the lateral speed were successively calculated over time along the different segments of its backbone extension. The lateral momentum of the fluid per unit length of the fish body is the product $m_{AM}(l,t) x w(l,t)$, where m_{AM} is the added-mass of a cross-section and w is the lateral velocity perpendicular to the centerline of that section (Fig. 1B). The added mass per unit length of a rectangular section can be shown to be (Brennen 1982) as:

$$m_{AM} = \tfrac{1}{4} \pi \rho h^2 \beta \qquad (1),$$

where h is the cross-section height and β is a constant close to unity. The value of h was measured from the selected fish at different positions across the body length, with h also separately measured at different positions across the sword.

The added mass force acting on the fish is equal to:

$$\mathbf{F}_{\mathrm{AM}} = -\frac{\partial}{\partial t}\int_{0}^{L} m_{\mathrm{AM}}\, w\mathbf{n}dl \qquad (2),$$

where L is the total length of the fish, and $\mathbf{n}$ is the unit vector perpendicular to the coordinate l. Hence, $h(l)$ and most importantly, the evolution of w in time and along l, must be known to calculate $\mathbf{F}_{\mathrm{AM}}$. Figure 1B shows the coordinate system used for these calculations.

To obtain $w(l,t)$ the following procedure was adopted. The different segments of the line running along the backbone of the fish were tracked for each frame. The fitting was made such that L was kept constant. The position l_i (x,z,t) and orientation of each segment were determined, such that the normal vector of each segment, $n_i(t)$, could also be calculated. In this manner, the lateral displacement of each segment was calculated as a projection of the displacement vector onto the normal vector. Therefore, the lateral velocity w was calculated as:

$$w_i(t) = \frac{1}{\Delta t}\left(x_i(t+\Delta t) - x_i(t), z_i(t+\Delta t) - z_i(t)\right)\cdot\left(n_x(t), n_z(t)\right)_i \qquad (3),$$

where Δt is the time step in between frames. Knowing w at each segment, i gives the variation with respect to l.

The values of w and m_{AM} can be used in Eqn.2 to calculate $\mathbf{F}_{\mathrm{AM}}$ (considering $\beta=1$) for a given specimen. This analysis was made for the fish body and sword separately to determine their contribution during the C-start maneuver. In our study only the net effect of the added mass force was considered. Our interest was in estimating the size of this force rather than in its direction. Therefore $\mathbf{F}_{\mathrm{AM}}$ showed positive and negative values that caused either acceleration or deceleration. The estimated uncertainty in this measurement was around 30%, which arose from the imprecision in the measurement of w (Eqn. 3) and the calculation of the time derivative in Eqn. 2. Note that no other forces resulting from lateral fins were calculated. Such forces could be estimated considering the complete analysis of Weihs (1971), however we chose to ignore such effects. The experiments were aimed mainly to determine the effect of the sword on the speed and acceleration of the head turning on the C-start maneuver. The only change in the specimen between experimental tests was the presence or absence of the sword, hence forces resulting from other fins should have in principle remained unchanged.

Results

The body and sword size of the males used for this study are shown in Table 1. Total body length and fish height were highly correlated (Pearson's correlation coefficient = 0.98, $P < 0.01$). The sword length showed no correlation with any body-size measurement (weight, total body length, or height; $P > 0.05$).

EVOLUTION OF THE BODY SHAPE DURING THE C-START MANEUVER

The motion during the C-start maneuver were similar in males with the natural sword and with the sword excised. For both, fish bent into a C-shape and then propelled their bodies forward. The fish with natural swords in their fastest escape trial achieved a close C-shape at a mean time of 16 ms (Table 2). During this initial phase, the sword remained motionless. However, the swordtails with the sword excised achieved this position in less time (Table 2; Wilkoxon signed-rank test $Z_{(\alpha = 0.05)} = -3.07$; $P < 0.01$; $n = 17$). The complete motion of the escape maneuver of a fish with and without the sword is shown in Figure 2. In this example, the maneuver of an organism carrying the sword took 72 ms, a time during which the fish was still unfolding from the C-shape as the sword dragged behind (Fig. 2A). At the time of 72 ms, the specimen with the sword excised had completed the C-start maneuver and was already swimming forward in a straight line (Fig. 2C). Figures 2B, and D show how the escape maneuver is achieved in less time in a fish without the sword than when carrying this ornament. Similar differences in the time of completion of the escape maneuver occurred in 90% of the males tested in this study.

SPEED AND ACCELERATION OF THE HEAD TURNING

The speed of the head turning in the C-start maneuver evolved from the rest position (speed zero) until it reached a maximum, both with and without the sword. The acceleration increased sharply reaching a maximum before achieving the maximum speed. The maximum values of acceleration during the maneuver appear as a result of the body of the fish bending into the C-shape, producing an increase in the speed of the fish movement as the body unfolds from this position. A similar speed and acceleration pattern occurred in all experimental males in their fastest escape trial, an example is shown in Figure 3.

Males with and without the sword showed different maximum speeds and accelerations during the C-start maneuver. Males with the sword excised increased their performance (Figure 3). Swordless males reached a higher acceleration (Wilkoxon signed-rank test $Z_{(\alpha = 0.05)} = -2.44$; $P = 0.01$; $n = 17$) and a higher speed (Wilkoxon signed-rank test $Z_{(\alpha = 0.05)} = -2.37$; $P = 0.02$; $n = 17$) than the same males with the intact sword (Table 2). In males with the sword, the maximum speed during the C-start maneuver was correlated with body length (L; Pearson's correlation $r = 0.63$; $P < 0.01$) and maximum body height (h_{max}; Pearson's correlation $r = 0.62$; $P = 0.01$); there was a combined effect of body length and height on the maximum speed of head motion during a C-start ($r^2 = 0.39$; $F_{(\alpha = 0.05)} = 3.90$; $P < 0.05$). However, only fish-body height had an effect on the maximum speed in males with the sword excised (Pearson's correlation coefficient = 0.51; $P < 0.05$).

LATERAL SPEED AND ADDED MASS FORCE

Figure 4 (A, B) show the measurements of the lateral speed as a function of body length for different times during the C-start maneuver for a male with and without the sword. The specimen with the intact sword moved faster ($l/L<0.2$) at the onset of the C-start maneuver, at the point when the fish body bends on one side and before achieving the C-shape. The swordtail's maximum lateral speed during this process was approximately $\sqrt{gL}$. The same male with the sword excised moved faster during this initial phase in the maneuver, but reached a lateral speed that was 50% higher than when carrying its sword intact (Fig. 4A and B).

For both, the added mass force generated by the caudal fin (that included the sword in males before surgery) was smaller than that generated by the body (Fig. 5). The added mass force of the fish without the sword was considerably larger than one with an intact sword. Although only one case has been shown, measurements for the other males showed the same general trend. The duration of the maneuver was longer for the specimen with the sword, though the period of time when the force had large values was smaller than without its elongated fin.

Discussion

The kinematics of the C-start maneuver was similar in males with the sword and with the sword excised. For both, the males rapidly adopted a C-shape and propelled themselves forward, as has been widely described (Weihs 1973). However, a negative contribution of the sword was seen during the first stage of the maneuver. The specimens with their sword intact fully adopt the C-shape in a longer time than the males without the sword. The same seems to happen after the fish has completed the C-shape, during the change in direction of tail motion as the fish unfolds from this position. In consequence, completing the C-start maneuver lasted less time for the organisms after the swords were excised. When males without the sword had completed the maneuver and were swimming away in a straight line, the males with swords were still making the maneuver (see Figure 2). The differences in the C-start performance may be a direct consequence of the turning angles relative to the body axis. Turning angles can vary greatly in fish of the same species depending on several factors, such as the stimulus (Webb 1976), the social context (Domenici & Batty 1997), and the fish size (Domenici & Blake 1993). For instance angelfish (*Pterophyllum eimekei*) uses different types of fast-start motions depending on their size. Small fish tend to use a double-bend type of fast-start more frequently, being characterized by a higher escape performance (distance traveled, speed, and acceleration) than a single bend, which is mostly used by large fish (Domenici & Blake 1993). The time of completion of the escape maneuver is body size-dependent and linearly dependent on turning angles, where larger fish require longer times to complete them (Domenici & Blake 1991; 1997; Domenici & Batty 1994). Based on these arguments, it is feasible that fish with swords had slower maneuvers by having longer bodies than when the sword was excised. This could be also supported by the positive relationship between speed of the head motion and body length in sworded males. Additionally, although differences in turning rates and latency of the C-start might be attributed to responses mediated by different neuronal effectors (Mauthner cells or other reticulospinal neurones; Eaton, Nissanov & Wieland 1984), the presence or absence of the sword should not modify the neural commands involved. Thus, we assume that differences between sworded and non-sworded males result from hydrodynamic effects.

The C-start maneuver occurs in a short-time span, shorter than the viscous relaxation time so that inertial forces are dominant (Weihs 1973), in manner that the added mass force is responsible for the ability to move quickly. We predicted that the sword could be used to improve the ability to escape faster by being able to increase the added mass force that results from the ability of a body to accelerate the surrounding fluid (Weihs 1971; Brennen 1982). One could expect that if a fish has a greater area, resulting from the presence of the sword, a higher added mass force could be achieved through moving with unsteady swimming modes. However, our results showed that the angular velocity and acceleration of the head turning increased after the sword excision. Additionally, the specimen with the intact sword produced a smaller added mass force with this caudal fin extension, despite its significant length. The added mass force is also responsible for the escape propulsion of carridean shrimps and lobsters. In these animals the hydrodynamic forces that result from rapid flexion of the abdomen lead to body accelerations (Daniel & Meyhofer 1989). In both, size of the tail is very important in thrust production, although the longer and wider tails have morphological advantages by producing predominantly added mass forces and in consequence higher thrust (Nauen & Shadwick 2001). In contrast to these crustaceans´ tails, the caudal fin elongation (sword) of *Xiphophorus* is a flexible structure that is dragged rather than moved significantly or held stiff during the maneuver, hence it represents a burden rather than an advantage as shown in our results.

