

Population ecology
and sexual preferences
in the mating complex of the
unisexual Amazon molly
Poecilia formosa
(GIRARD, 1859)

von

Katja U. Heubel

**Population ecology
and sexual preferences
in the mating complex of the
unisexual Amazon molly
Poecilia formosa (GIRARD, 1859)**

Dissertation
zur Erlangung des naturwissenschaftlichen Doktorgrades
des Fachbereiches Biologie
der Universität Hamburg

vorgelegt von

Katja U. Heubel

aus

Ludwigsburg

Hamburg im Januar 2004

Genehmigt vom
Fachbereich Biologie der
Universität Hamburg
auf Antrag von Herrn Professor Dr. J. PARZEFALL
Weitere Gutachter der Dissertation:
Herr Priv. Doz. Dr. I. SCHLUPP

Tag der Disputation: 06. Februar 2004

Hamburg, den 23. Januar 2004



Professor Dr. A. Frühwald
Dekan

TABLE OF CONTENTS:

<u>Outline of this thesis</u>	1
<u>Chapter 1: General Introduction</u>	3
Coexistence and persistence in the mating complex of the Amazon Molly, <i>Poecilia formosa</i> and its sexual host species	3
The system	4
Evolution of sex: advantages and disadvantages of asexual reproduction	5
Niche partitioning and character displacement	7
Frozen niche variation model	8
Alternatives to frozen niche	9
<u>Chapter 2: Population ecology in the mating complex of the unisexual Amazon molly <i>Poecilia formosa</i></u>	10
Introduction	10
Gaps in our knowledge	10
What explains the success of Amazons?	10
Heterogeneity and variation of habitat and fish community	11
Temporal or spatial population patterns within the mating complex	11
Frozen Niche Variation	12
The role of males	12
Long-term success of Amazons: Disadvantages of asexual reproduction	13
Abiotic parameters: a key to Amazons?	13
Study area	14
Central Texas	15
South Texas	18
Materials and Methods	21
Fish sampling	21
Processing of <i>Poecilia</i>	22
Physical and chemical parameters of water quality	23
Data handling	24
Results	26
Community sampling at field sites	26
Species diversity	28
Significance of <i>P. formosa</i> in the fish community	29
A closer look at mollies: The sexual-asexual mating complex	30
Selected parameters that affected frequency of <i>P. formosa</i>	38
Population ecology in the complex: Integrating parameters to explain variation	44
Discussion	47
Community and the success of Amazons	47
Representativeness and validity in comparison to other studies	47

Properties of habitats and environmental fluctuation	49
A closer look: dynamics and patterns within the complex	50
Advantage of asexuals	51
Life history patterns in the complex	52
A temporal niche? The success of <i>P. formosa</i>	54
Population ecology in the complex: Parameters to explain habitat variation	55
Which parameters explain frequency of Amazons?	55
Evolutionary stability caused by ecological instability?	57
<u>Chapter 3: Males are choosy when it matters</u>	59
Abstract	59
Introduction	59
Materials and Methods:	63
Results	65
Discussion	67
<u>Chapter 4: Turbidity affects association behaviour in male Sailfin mollies (<i>Poecilia latipinna</i>)</u>	70
Abstract	70
Introduction	70
Materials and Methods	72
Results	74
Discussion	75
<u>Chapter 5: Geographic variation in female mate-copying in the species complex of a unisexual fish, <i>Poecilia formosa</i></u>	78
Abstract	78
Introduction	78
Materials and Methods	81
Results	85
Discussion	88
<u>Chapter 6: When does it pay off for males to discriminate?</u>	91
A first matrix	93
Perspectives	95
<u>Chapter 7: General Discussion and Conclusion</u>	96
Summary	99
Zusammenfassung	102
Literature	105
Danksagung / Acknowledgments	122
Appendix	124
Curriculum vitae	136
Erklärung	137

Population ecology and sexual preferences in the mating complex of the unisexual Amazon molly *Poecilia formosa*