The ability to push the fluid around is also dependent on the lateral velocity (*w*) that fish can generate at different points all along the body. This is the key element to produce a force of importance in terms of magnitude. The lateral speed produced by this caudal fin extension seems to be unimportant to produce a propulsion force that enhances the C-start maneuver. Although the caudal fin plays an important role on a C-start, the fin stiffness would be required to produce thrust (Domenici & Blake 1997; Zhao *et al*. 2006). Ahlborn and collaborators (1997) employed a simulated fish-tail apparatus to visualize the flow during a fast-start. They found that the tails of intermediate flexibility produce larger impulses than either stiff or very flexible tails. Additionally, a classical hypothesis suggests that the stiffening of the axial skeleton of early fish is an adaptive function increasing swimming speed (Gibb *et al*. 2006; Summers & Long Jr. 2006). The sword is formed by flexible rays that seem not to be stiff enough to generate thrust.

The relatively low contribution of elongated caudal fins on the thrust during fast-start swimming has been also described through manipulation experiments with *Hyla versicolor* tadpoles. In these tadpoles, the artificial reduction of the tail by 34% had no effect on swimming speed in burst swimming. However, when a higher percentage of the tail was removed, the escape performance decreased (speed and escape time). These results show that the deepest part of the tail during steady swimming are mostly used for generating thrust, whereas the distal portion of the tail is not sufficiently stiff to contribute to forward propulsion (Wassersug & Hoff 1985; Weihs 1989; Liu, Wassersug & Kawachi 1996; Van Buskirk & McCollum 2000). Although the sword may increase the exposed area to the fluid in the C-start, it seems that it is too long and flexible to contribute to escape quickly.

The force produced by the body during a C-start maneuver was significantly greater than that produced by the sword, or by the part of the sword that remained after the excision (caudal fin without the elongation). In contrast, the body depth showed to have a great contribution to the maximal velocity and acceleration of the head turning during the C-start maneuver. The positive relationship of the body depth (height) with the angular velocity is likely to be then a direct result of the increased added mass force, because greater height increase the area exposed to the flow that determines the speed at which an object is accelerated in a liquid (Brennen 1982). Similar results are reported by Royle, Metcalfe & Lindström (2006) for *X. helleri*, where the maximum escape performance was positively correlated with body depth.

A previous study has assessed the role of the sword during the escape performance in males of the genus *Xiphophorus*. Baumgartner *et al*. (2011) reported that the sword in *X. helleri* does not affect the male's ability to escape predators; However, the different results obtained in both studies should be further explained. First, there are significant differences in the sword size of these two species. The males of *X. montezumae* (Rio Gallinas; México) have a mean sword extension of 36 mm and a sword index of 1.3 (SI = standard length/sword extension; Rauchenberger *et al*. 1990) whereas the commercial specimens of *X. helleri* had smaller swords (12 mm; SI = 0.6; Baumgartner *et al*. 2011). It is possible that the sword of *X. helleri* is not long enough to produce significant hydrodynamic costs; but our study showed unequivocally that it reduces the escape performance of the Montezuma swordtails. Other explanations for the different results reported by Baumgartner *et al*. (2011) and those reported here could arise from the type and orientation of the stimulus in trials. Additionally, the procedure and the measurements estimated were very different; specifically we measured the performance of the C-start maneuver while Baumgartner and collaborators estimated the outcome of the overall escape performance.

Fast-start swimming in wild animals is important to fitness because it is closely linked to survival probability (Walker *et al*. 2005; Royle *et al*. 2006), being the turning rate one crucial factor of escaping success (Dadda, Koolhaas & Domenici 2010). Our data show that the presence of the sword produces hydrodynamic costs for mature males, which is opposed to the benefits of the sword by sexual-selection processes (Basolo 1995). According to our data, long swords like the sword in *X. montezumae* are far away from being an evolutionary shaped ideal ornament as proposed by Baumgartner *et al*. (2011). Previous studies have shown that this sexually selected trait has a negative effect during steady swimming (Kruesi & Alcaraz 2007) and that it is energetically costly during routine and courtship swimming modes (Basolo & Alcaraz 2003). Previous studies plus the evidence generated here suggest that only high quality males may pay off the costs of bearing an exaggerated ornament, with the male sword being a signal of overall condition and genetic quality, as suggested by the handicap principle (Zahavi 1975).

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LIST OF SYMBOLS AND ABBREVIATIONS

m_{AM} : added mass

ρ : liquid density

h : fish cross-section height

h_{max} : fish maximum height

L : fish total length

S : fish sword length

SI: sword index

g : gravitational acceleration

V : normalized speed

A : normalized acceleration

l : coordinate along the fish backbone

t: time

(x,z): spatial coordinates

w: the velocity component perpendicular to the coordinate l

β: numerical coefficient

$\mathbf{F}_{AM}$: added mass force

n: unit vector, normal to coordinate l

Δt: time step

i: the i-th position along coordinate l

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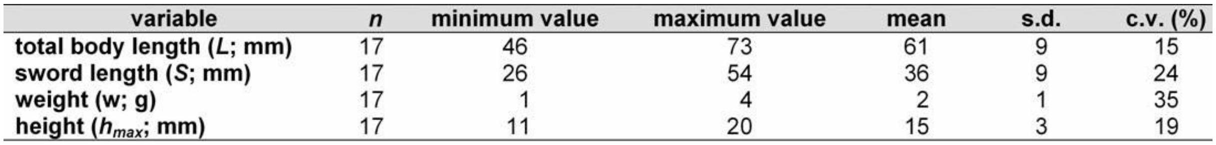
Tables

Table 1. Morphometric measurements of the males used in this study. n = sample size, mean = geometrical mean, s.d. = standard deviation, c.v. =coefficient of variation.



variable	*n*	minimum value	maximum value	mean	s.d.	c.v. (%)
total body length (*L*; mm)	17	46	73	61	9	15
sword length (*S*; mm)	17	26	54	36	9	24
weight (w; g)	17	1	4	2	1	35
height (h_{max}; mm)	17	11	20	15	3	19

Table 2. Statistics describing the dimensionless speed and acceleration of the head during the C-start, and the time (in seconds) to achieve the C-shape in *Xiphophorus montezumae* males with the sword and after the sword excision. n = sample size, mean = geometrical mean, s.d. = standard deviation, c.v. = coefficient of variation.

variable	*n*	minimum value	maximum value	mean	s.d.	c.v. (%)
with sword						
speed [$V/(gL)^{1/2}$]	17	1.6	2.6	2.1	0.3	13
acceleration (*A*/*g*)	17	4.9	9.1	6.7	1.2	18
time to achieve C-shape (s)	17	8.0	24.0	16.2	4.5	27
swordless						
speed [$V/(gL)^{1/2}$]	17	1.9	2.6	2.3	0.2	10
acceleration (*A*/*g*)	17	4.8	9.8	7.6	1.2	16
time to achieve C-shape (s)	17	8.0	18.0	12.7	2.9	23

Figures

Figure 1

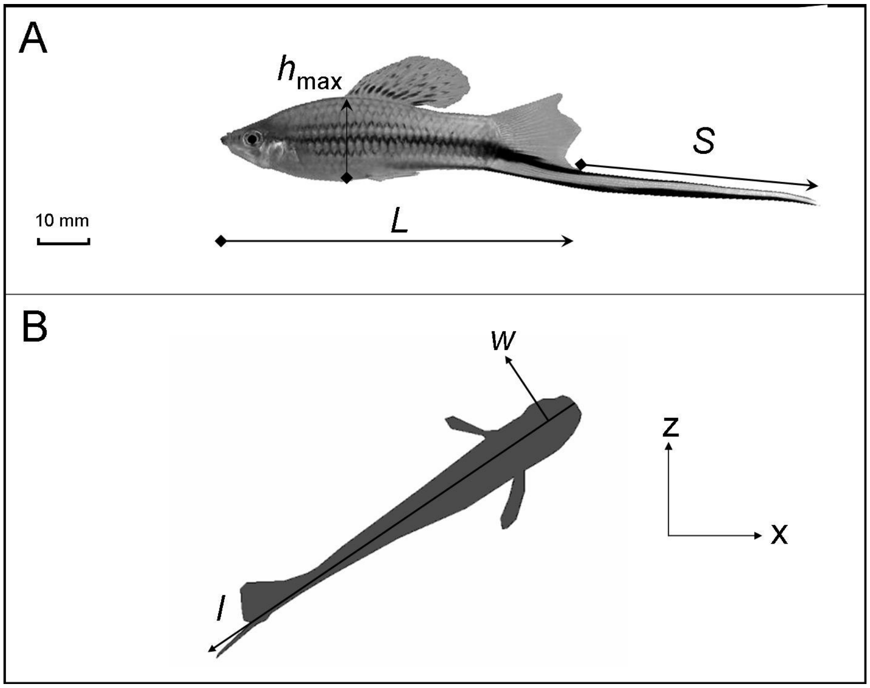


Figure 2

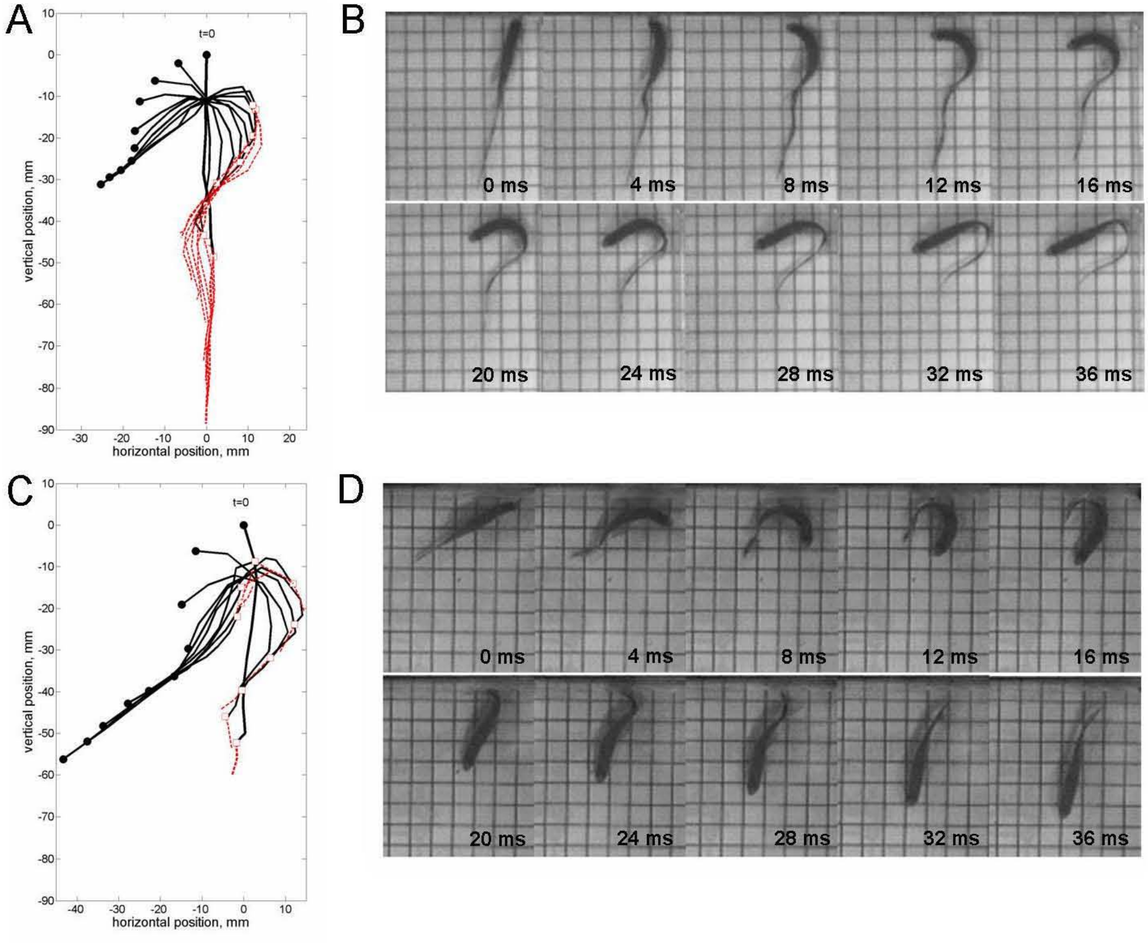

A
t=0
vertical position, mm
horizontal position, mm
10
0
-10
-20
-30
-40
-50
-60
-70
-80
-90
-30
-20
-10
0
10
20
B
0 ms
4 ms
8 ms
12 ms
16 ms
20 ms
24 ms
28 ms
32 ms
36 ms
C
t=0
vertical position, mm
horizontal position, mm
-40
-30
-20
-10
0
10
D
0 ms
4 ms
8 ms
12 ms
16 ms
20 ms
24 ms
28 ms
32 ms
36 ms

Figure 3

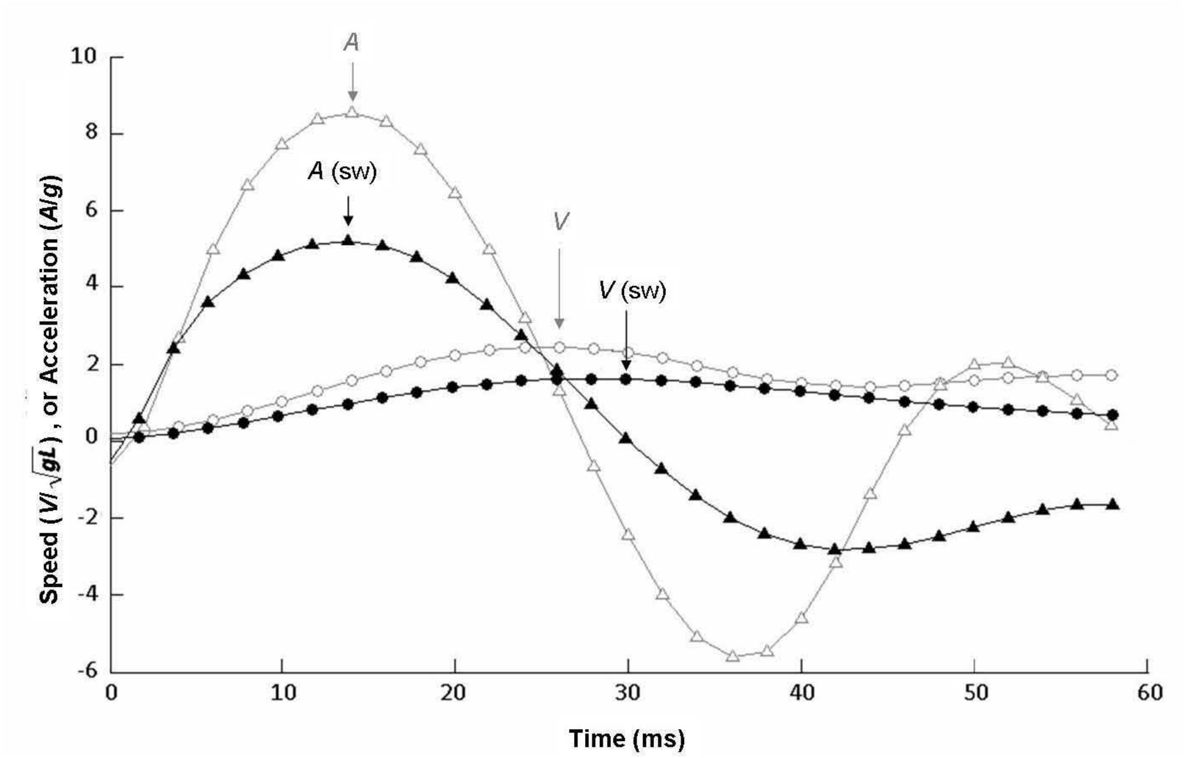

A
A (sw)
V
V (sw)
10
8
6
4
2
0
-2
-4
-6
0
10
20
30
40
50
60
Speed ($V/\sqrt{gL}$) , or Acceleration (A/g)
Time (ms)

Figure 4

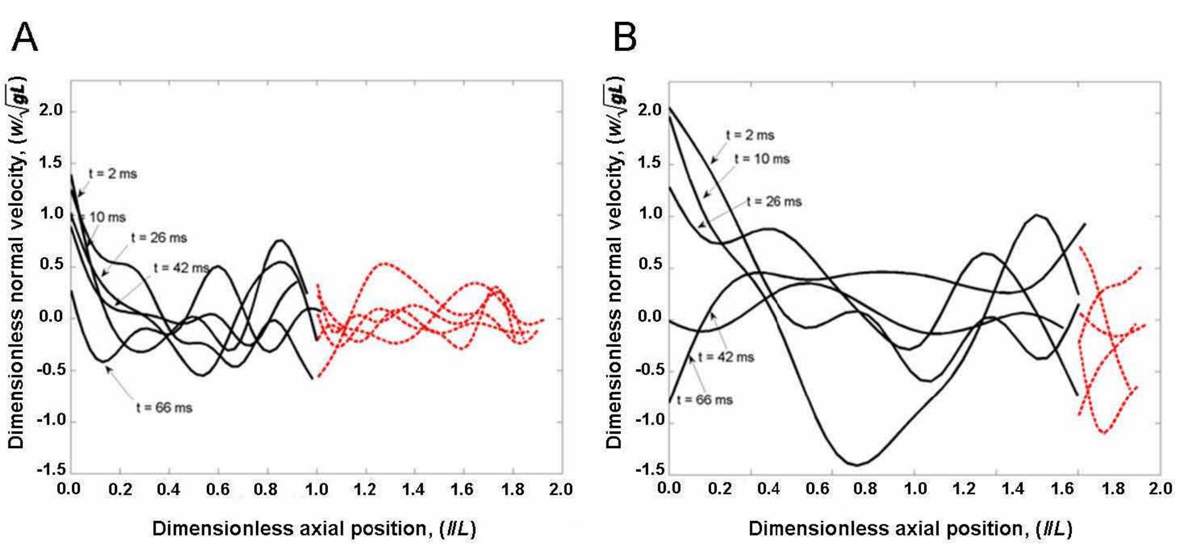
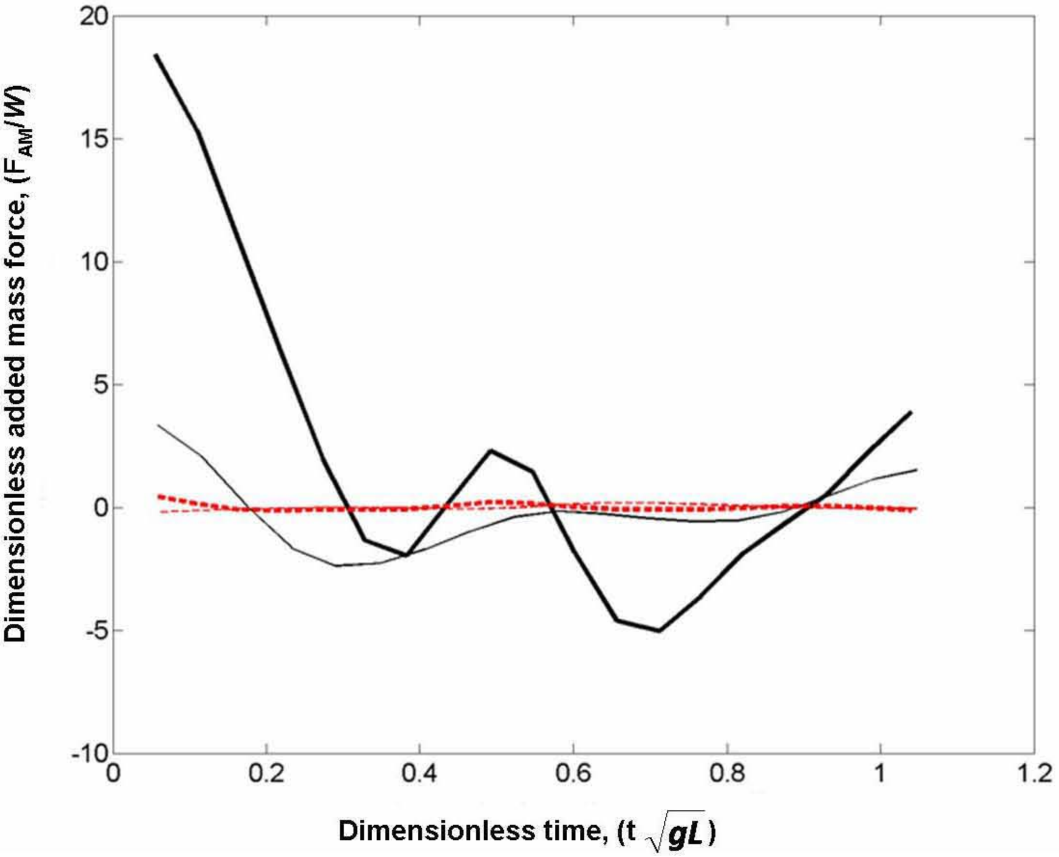

A
Dimensionless normal velocity, $(w/\sqrt{gL})$
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
t = 2 ms
10 ms
t = 26 ms
t = 42 ms
t = 66 ms
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Dimensionless axial position, (l/L)
B
Dimensionless normal velocity, $(w/\sqrt{gL})$
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
t = 2 ms
t = 10 ms
t = 26 ms
t = 42 ms
t = 66 ms
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Dimensionless axial position, (l/L)

Figure 5



Dimensionless added mass force, (F_{AM}/W)
20
15
10
5
0
-5
-10
0
0.2
0.4
0.6
0.8
1
1.2
Dimensionless time, $(t\sqrt{gL})$

Figure legends

Figure 1. A) Male *Xiphophorus montezumae* showing a long sword. All morphometric variables considered in this study are marked here. B) Reference frame for the determination of the added mass forces during the C-start maneuver of a fish.