Abstract The Amazon molly *Poecilia formosa* is a gynogenetic all-female ovoviparous fish. Gynogenesis is a special form of parthenogenesis; sperm is needed to trigger embryogenesis. Males do not contribute to the genome of ameiotically produced all-female offspring. In this unique mating system, asexually reproducing females have to rely on heterospecific matings with males of two closely related sexual host species, *P. latipinna* and *P. mexicana*. This asexual / sexual species complex is a unique model system to study the stability of coexistence of closely related bisexual and unisexual species. In mixed shoals of a sexual host species and the sexual-parasite *Poecilia formosa*, sperm donating males mate with conspecific sexual females and heterospecific asexual females. Obviously, males benefit from mating with conspecific females, whereas mating with the unisexual *P. formosa* does not increase a male's fitness. Therefore, males should discriminate between the two types of females. Under perfect mate discrimination, the Amazon molly *P. formosa* would disappear. On the other hand, asexually reproducing females theoretically have a faster population growth than sexually reproducing females because they do not have to incur the cost of producing males. This advantage of asexual reproduction would lead to increasingly high proportions of asexual Amazon mollies (*P. formosa*) in mixed populations. By outcompeting its sexual host species, the sexual-parasite *P. formosa* would also disappear.

The aim of this thesis is to study the coexistence and stability of the asexual / sexual mating complex of *P. formosa* and how it can be maintained. Therefore, I studied the ecological situation and patterns of coexistence in several mixed populations in the field and conducted experiments on mate choice behaviour in the asexual / sexual species complex of the Amazon molly *P. formosa*.

Outline of this thesis

This thesis is organized in seven chapters. The technical details of each study can be found in the specific chapters. Chapter one is an introduction and thus written in the form of an essay. Chapter 2 -5 are structured in summary, introduction, methods, results, and discussion. Chapter six is a short communication and chapter seven a general discussion and conclusion. This outline is a very general introduction to the concepts of the research questions.

Chapter 1 presents a general introduction to the evolution of sex, advantages and disadvantages of asexual reproduction, and persistence of the gynogenetic Amazon molly, *Poecilia formosa*. Some existing general hypotheses on advantages and disadvantages of asexual reproduction are discussed with particular reference to those models that may also apply to sperm dependent unisexual fishes.

In **chapter 2**, an ecological field study is presented and discussed. The aim of this study was to investigate possible niche differentiation and population dynamics in this species-complex. Therefore, the ecology of the coexistence of the Amazon molly and the closely related sperm donating bisexual species *P. latipinna* has been studied in several sympatric populations in

South (old sympatry) and Central (young sympatry) Texas. Environmental heterogeneity, the spatial and temporal variation and stability of habitat properties, community structure, species diversity, predation risk and life-history parameters (e.g. sex-ratios, juveniles, body size) within the asexual / sexual mating complex, and relationships of frequency of *P. formosa* with other observed variables were thoroughly investigated. Besides factors of the fish community and interactions with its sexual host species that turned out to have an impact on frequency of Amazons, I present a variety of measured abiotic parameters and test their potential relevance to explain the persistence of the Amazon molly. Environmental stochastic disturbances are discussed as a possible explanation to maintain the coexistence of the Amazon molly *P. formosa* and its host.

While chapter two concentrates on ecological factors that might explain the stability of this asexual / sexual mating complex, **chapter 3, 4, and 5** focus on behavioural aspects that might contribute to the persistence of Amazon mollies.

In **chapter 3**, seasonal variation of male mating preferences for conspecific sexual females *versus* asexual *P. formosa* in several, regularly sampled sympatric populations in South and Central Texas has been tested. This chapter shows that male mating preferences are neither male-size dependent nor depending on the frequency of asexual females within the population. Males did not have general preferences for conspecific females, but preferences were seasonally influenced. Males had mate preferences for conspecific sexual females during the natural peak season of reproduction.

Chapter 4 studies the impact of turbidity as an environmental factor that is highly variable among different sympatric populations on male mating preferences of the bisexual-unisexual *P. latipinna* / *P. formosa* species complex. Most habitats of visually communicating mollies are considerably turbid throughout the year. I tested how turbidity influences male mating preferences for sexual and asexual females.