Figure 2. Evolution of fish motion during the C-start maneuver. On the left side, the schemes A and C show the measurements from the digital analysis. On the right side (B and D), the original sequences of images. The time interval inbetween images is 4 ms. The top (A and B) and bottom (C and D) rows show the results for the same fish with its natural sword and with the sword excised. The measurements shown on the plots on the left were alligned and rotated for clarity, such that in both cases the initial position is vertical and the maneuver is in the counter-clockwise direction. For these plots, the black circle and continuous line denote the position of the fish head and and the body shape. In the same manner, the red square and dashed line show the onset of the sword and the fit to its shape. Each set of lines represents the position of the fish at different times. The time step inbetween lines is 8 ms.

Figure 3. Speed and acceleration of the head of the fastest trial of one male *X. montezumae* with natural sword and with the sword excised. Both variables are presented in dimensionless forms, considering $\sqrt{gL}$ and g (gravitational acceleration) as the characteristic individual speed and acceleration.

Figure 4. Evolution of the normal velocity of a male Montezuma swordtail (w) along its body length with (top) and without the sword (bottom). The continuous black lines show the measurements for the body at different time instants and the red dashed-lines show the

measurements for the sword. The results shown here correspond to the same model fish used at this study.

Figure 5. Change in time of the magnitude of the added mass force, F_{AM}, obtained from Eqn. 3. The force is normalized by the weight of the model specimen. The continuous black lines show the force resulting from the motion of the body; the red dashed lines show the added mass force produced by the sword. The thick and thin lines show the results for the specimen with and without sword.

4. PREFERENCIA FEMENINA

K. Kruesi y G. Alcaraz

(manuscrito enviado)

A threshold in the preference for the sword: female assessment of an exaggerated male trait

Kruesi K., and G. Alcaraz

Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, México City, Zip Code: 04510, Ciudad Universitaria

E-mail: kkc@fciencias.unam.mx and alcaraz@ciencias.unam.mx.

Running title: Preference for sword length in female Montezuma swordtail

Total number of words: 4688

ABSTRACT

Female preference for exaggerated traits may be accompanied by the evaluation of male performance. A female bias favouring the elongation of the caudal fin (sword), which is suggested to signal increased apparent male size, is present in many species of the genus *Xiphophorus*. The Montezuma swordtail males are among this group the ones that develop the longest swords, often longer that their body itself, but female preference in this species has never been tested. In this study we estimated female preference to the longer-sworded males in dichotomous choice tests using live-courting males of similar age and body size. The results showed that female preference does not correlate with sword length. They preferred longer-sworded males when the difference between stimuli males ranged between 27 to 32 mm (sword estension) but dropped when 37 mm or longer. Sword length increases the costs of courtship swimming modes probably due the opposite drag forces elicited by this exaggerated male trait. We suggest that females may assess differences in male courtship performance in order to make mating decisions. However, further research should be done in order to confirm this.

INTRODUCTION

Female preference plays an important role in male fitness by means of sexual selection, by conferring reproductive success to the males having the most attractive traits (Darwin 1871; Andersson 1994). These traits might be either morphological or behavioral and their expression could be associated with certain genes, physiologic processes, and with other traits that cooperate to increase individual fitness of males in a particular environment like condition-dependent characteristics (Zahavi 1975; Hamilton & Zuk 1982; Birkhead et al. 2006). The expression of sexual traits that reach exaggerated proportions often pose challenges to males, being energetically costly to produce and maintain (Rubenstein & Hauber 2008) or because they compromise male performance and survival (Arnold 1983; Mø ller 1989; Barbosa & Mø ller 1999). By associating with males with elaborate traits females may incur direct fitness costs, e.g. of being preyed on because of the male's conspicuousness (Rosenthal et al. 2001; Hernandez-Jimenez & Rios-Cardenas 2012) or being involved in male-male aggressive encounters (Tudor & Morris 2011). Alternatively, by associating with males capable of paying the costs of expressing exaggerated traits, females may gain direct or indirect benefits in the form of parental effects or quality offspring (Trivers 1972; Zahavi 1975). Hence, females must assess the costs and benefits of their mate selection and discriminate between a sexual character which expression is informative of the male's quality, or too expensive.

How female preference works is complex. The evaluation of potential mates includes processes that may be influenced by a variety of mechanisms of sensory perception, for example color vision (Hunt et al. 1998; Rosenthal 2007) or mate recognition through chemical cues (Hankison & Morris 2003). Additionally, cognitive processes play an important role in female preferences and the assessmet of male performance, as well as past experiences and evesdropping on other females decisions are implicated in the decision-making of associating with the available reproductive mates (Ryan 1998).

In recent decades, the genus *Xiphophorus* has been widely studied in terms of sexual selection and the evolution of sexually selected traits (Basolo 1990a; Meyer et al. 1994; Basolo 1995; Rosenthal et al. 1996; Robinson et al. 2011). This is a complex group with regard to the expression of sexual traits and social behavior (Farr 1989). To access females, males must perform a set of conspicuous courtship displays (Haas 1993) and furtive gonopodial thrusting (Ryan & Wagner 1987) while exhibiting multiple morphological traits that are the subject of female preference such as body and dorsal fin size (Rosenthal & Evans 1998; MacLaren & Daniska 2008), vertical melanin bars (Morris et al. 2003), and the presence and length of the sword (Basolo 1990b). The sword is a secondary sexual characteristic that mainly consists of a pigmented elongation of the inferior caudal fin rays (Basolo 1995). Earlier studies have demonstrated that females of various *Xiphophorus* species share a preference for sworded males, which has been confirmed in species where the ornament is long (*X. helleri*; Basolo 1990b; Rosenthal & Evans 1998), short (*X. nigrensis*; Rosenthal et al. 2002), and in species whose males do not develop a sword (*X. maculatus*; Basolo 1990a) and *X. variatus* (Basolo 1990c; Haines & Gould 1994). In a species like *X. helleri*, where males develop long swords which increase its probability of being predated (Hernández-Jiménez & Ríos-Cárdenas 2012), females show high preference for this trait but are able to evaluate the costs of the sword and change their preferences according to past experiences (Johnson & Basolo 2003).

Males of the Montezuma swordtail *Xiphophorus montezumae* develop the longest swords in the genus (Rauchenberger et al. 1990), however female preference for this trait has not yet been studied. The sword in this species is a character that, under laboratory conditions, may increase in size continually along a male's life (Kruesi et al. 2011), increasing the energetic demands during courtship (Basolo & Alcaraz 2003) and steady swimming modes (Kruesi & Alcaraz 2007). Our study estimates the preference for the sword in *X. montezumae* using reproductively naïve females. Females were given the choice between a pair of males differing naturally in sword length. As females have not had the experience of evaluating the costs of selecting males of exaggerated sword size, we predicted that since this species expresses the longest sword and if sword evolution is a consequence of female preference, this would increase with sword length.

METHODS

Fish collection and maintenance

Adult *X. montezumae* males and females were captured in the Capuchinas spring (21°46'30.5" N; 99°18' 13.2" W), located in the Huasteca region of San Luis Potosi, Mexico. All fish were transported to the Ecophysiology Laboratory at the Universidad Nacional Autonoma de Mexico and maintained individually in 18-l tanks fitted with a gravel substrate and dechlorinated water with constant air supply. Fish were fed with Tetramin® flakes (46% protein) twice a day and alternatively, we fed them *ad libitum* live *Tubifex sp.* worms (commonly used to feed tropical freshwater fish) once per week. The water temperature was held at 25 ± 1 ºC, with a concentration of 5 ± 0.6 mg l^{-1} dissolved oxygen, salinity of 5 pps and under a 12 h:12 h light-dark period, similar to the physical and chemical conditions of water at the collection site.

Females tested for mate choice and males used as stimuli were born between august and september 2005; they were first generation descendants of the colected organisms and all came from different breeding pairs. To ensure the use of adult virgin females and non experienced males, juveniles were isolated and reared until the onset of maturation. In females, until the gravid spot was clearly observed, which occured five to six months after birth. The gravid spot is a small abdominal dark patch that signals gonadal maturation in female livebearing fish (Gordon 1943). Experimental fish were similar in size (females: n = 9; standard length = 53 ± 3 mm, coefficient of variation = 0.04; males: n = 12; standard length = 53 ± 8 mm, coefficient of variation = 0.15). All females were 7 months old and the male's age ranged between 8 an 11 months.

Morphometric measurements

Body size was measured for males and females as mass (M; g) and standard length (SL; mm); SL was defined as the distance from the tip of the mouth to the proximal edge of the caudal fin. With the purpose of forming pairs of males to be used in choice trials, other morphological characters as the dorsal fin length ($L_{dorsal\ fin}$), body depth (H), peduncle depth ($H_{peduncle}$), sword-extension length (E; mm) and coloration (whole body, peduncle and sword) were measured (Fig. 1). The sword extension E was defined as the length of the sword posterior to the inferior limit of the caudal fin (Rosenthal & Evans 1998). To record this measurements, the organisms were weighed to the nearest gram in a digital plate balance (OHAUS; ± 0.01 g) and photographed outside the water over a plastic white surface which creates a contrast with fish coloration. The pictures (24 bit RGB color) were taken using a digital camera and a scale reference. We used the image analyzer program for Windows '98 "Image J" to estimate the morphologic and coloration measurements described above. Coloration data were the modal relative number of pixels at each of the 250 tonal values of red, green and blue of the fish body (lateral surface), peduncle (inferior portion of the peduncle) and sword (from the distal part of the peduncle to the end of the caudal fin; Fig. 1). The fish were measured one week prior to the experimental trials.

Experimental setup

The experimental tank (55 cm long, 31 cm wide, and 29 cm tall) was fitted for dichotomous selection trials using two divisions to separate it into three sections; two smaller external sections (12 cm wide) and one extended central section (31 cm wide). The tank was divided using two acrylic walls per side, one clear wall fixed to the tank and one removable opaque screen to avoid visual communication between tank chambers during the acclimation period. The central section was externally marked by two black lines drawn in the front wall (only visible to the observer) to virtually separate three zones: two 'preference zones', each representing a space where the females attended to each male, and a 'neutral' central location (Fig. 2a). Water conditions as well as a gravel substrate were set as discribed above. The tank was enclosed in a chamber with Styrofoam walls to keep it isolated from natural light and to reduce disturbance caused by any noise or movement during the experimental trials. Illumination was provided by an aquarium lamp with two opaque light bulbs (100 W) placed 40 cm above and centered over the tank. Using a digital video camcorder (Canon Elura) located at a distance of 60 cm at one side of the experimental tank (Fig. 2b), the female's behavior was recorded.

Experimental design

Six pairs of swordtail males were formed taking into account similarity in body size, shape, and coloration. After testing for normal distribution of the values describing male characters, a series of Student t tests were performed to confirm similarity between long- and short-sworded males (Table I). We also checked for relationships between male characters corrected for allometric effects of body size (Lleonart et al. 2000). There is a correlation of sword extension (E) with peduncle depth ($H_{peduncle}$; Pearson correlation analysis, $r = 0.70$, $p = 0.01$) but not with the rest of the morphometric or coloration characters measured ($p > 0.05$).

With the purpose of testing female preference for males according to their difference in sword length, the differences in sword extension (ΔE) between males in pairs varied from 2 to 43 mm. The variable ΔE was defined as the sword extension length (E) of the longer sworded male minus that of the male with the shorter sword. Females were presented to choose between pairs of males with ΔE of 2, 15, 27, 32, 37, and 43 mm. Among pairs of males, the sword extension of the longer-sworded males was similar (E = 60 ± 9 mm; coefficient of variation = 0.17).

Fish were fed *ad libitum* with live *Tubifex sp.* worms before the trials and then kept in the experimental tank for an acclimation period of 30 minutes. The males were placed randomly in the external sections of the tank. An experimental female was placed in the central chamber and after the acclimation period, the opaque barriers were released allowing visual but no chemical communication with both males. The trials were divided into two periods. During the first period female behavior was recorded for 10 minutes and afterwards the opaque barriers were replaced.

The males then were exchanged in their chambers reversing their places for a second acclimation period (30 min). This was done to control for any side bias in the female's choice. After this, a second 10-minute period of female behavior was recorded. All females (n = 9) were tested once a week with each pair of males (six trials per female; 54 total trials). Each female was tested with all pairs in a different random sequence and all trials were performed each day between 11:00 and 15:00 hours.

Female preference

Trials started when the females had spent at least 10 seconds interacting with the male in each side of the tank. Interaction with males was when the female swam with her head directed towards one of the males, inside the preference zones of the central chamber and only when the male was not more than 3 cm away from the clear wall and with its head directed towards the female, while courtship occurred (Haas 1993). The cumulative interaction time of females with the short- and the long-sworded male was recorded and summed among both 10-minute periods of each trial. The amount of time that a female spent at a male's side when there was no interaction was not recorded.

We estimated the proportion of time that females interacted with both males in each trial as a measure of female activity during mate selection

I = total interaction time ($i_{\text{long sword}} + i_{\text{short sword}}$ s) / total trial time (1200 s),

where i is the interaction time, either with the short- $i_{\text{short sword}}$ or the long-sworded male $i_{\text{long sword}}$. To assess the female preference (P) for the long-sworded male in each pair, the proportion of time that females interacted with this male in relation to the total time of interaction (with both males) in each trial was calculated

$$P = (i_{\text{long sword}}) / (i_{\text{long sword}} + i_{\text{short sword}}).$$

The proportion of females having more interaction with the longer-sworded males was calculated for each pair of males.

Statistical analysis

All trials were included in the statistical analysis because there was no observation of lack of female activity or weak-male courtship rate. However, the number of females was reduced in one trial (ΔE = 32 mm) because one died for an unknown cause during maintenance periods.

One-way analysis of variance (ANOVA) was made to test for possible effects of female size (SL) in total interaction time (*I*) during trials, and in female preference for the longer-sworded males (*P*). Correlation analysis (Pearson) was carried out to look for linear effects of ΔE on the female preference (*P*). To estimate other (non-linear) effects of ΔE on female preference for the longer-sworded males, we conducted a linear mixed model, which is adecuate for longitudinal data (repeated measures). The variable ΔE (categoric) was set as the fixed effect and *P* as the dependent variable. A post hoc test (Least Squares Differences; $\alpha = 0.05$) was conducted to identify the relationships between subgroups.

The relationship among *P* and the proportion of females preferring the longer-sworded males was estimated with a Pearson correlation analisys.

RESULTS

Neither the total interaction time (*I*) nor preference (*P*) varied as a function of female size [$F_{(8, 44)} = 0.46$, MSE = 0.02, p = 0.88; $F_{(8, 44)} = 0.66$, MSE = 0.03, p = 0.72, respectively].

There was no linear correlation of female preference with ΔE (*r* = -0.11, p = 0.84), however there was an effect of ΔE on female response towards the longer-sworded males [$F_{(5,7.4)} = 15.52$, p = 0.001]. The post hoc tests of pairwise comparisons showed that the female preference for the longer-sworded males was significantly higher when ΔE = 27 and 32 mm ($p < 0.05$) and that there was no difference on preference when ΔE was 2, 15, 37 or 43 mm long ($p > 0.05$; see Table II for statistics). Preference was not affected by mean male size (Pearson correlation; *r* = -0.31, p = 0.55).

There is a positive relationship between the proportion of females selecting for the longer-sworded males and female preference, which is an index of the interaction time with these males in function of total interaction in trials.

DISCUSSION

In our study, the females had no previous experience in mating and were similar in age and size, therefore female total interaction time and preference were not a consequence of size and experience as demonstrated in *X. nigrensis* (Wong et al. 2011). The results in this study showed that the preference of female *X. montezumae* for long-sworded males does not increase with sword length. Instead, preference was significantly higher when the difference in sword length was from 27 to 32 mm. At least for *X. helleri*, it has been demonstrated that small differences in sword size (6 mm) are enough to bias selection towards longer-sworded males in paired-stimulus choice tests using live males (Basolo 1990b) and that female preference increases with sword length. The females of *X. montezumae* seem to be less responsive to the difference in sword size than *X. helleri*, despite the males in this species exhibiting the most exaggerated expression of the characteristic within the swordtail group.

These results showed that when in the presence of males with a larger difference in sword size the females lost the preference for the long-sworded males, which is contrary to our predictions according to the female's lack of experience. Similarly, female guppies (*Poecilia reticulata*) prefer males with long dorsal fins, but when presented to live males with a supernormal expression of this trait then that preference became unlikely, which may restrain the evolution towards more exaggerated dorsal fins (Karino et al. 2011). The mating preferences may be influenced by many factors that form part of the environmental context in which the selective gender must decide. In this study, where females were reproductively naïve, the loss of preference for the most conspicuous males should have been caused by the female's evaluation of other features of the males during trials.

Because we used males with a natural sword size, it is likely that females responded to male traits correlated with sword size in a form that was not evident to us. Although manipulaion is necessary to exclude the possibility of mate choice based on characters that covary with visual signals, we used males with its natural sword length to avoid an effect of sword excision or artificial swords on courtship displays (which has not yet been tested). The males in this study spent all of the time in trials courting, independently of their sword length. However, we did not estimate courtship qualitatively. Basolo (1990b) reported that after making reversal experiments in which sword length was modified by sword excision after a previous trial, the time that both males courted was not affected. In this reversal experiment females reversed its choice too, confirmirming that they select mates based on sword size. Female assessment of visual characters might be correlated with signals involving individual performance, moreover in species in which courtship is an important feature on mate choice. In *Xiphophorus*, male courtship involves frontal arching displays as well as backup swimming (Haas 1993) among other maneuvers. The methods used to control for correlated characters in behavioral observations may also carry some difficulties. The use of video playbacks should consider motion vision in animals and a sequence of images in screens may difficult spatial acuity and affect animal responses (Nelson et al. 2010; Nelson & Fijn 2013). Artificial stimuli and phenotypic manipulation has shown to result in low experimental repeatability and in the possibility of misunderstanding the qualitative characteristics of behavior due to compensatory mechanisms (Robinson et al. 2011; Rosenthal et al. 2002).

Females may discern the elaboration of courtship displays (Engström-Öst & Candolin 2007). All these are traits that give them some information about the male performance in their environment. The sword in *X. montezumae* generates costs to the bearers in various aspects of fish locomotion. The sword length reduces critical swimming speed by 20% (Kruesi & Alcaraz 2007) and increases the cost of routine and courtship swimming (Basolo & Alcaraz 2003). Additionally males with longer swords are slower during the preparatory phase of the escaping maneuver (C-starts; Kruesi et al., own data). Hence, boundaries may arise when the costs of the sexually selected traits exceed the individual's possibilities to perform adequately. Females may evaluate performance between competing males correlated with structural traits. In this study, the use of live males with natural differences in sword size instead of video play back as stimuli provided additional information to females.

Male pairs were formed maintaining the sword extension of the long-sworded males constant, hence variation was provided by the difference with the short-sworded male in each treatment. The females exposed to male pairs with similar swords and with a small difference between them (ΔE = 0 and 15 mm) have probably had to chose between males which could be similarly affected in their courtship performance. Instead, when females were exposed to male pairs exhibiting the two largest differences in sword size they were exposed to a long-sworded male that was conspicuous but likely with a low performance compared to the short sworded males in those treatments. However, they did not show a preference for the shorter-sworded males either. Moreover, there was also a major proportion of females interacting more time with the longer-sworded males when the preference increased. This, suggests that the decrease in preference observed when males exhibit longer swords (with a difference over 32 mm) is acompanied by a rejection of the longer-sworded males.

Having exaggerated traits may produce displays that are relatively less attractive to females, making them to desist from choosing conspicuous males when the expression of the structural trait reaches a threshold between morphological cues and performance. It is likely that costly sexually selected characteristics represent a handicap that when successfully overcome indicate the quality of the bearers (Zahavi 1975). However, in some species females even show disdain for exaggerated traits (Saetre et al. 1997; Griffith et al. 1999; Shenoy & Crowly 2011). To evaluate to what point female preference costists of a bias towards visually attractive traits and if it is regulated by the assessment of male performance bearing costly traits, further experiments shoult be done and the functional costs of cospicuous characters have to be estimated.