Males might benefit from mating with *P. formosa* due to heterospecific imitation behaviour of sexual females that copy mate choice decisions of the unisexual *P. formosa* increases males' attractiveness and thus enhances probability to obtain future matings with conspecific females (Schlupp et al. 1994). Males mating with Amazons increase their attractiveness to sexual conspecific females that observe those interactions by such "wrong" matings.

In **chapter 5**, the extent of heterospecific and conspecific mate-copying behaviour has been studied in sympatric and allopatric populations of *P. mexicana* and *P. latipinna* and its gynogenetic associate *P. formosa*. I compared mate-copying scores, the degree to which female *P. latipinna*, *P. mexicana*, and *P. formosa* alter their preference after observing another (heterospecific *P. formosa* or conspecific) female mating with the initially less preferred male. In both systems (*P. latipinna* / *P. formosa* and *P. mexicana* / *P. formosa*), sexual and asexual females copy each other's mate choice decisions in sympatry, but heterospecific mate-copying seems to be absent in allopatry.

The different behavioural aspects of the previous chapters lead to the fundamental question: When does it pay off for males to discriminate between sexual and asexual females as potential mates in the mating complex of *P. formosa*? In **chapter 6**, an asymmetric game theoretical model is suggested to address this question by integrating male and female behaviour. As a starting point, I present the prospective pay-off matrix for future theoretical modelling work on the stability of this mating complex.

Chapter 1: General Introduction

Coexistence and persistence in the mating complex of the Amazon Molly, *Poecilia formosa* and its sexual host species

One of the unanswered questions in ecology is how coexistence of closely related bisexual and unisexual species can be maintained. Unisexual vertebrates are extremely rare (Vrijenhoek et al. 1989). Asexually reproducing fishes or amphibians are always sperm dependent unisexual organisms and therefore coexistence of closely related sexually and asexually reproducing individuals is a necessity for the persistence of these asexual lineages. Besides coexistence in the mating complex of *Poecilia formosa* (Hubbs & Hubbs 1932; Balsano et al. 1981), it has also been studied in other complexes of unisexual-bisexual fishes, e.g. in *Poeciliopsis* (Moore & McKay 1971; Moore 1975), *Menidia* (Echelle & Echelle 1997), and *Phoxinus* (Schlosser et al. 1998). See Schultz (1989) and Vrijenhoek (1994) for reviews of unisexual-bisexual species complexes in fishes.

Balsano et al. (1989) summarise and discuss two hypotheses that might account for bisexual – unisexual coexistence. The first hypothesis, “**the behavioural regulation hypothesis**”, explains coexistence *via* behavioural regulated density or frequency dependent mating success (Moore & McKay 1971; Stenseth et al. 1985) or *via* regulating effects due to general weak mate discrimination (McKay 1971; Moore & McKay 1971; Kawecki 1988). A frequency dependent regulation assumes that male dominance hierarchies regulate sperm availability to unisexuals. In the *Poeciliopsis* complex, males have an underlying preference for conspecific sexual females. However, it is less pronounced in subordinate males. They are less discriminating and more likely to mate with unisexuals. Consequently, they are not likely to exclude their bisexual host species (McKay 1971; Moore & McKay 1971).

For the asexual / sexual mating complex of *P. formosa*, male dominance hierarchies are also documented for males of the sexual host species *P. mexicana* (Parzefall 1969; Balsano et al. 1985) and *P. latipinna* (Baird 1968). However, in neither species, dominance hierarchies among males restrict access to females.

Behavioural aspects of asexual – sexual coexistence in the mating complex of *P. formosa* are studied in chapter 3, 4, 5, and 6.

The second hypothesis on the stability of coexistence of bisexual and unisexual species is adopted from general assumptions on **niche segregation** among closely related species (e.g. MacArthur & Lewins (1967). The “**resource-partitioning hypothesis**” assumes that bisexual and unisexual taxa are sufficiently distinct to not compete for common limiting resources and therefore coexist by resource partitioning (Vrijenhoek 1978; Schenck & Vrijenhoek 1986; Wetherington et al. 1989).