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Figures and Tables

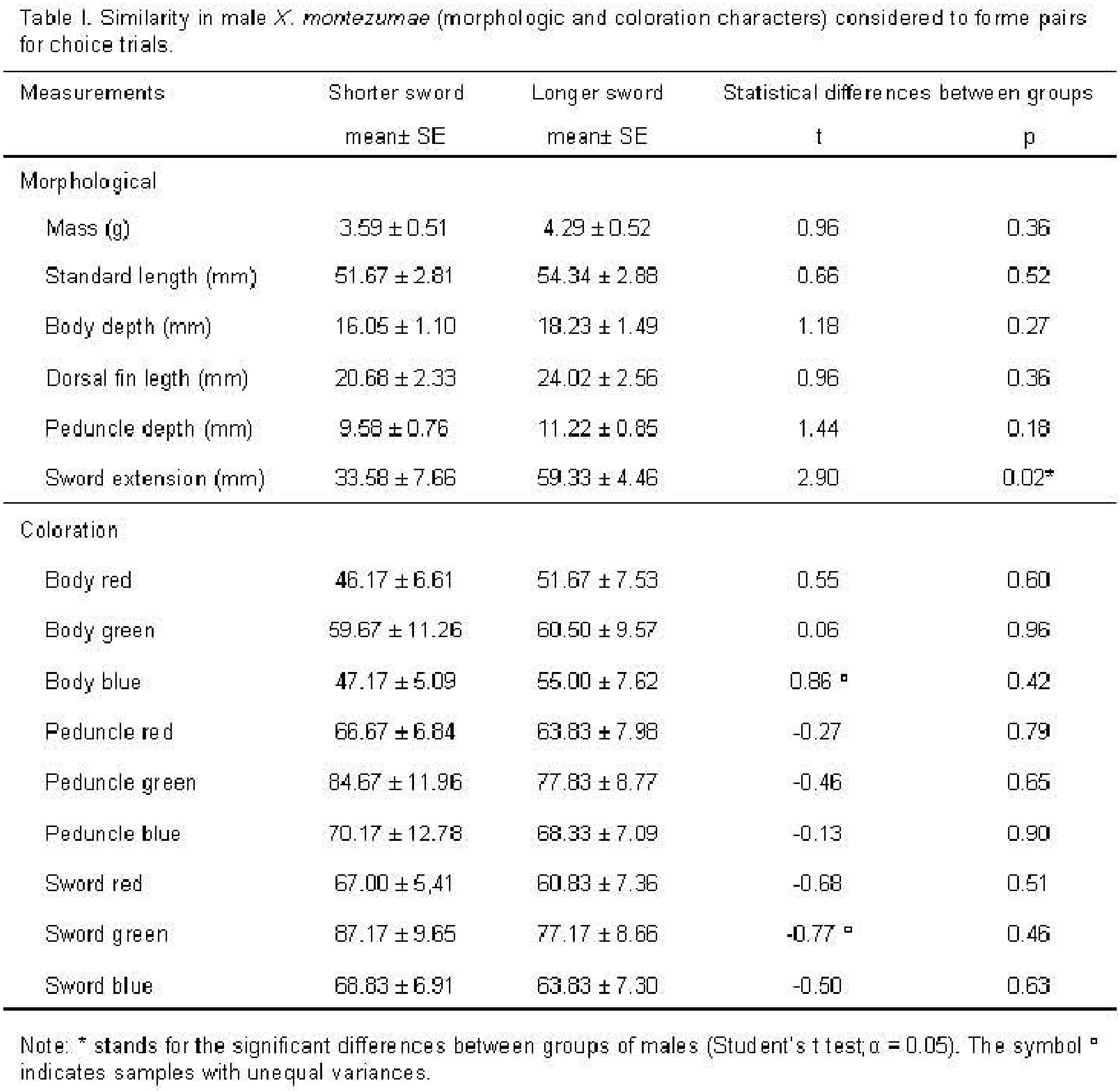

Table I. Similarity in male *X. montezumae* (morphologic and coloration characters) considered to forme pairs for choice trials.

Measurements	Shorter sword mean± SE	Longer sword mean± SE	Statistical differences between groups t	 p
Morphological				
Mass (g)	3.59 ± 0.51	4.29 ± 0.52	0.96	0.36
Standard length (mm)	51.67 ± 2.81	54.34 ± 2.88	0.66	0.52
Body depth (mm)	16.05 ± 1.10	18.23 ± 1.49	1.18	0.27
Dorsal fin legth (mm)	20.68 ± 2.33	24.02 ± 2.56	0.96	0.36
Peduncle depth (mm)	9.58 ± 0.76	11.22 ± 0.85	1.44	0.18
Sword extension (mm)	33.58 ± 7.66	59.33 ± 4.46	2.90	0.02*
Coloration				
Body red	46.17 ± 6.61	51.67 ± 7.53	0.55	0.60
Body green	59.67 ± 11.26	60.50 ± 9.57	0.06	0.96
Body blue	47.17 ± 5.09	55.00 ± 7.62	0.86 ▫	0.42
Peduncle red	66.67 ± 6.84	63.83 ± 7.98	-0.27	0.79
Peduncle green	84.67 ± 11.96	77.83 ± 8.77	-0.46	0.65
Peduncle blue	70.17 ± 12.78	68.33 ± 7.09	-0.13	0.90
Sword red	67.00 ± 5,41	60.83 ± 7.36	-0.68	0.51
Sword green	87.17 ± 9.65	77.17 ± 8.66	-0.77 ▫	0.46
Sword blue	68.83 ± 6.91	63.83 ± 7.30	-0.50	0.63

Note: * stands for the significant differences between groups of males (Student's t test; α = 0.05). The symbol ▫ indicates samples with unequal variances.

Table II. Female preference and interaction time with the short and long-sworded males in each pair.

ΔE between males	Female interaction time (i) mean± SE (s)		Preference (*P*) mean± SE	Females selecting longer-sworded males	N
(mm)	Shorter	Longer		(%)	
2	347 ± 56	335 ± 53	0.50 ± 0.08^{a}	44	9
15	218 ± 47	223 ± 41	0.49 ± 0.08^{a}	56	9
27	135 ± 38	218 ± 27	0.68 ± 0.06^{b}	89	9
32	184 ± 60	288 ± 83	0.63 ± 0.07^{b}	86	8
37	264 ± 72	277 ± 64	0.44 ± 0.06^{a}	44	9
43	387 ± 47	298 ± 47	0.42 ± 0.06^{a}	44	9

Note: The letters in column *P* describe significant differences between preference values (Least squares post hoc test for linear mixed model analysis; $\alpha = 0.05$).

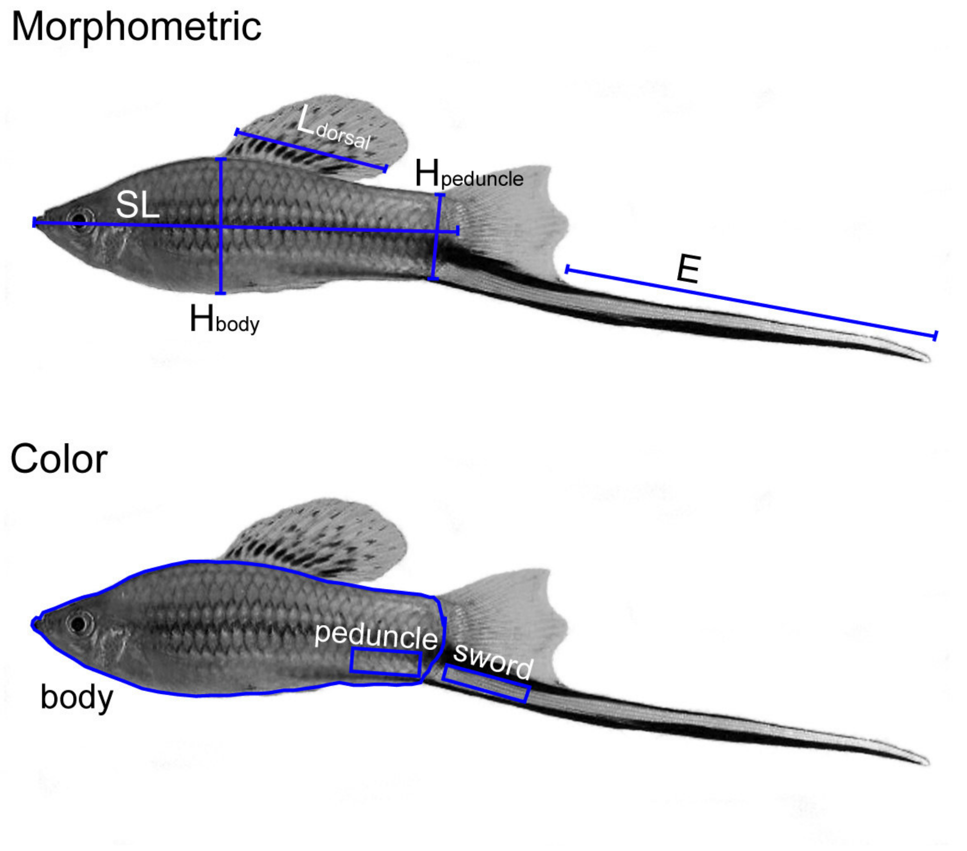

Fig. 1. Morphometric measurements taken on mature Montezuma swordtail males: (SL) standard length, (H) body depth, measured perpendicularly to SL line, from the anterior insertion of the dorsal fin to the vendral surface of the fish, (L_{dorsal}) dorsal fin length, from the anterior to the distal tip in its longest portion and horizontal to the base line, ($H_{peduncle}$) peduncle depth, in its most posterior portion, (E) sword extension, blabla. The dotted lines mark the surface areas selected to measure coloration: (body) whole body lateral surface, (peduncle) measured as the area below the lateral pigmented line from the most posterior insertion of the dorsal fin to the onset of the caudal fin, and (sword) area below the

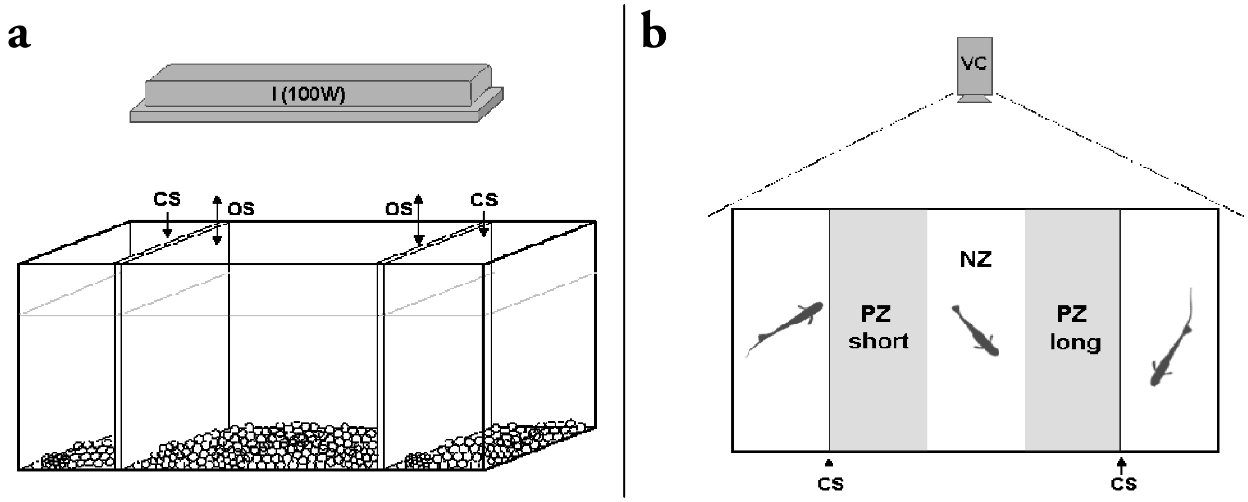

Fig. 2. Experimental setup showing (a) a lateral view of the experimental tank divided by two sets of clear fixed (CS) and opaque removable (OS) screens, gravel substrate and a lamp 40 cm above it, and (b) an upper view of the tank showing the external compartments where the males of each pair were set and the three central zones, two external (PZ) where females attended either de long- or the short -sworded males and a central neutral zone. A video camcorder was set 60 cm from one side of the tank to register behavior.

5. DISCUSIÓN GENERAL Y CONCLUSIONES

“El costo de la espada y su función en la selección sexual de *Xiphophorus montezumae*.”

Una manera de estudiar el origen y la evolución de los caracteres sexuales secundarios (CSS) es a través de la historia evolutiva o filogenética del grupo. Este tipo de información conforma la base para entender la función de estos caracteres y las fuerzas selectivas que han dirigido su evolución y determinan su permanencia en un grupo taxonómico, siendo la selección intersexual uno de los mecanismos involucrados en estos procesos. De manera general, la preferencia por los caracteres seleccionados sexualmente puede estar asociada a que éstos funcionan como señales indicadoras o amplificadoras que facilitan al receptor la evaluación genuina de la pareja potencial, a caracteres genéticamente correlacionados (expresión de CSS y conductas de preferencia) o bien a la expresión de señales honestas que pueden resultar en beneficios indirectos para las hembras. De esta manera para intentar entender la evolución de los CSS es necesario ahondar en la preferencia de las hembras, en la relación entre la preferencia y el grado de expresión de los CSS, en el costo asociado a la expresión de los ornamentos y en la relación de estos con alguna respuesta asociada a la adecuación de los individuos.

LA EXPRESIÓN DE LA ESPADA COMO SEÑAL AMPLIFICADORA

La preferencia asociada a caracteres que funcionan como señales amplificadoras exige que éstas estén ligadas genéticamente al potencial del macho que las porta, de manera que su expresión no resulta costosa. Estas señales son por definición honestas debido a que grado de expresión está positivamente correlacionado con la cualidad que señala (Hasson 1991). En muchas especies, como también sucede en las hembras del género *Xiphophorus*, la talla corporal es uno de los CSS más importantes en la selección de pareja (Ryan y Keddy-Hector

1992; MacLaren y Daniska 2008); por lo que no es de extrañarse que muchas de las señales amplificadoras están directamente ligadas a la talla de los animales, es decir el cambio de su expresión está directamente ligada al crecimiento. De esta manera, el grado de desarrollo de la espada de los machos y su máxima expresión podría estar ligados a la talla corporal de los individuos. Los resultados de este trabajo no apoyan esta hipótesis dado que muestran que el crecimiento corporal y la talla máxima de los machos de *Xiphophorus montezumae* no se relaciona de con la longitud del ornamento. La espada en machos de *X. montezumae* es una estructura ornamental que está estrechamente relacionada con la historia de vida de los individuos. La expresión y el desarrollo de algunos caracteres sexuales secundarios están relacionados con la historia de vida temprana de los organismos; como el tamaño o la simetría corporal que son producto de una adecuada obtención de recursos en etapas del ciclo de vida tempranas y pueden ser afectados por estrés ambiental durante el desarrollo (De Coster et al. 2013). Este estudio mostró que en *X. montezumae* la espada crece más rápido cuando se alcanza una mayor talla a la edad de maduración y al inicio del desarrollo de los caracteres sexuales secundarios, de manera similar a lo que ocurre entre otras especies del género *Xiphophorus* (Marcus y McCune 1999). Esto, por un lado muestra que la inversión de los individuos en el desarrollo de caracteres sexuales es menor a la que se asigna al crecimiento corporal y se incrementa solo hasta alcanzar cierta talla corporal. Es decir, al menos bajo condiciones controladas (en ausencia de presiones ambientales que beneficien la maduración temprana), los individuos asignan los recursos primero al crecimiento somático y posteriormente al alargamiento de la estructura. Por otro lado, es probable que estos organismos compensen el retraso en el desarrollo de la espada con tasas más aceleradas de crecimiento del carácter, obteniendo de manera similar los beneficios de este ornamento.

La talla es importante en los organismos debido a que incrementa las posibilidades de ganar la competencia por recursos como alimento, territorio, pareja reproductiva, además de que puede resultar ventajosa en la defensa anti-depredatoria. Esto se debe entre otras razones a que la masa corporal tiene un efecto importante en la fuerza y resistencia de los organismos ante las condiciones desfavorables (Taylor et al. 2000). En los procesos de selección sexual también brinda beneficios ya que tener una talla corporal mayor implica ganar los encuentros agonísticos en la competencia directa por una pareja reproductiva (combate) y controlar el territorio libre de competidores. En este estudio, los individuos con mayor talla al inicio del desarrollo de los caracteres sexuales secundarios presentaron tasas de crecimiento de la espada más aceleradas. Sin embargo, el crecimiento acelerado del ornamento no fue suficiente pues la talla corporal tuvo una correlación negativa con la longitud de la espada al final de nuestro experimento. Estos resultados sugieren que los machos de *X. montezumae* que a la edad de maduración alcanzan una talla menor podrían incrementar su talla aparente a través del efecto óptico que causa la espada y como consecuencia obtener beneficios. No existen estudios que confirmen que la espada les ayuda a contrarrestar las desventajas de tener un cuerpo más pequeño, sin embargo aquellos que alcanzan una talla mayor son dominantes en los encuentros agonísticos (Beaugrand y Zayan 1985). Las hembras de muchas especies de animales (entre ellas mamíferos, aves, anfibios y peces) muestran preferencias consistentes por los machos con mayor talla corporal y los peces del género *Xiphophorus* no son la excepción (Basolo 1990). Una de las hipótesis de por qué las hembras favorecen la expresión de la espada señala que esta estructura incrementa el tamaño aparente de los individuos (Rosenthal y Evans 1998). Sin embargo al no verse ligada su expresión al tamaño real podemos descartar que se pueda considerar como una señal amplificadora.

Aunque la espada no tenga una función como indicador de la historia de vida exitosa de los organismos en etapas tempranas, existen evidencias de que las hembras de éste género pueden utilizar otros caracteres para evaluar a las parejas reproductivas disponibles. Morris y colaboradores (2012) estimaron que la expresión de las líneas de melanina laterales, que constituyen un carácter sexual secundario en muchas especies de *Xiphophorus* es asimétrica cuando existe una deficiencia durante el desarrollo del individuo. Esta asimetría tiene consecuencias en los machos en etapa adulta ya que las hembras los rechazan en presencia de individuos con un número simétrico de líneas en ambos lados del cuerpo. Al seleccionar machos simétricos las hembras se aparean con los machos de mejor calidad.

LA ESPADA COMO CARÁCTER HONESTO

Una segunda opción para explicar la expresión de la espada en estos peces se fundamenta en la expresión del carácter como un indicador asociado a una señal honesta de la calidad del macho. La espada es un carácter que se ha demostrado resulta costoso en diferentes aspectos para los machos del género *Xiphophorus*. Basolo y Alcaraz (2003) estimaron los costos metabólicos de la espada durante el cortejo y el nado de rutina en esta misma especie. Además, la presencia de esta estructura genera arrastre hidrodinámico reduciendo la capacidad crítica de nado de los portadores (Bonilla 2005; Kruesi y Alcaraz 2007). Los costos de la espada en machos de este género también se han demostrado en función de que este carácter atrae tanto a las hembras como también a uno de sus predadores naturales, el pez tetra mexicano (*Astyanax mexicanum*; Rosenthal et al. 2001; Hernández-Jiménez y Ríos-Cárdenas 2012).

Un ornamento que es costoso no puede funcionar como un engaño, o si lo hace tiende a permanecer únicamente por un tiempo (evolutivo) relativamente corto (Lotem 1993). De acuerdo con Zahavi (1975), la calidad genética de los individuos puede ocasionar que solo aquellos miembros de la población que son suficientemente capaces puedan sobrevivir pagando los costos de emitir una señal eficiente en términos del éxito reproductivo. Aunque los costos de la espada habían sido evaluados a través de la reducción en la velocidad crítica de nado durante nado lineal, los costos de la espada asociados directamente a la adecuación como la habilidad de escape ante un predador pueden brindar información de mayor relevancia para explicar la expresión del carácter. De acuerdo con Baumgartner y colaboradores (2011) la longitud de la espada en peces cola de espada de la especie *X. helleri* no afecta la sobrevivencia de los machos portadores porque no disminuye su velocidad de escape. Sin embargo, los resultados en este estudio mostraron que la espada en *X. montezumae* afecta de manera importante al desempeño de la maniobra de escape. La fase preparatoria del escape es disparada por vía neuronal produciendo la contracción de los músculos de un lado del cuerpo hasta lograr una posición con forma de “C”; los resultados mostraron que la presencia de este ornamento dificulta la ejecución de la posición en “C” ya que el tiempo en alcanzarla es mayor. Domenici (2007) asegura que esta fase de la maniobra es muy importante y determina la velocidad, trayectoria y eficacia del escape. Adicionalmente, la presencia de esta estructura ornamental disminuye la aceleración y velocidad para completar la maniobra durante la segunda fase, comprobando que este carácter representa un costo en el desempeño de la maniobra de escape, lo que podría afectar su supervivencia. Hernández-Jiménez y Ríos-Cárdenas (2012) estimaron que los individuos con espadas largas no solo son más atractivos para el predador *A. mexicanus*, como propuso Rosenthal et al. (2002), sino que también son más propensos a fallar en el intento de escape. Aunque este estudio no reveló un efecto concreto de la longitud de la espada en el desempeño de los machos es posible que existan pequeñas diferencias en factores que no pudimos observar.