Balsano et al. (1985, 1989) favour the resource-partitioning hypothesis: Despite highly skewed sex ratios in favour of females, they state that sperm availability is not a limiting resource. These ecological aspects of bisexual – unisexual coexistence are presented in chapter 2.

The system

Amazon mollies, *Poecilia formosa* (GIRARD, 1859), are all-female gynogenetic fish of the live-bearing family Poeciliidae (Hubbs & Hubbs 1932) (Fig. 1.1). A characteristic trait of Poeciliids is internal fertilisation and ovovivipary. Females have a pronounced sexual cycle (Parzefall 1973). Males are characterised by their typical copulatory organ, the gonopodium, which is the modified anal fin (Rosen & Bailey 1963).



Fig. 1.1: unisexual Amazon molly *P. formosa*.

Gynogenesis is a special form of parthenogenesis in which sperm of a host species serves as a physiological stimulus to trigger embryogenesis. This sperm normally is not incorporated into the genome of the offspring (Schlupp et al. 1998, but see Schartl et al. 1997; Lamatsch et al. 2000). Amazons asexually produce all-female offspring from diploid eggs (Rasch & Balsano 1989). In the case of *P. formosa*, sperm is usually provided by males of one of two species, *Poecilia mexicana* STEINDACHNER, 1863 or *Poecilia latipinna* (LE SUEUR, 1821) (Hubbs & Hubbs 1932; Schlupp et al. 1998). A third natural host species (Niemeitz et al. 2002), *Poecilia latipunctata* MEEK, 1904, has a very limited biogeographic range in Tamaulipas, Mexico (Miller 1983).

Like other unisexual vertebrates (Turner 1982; Vrijenhoek et al. 1989), *P. formosa* speciated via hybridisation (Turner 1982). The Amazon molly is most likely derived from a single hybridisation event of a *P. mexicana* female and a *P. latipinna* - like male ancestor (Turner 1982; Avise et al. 1991; Schartl et al. 1995; Möller 2001).

Amazon mollies range from southeast Texas to northeast Mexico. *P. formosa* is sympatric with *P. latipinna* in Texas and a few areas in northeast Mexico, while it is sympatric with *P. mexicana* in Mexico (Darnell & Abramoff 1968; Schlupp et al. 2002).



Fig. 1.2: Female Sailfin molly *Poecilia latipinna*.



Fig. 1.3: Male Sailfin molly *Poecilia latipinna*.

Evolution of sex: advantages and disadvantages of asexual reproduction

PERSISTENCE OF GYNOGENESIS

As explained above, gynogenesis is a special form of parthenogenesis in which sperm of a host species serves as a physiological stimulus to trigger embryogenesis. This sperm normally is not incorporated into the genome of the offspring and all-female offspring is produced from diploid eggs. Pseudogamous (or gynogenetic) organisms have therefore a need for continued coexistence with sexual associates. Ridley (1993) expects that there must be an underlying constraint for fishes and amphibians not to become parthenogenetic, in contrast to asexually reproducing reptiles.

TWO-FOLD ADVANTAGE OF ASEXUAL REPRODUCTION

Asexual reproduction has an immanent advantage: The asexual female multiplies at twice the rate. Therefore, the sexual female has only 50% of the fitness of an asexual female, assuming males make no energetic contribution to reproduction and there is no parental care (e.g. in some birds the cost of sex therefore is lower than 50%). To outweigh the cost of sexual reproduction, females must produce offspring via sexual reproduction that is twice as fit as clonal copies of themselves. Williams (1975) called this „the outstanding puzzle in evolutionary biology“.

Costs and benefits of asexual reproduction have been intensively discussed (Ghiselin 1974; Williams 1975; Maynard Smith 1978; Bell 1982). Only few studies report actual evidence for the cost of sexual reproduction (Dunbrack et al. 1995; Jokela et al. 1997a).

However, there must be a selective advantage of sexual reproduction overcoming this two-fold cost of sex (Williams 1975; Maynard Smith 1978) because the overwhelming majority of animal species still has sex.