El costo de la espada relacionado directamente con el grado de expresión del carácter ha sido demostrado en *X. montezumae*. La longitud de la espada tiene un efecto negativo en la velocidad crítica de nado y los machos con una mayor tasa metabólica estándar (compensando por talla) son aquellos que tienen un mejor desempeño en esta actividad (datos no publicados). La relación entre la longitud del carácter y sus costos, aunados a la relación positiva entre el grado de expresión del CSS y el potencial metabólico de los animales apoyan la idea de que el ornamento funciona como un indicador directo de la calidad del macho. Es posible que además de existir costos energéticos asociados al cortejo en estos peces, existan diferencias en su desempeño asociadas con los costos o bien que sean compensadas y que las hembras puedan evaluarlas, como sucede en algunas aves que evalúan el cortejo de los machos que consiste en brincar rápidamente de una rama a otra, que es una actividad costosa (Barske et al. 2011). Los machos de *Xiphophorus* llevan a cabo un cortejo complejo (Haas 1993) con el que quizás señalen su talla aparente y la habilidad del desempeño de estas maniobras puede ser un factor importante en la eficiencia de la emisión de la señal.

Se ha demostrado que la espada representa una ventaja para los machos al permitirles aparentar una mayor talla corporal (Rosenthal y Evans 1998). Es decir, este carácter podría ser explotado por los machos como una señal deshonesta de su calidad individual (talla corporal). Sin embargo, al menos para las dos especies con espada más larga en el grupo (*X. helleri* y *X. montezumae*) lo anterior no es posible porque ya se han comprobado los costos de portar espadas, lo que inhabilita el engaño ya que los individuos que emitan una señal eficiente pagan de cualquier manera un costo por esta señalización. Es decir, son varias las evidencias que podrían apoyar la función de la espada como un carácter honesto que evidencia la calidad del portador más que un carácter correlacionado, una señal de engaño o un carácter amplificador.

LA EXPRESIÓN DE LA ESPADA COMO CONSECUENCIA DE LA FUERZA DE PREFERENCIA EN EL GÉNERO

Si la fuerza selectiva que favorece la elongación de la espada es la preferencia de las hembras por este carácter se esperaría que las especies con machos de espada más exagerada correspondieran a las especies con hembras que denotaran mayor preferencia por el carácter. En el caso de *X. montezumae* se esperaría que la preferencia de las hembras por este carácter fuera muy evidente en las hembras de esta especie respecto a otras especies de *Xiphophorus* y que la fuerza de preferencia en esta especie se incrementara con la longitud del ornamento de manera similar a lo que ocurre entre las hembras de *X. helleri*. Los resultados revelaron que la preferencia de las hembras es modulada (está determinada) por la diferencia entre la longitud del ornamento de los machos. Es decir, en la especie en la que los machos desarrollan el carácter más exagerado en el grupo, la preferencia por el macho con espada larga decae cuando la diferencia entre estos es mayor de un aparente límite. La fuerza de preferencia de las hembras de *X. helleri* es mayor que la de las hembras de *X. montezumae*, cuando esta especie es la que presenta a los machos con mayor elongación del ornamento. Aunque este estudio no permite evaluar las diferencias en el desempeño de las maniobras de cortejo entre los machos, es posible suponer que al ser de edad, talla y condición aparentemente similares, la diferencia en la respuesta de las hembras se debe al efecto de la espada en el desempeño de los individuos al cortejar.

Adicionalmente, la literatura indica que la preferencia de las hembras por la espada es un carácter plástico que depende de factores cognitivos. Se ha registrado que existe una tendencia de las hembras en sus primeros estadios a copiar la selección de otras hembras, de la experiencia propia con depredadores, así como del riesgo que perciban de asociarse con machos conspicuos. En este estudio se evaluó la preferencia por la longitud de la espada de los machos en hembras de *X. montezumae* sin experiencia cognitiva previa en selección de pareja, por lo que la elección femenina no fue sesgada por factores de experiencia o sociales. En conclusión, la dirección inversa de la preferencia con la expresión de la espada a nivel interespecífico y la expresión plástica de la preferencia de las hembras por la expresión del carácter indican que la expresión del CSS en este grupo de peces no se asocia a la correlación de ambos caracteres (expresión de la espada y preferencia).

Siendo la preferencia femenina un carácter fundamental para mantener la expresión de los CSS es interesante que la preferencia por la espada de las hembras del género *Xiphophorus* sea tan baja. La débil preferencia femenina por la espada en *X. montezumae*, estimada en este estudio y comparada con un estudio similar en *X. helleri* (Basolo 1990), así como la pérdida de la preferencia cuando la longitud de la espada excede cierto límite, son respuestas que pueden estar asociadas a los costos que este ornamento representa al crecer de manera indeterminada en esta especie. El hecho de que la espada continua creciendo a lo largo de la vida de los organismos implica un sistema dinámico en el que tanto los beneficios como los costos de portar un ornamento de mayor dimensión son factores que el organismo debe enfrentar de manera cambiante y continua a lo largo de su vida. Es posible que este ornamento por su naturaleza dinámica no genere costos a menos que alcance proporciones determinadas y que sea entonces cuando este carácter representa una desventaja para los portadores en términos de adecuación (Zahavi 1975). Así, es probable que sólo cuando el ornamento alcanza ciertas dimensiones las hembras evalúan los costos (riesgo de depredación) y los beneficios (progenie con buenos genes) de asociarse con ellos para la reproducción. En cuanto a los machos, de manera similar a lo que podría suceder en las hembras, es probable que la espada represente una desventaja únicamente cuando la estructura alcance ciertos límites que resulten costosos. Este supuesto podría fundamentarse en las diferencias de los costos generados por la espada en *X. helleri* y en *X. montezumae*. Mientras que en *X. helleri*, teniendo una espada relativamente corta, no se observan costos de la espada en la habilidad del escape, en *X. montezumae* (con espadas más largas que los primeros), la estructura disminuye la habilidad de escape de los portadores. Es decir, los costos de la espada tanto para hembras como para machos podrían incrementarse durante la vida de los animales.

Los resultados de este estudio sugieren que mientras la permanencia de la espada en *X. montezumae* puede explicarse por la preferencia (aunque relativamente baja) de las hembras por este carácter, la disminución de la preferencia en esta especie puede explicarse en base al incremento de los costos que genera la estructura durante su desarrollo. Los análisis filogenéticos más recientes para el grupo revelan que la espada es un carácter derivado, que la preferencia femenina es un carácter ancestral y que la presencia de la espada en el grupo se ha perdido en varias ocasiones de manera independiente (Meyer et al. 2006; Cui et al. 2013). A la par con nuestros datos y considerando esta base filogenética es posible suponer que la preferencia por la espada ha disminuido a lo largo de la historia evolutiva el grupo como resultado del desarrollo de espadas más largas que implican mayor costo para los portadores. Esto concuerda con lo señalado con Cui y colaboradores (2013) quienes explican que la longitud de la espada no parece estar correlacionada con la historia evolutiva en el grupo (al menos no de manera positiva) y que se observa una tendencia evolutiva hacia la disminución de la preferencia femenina por este carácter. La información generada en el presente estudio, utilizando como modelo al pez cola de espada de Montezuma (*X. montezumae*), brinda evidencias para evaluar las dos hipótesis principales que pueden explicar la pérdida del carácter en el grupo: la disminución en la preferencia femenina por este ornamento y su relación con los costos asociados a su probabilidad de sobrevivencia (depredación).

Xiphophorus montezumae expresa el ornamento más largo entre los peces cola de espada a pesar de que su presencia requiere de una inversión energética para realizar algunas actividades como el cortejo y de disminuir la velocidad de nado y habilidad del escape (Basolo y Alcaraz 2003; Kruesi y Basolo 2007; este estudio). La longitud de la espada no es un factor que afecte el establecimiento de la dominancia entre machos que compiten por el acceso a un grupo de hembras (Beaugrand y Zayan 1985) y las hembras de *X. montezumae* no muestran una mayor preferencia por la espada que las demás especies del género. Su débil preferencia parece concordar con el resto de las especies del clado de los peces cola de espada del norte (Cui et al 2013). Es probable entonces que la selección sexual no sea el proceso principal en la evolución de la espada en esta especie hacia esta forma de expresión elaborada y que como sugirió Meyer (1994) en aquellas especies de *Xiphophorus* en las que la expresión del carácter se ha perdido, exista de manera latente el sesgo sensorial en las hembras. Por un lado, aun no se conoce si existen mecanismos genéticos que regulen el alargamiento de la espada en otras especies que característicamente desarrollan espada corta, como *X cortezi* y *X. malinche*, ni existe evidencia de que el crecimiento de la espada cese ante factores ambientales como el riesgo de depredación, la estructura social, etc. Por otro lado, *X. montezumae* al igual que *X. helleri*, pudo haber desarrollado mecanismos de compensación ontogénicos que enmascaran los costos de portar una espada (Møller 1996; Basolo 1998; Oufiero et al. 2012), aunque estos mecanismos también resultan costosos (Gowaty 2008). Es probable que si el crecimiento de la aleta caudal no cesa entonces la variación entre individuos en los mecanismos de compensación juegue un papel determinante para su adecuación, permitiendo el desempeño exitoso de actividades ecológicamente relevantes como el escape de los depredadores y la maniobra de cortejo, entre otras.

Se ha propuesto que la selección sexual puede actuar en contra de los procesos de selección natural, favoreciendo la expresión de caracteres sexuales secundarios que resultan costosos para los individuos en términos de adecuación. Sin embargo, aunque la competencia entre individuos por incrementar el éxito reproductivo es un proceso para dirigir la evolución de la expresión de un carácter en una dirección determinada y la selección natural regule el efecto de la selección sexual.

6. LITERATURA CITADA

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