MULLER'S RATCHET AND THE EVOLUTIONARY AGE OF AMAZON MOLLIES

Sexually reproducing *P. latipinna* and gynogenetic *P. formosa* have been coexisting in South Texas for more than 100.000 generations (Schartl et al. 1995; Möller 2001). According to Muller's ratchet (Muller 1964) sexually reproducing species should outcompete co-occurring closely related clonal organisms due to accumulation of deleterious mutations in the genome of the asexuals (Crow & Kimura 1965) and, theoretically, asexual lineages are expected to go extinct after approximately 10.000 – 100.000 generations (Lynch & Gabriel 1990). With Amazons, this seems not to be the case.

Why are Amazons so successful in maintaining a stable coexistence for such a long time? Assuming the age of *P. formosa* and mutation rate are estimated correctly, *P. formosa* must have developed mechanisms to compensate negative genetic effects of asexuality. Introgression of microchromosomes and occurrence of triploids are discussed as possible mechanisms of „occasional sex“ to maintain genetic diversity and keep deleterious mutations under a certain threshold (Turner et al. 1983; Balsano et al. 1989; Lewis et al. 1999; Lamatsch et al. 2002). To what extent these phenomena might contribute to the maintenance of co-existence, is unknown. So far, only one type of microchromosomes and at only one location (in the tributaries of the Rio Purification, Mexico) has been recognised (Lamatsch, pers. comm.). Triploids are rare in the *P. formosa* / *P. latipinna* complex compared to the sister-system in the drainages of Soto La

Marina, Mexico with *P. mexicana* as sexual host species, where triploids comprised 5-16% of Amazons (Schartl & Lamatsch, pers. comm.). Out of 5000 mollies, less than 0.1% were triploid (Rasch & Balsano 1989). Additionally, there is evidence that triploids are genetically even less variable than diploids and therefore unlikely to be *P. formosa*'s main strategy against Muller's ratchet (pers. comm. Lampert & Lamatsch).

OTHER MODELS ON ADVANTAGES OF SEX: TANGLED BANK HYPOTHESIS

Bell (1982) proposed the tangled bank hypothesis. He argued that sexual reproduction is beneficial because it allows adaptations to a fast changing environment. Asexually reproducing organisms would be more likely to go extinct in a changing habitat. However, there are only very few cases that support the tangled bank hypothesis (Hestmark 1992; Dybdahl & Lively 1995). The strongest argument against tangled bank is that also stable, more predictable habitats (e.g. caves, deep sea, arctic) do not harbour more asexually reproducing organisms than elsewhere. The long-term success of *P. formosa* (Schartl et al. 1995; Möller 2001) also contradicts the tangled bank hypothesis.

RED QUEEN

The Red Queen hypothesis (van Valen 1973; Ridley 1994), as an arms race between hosts and their parasites (Dawkins & Krebs 1979), is one of the recently best studied hypotheses on the maintenance of sex (e.g. Lively 1990; Ladle et al. 1993; Leberg & Vrijenhoek 1994; Dybdahl & Lively 1998; Hakoyama et al. 2001; Dries 2003). Sexuality provides more genetic variation and thus sexually reproducing organisms evolve faster than clonal organisms. Sexually reproducing organisms therefore have a headstart in escaping from coevolving parasites in comparison with asexual organisms that are expected to be genetically less diverse and evolve more slowly (reviewed in Hamilton et al. 1990).

But this has to be studied carefully since the basic assumption of poor genetic diversity is not always true: unisexual organisms possess some of the highest levels of heterozygosity known among vertebrates (Moore 1976) resulting in spontaneous fitness advantages to unisexuals (Schultz 1971; Schultz 1989).

Niche partitioning and character displacement

One hypothesis explaining presence of two competing species in syntopy is niche partitioning (Roughgarden 1972; Tokeshi 1999). In bisexual – unisexual mating complexes of vertebrates, this mechanism becomes important because the sperm-dependency of asexuals requires coexistence of the two closely related species. In livebearing fish, sexual males and asexual females have to meet and copulate since eggs are internally (pseudo-) fertilised.

Ecological specialisation on limited spatial and trophic resources and subtle microhabitat partitioning could allow unisexual / bisexual coexistence (Vrijenhoek 1978; Vrijenhoek 1984; Schenck & Vrijenhoek 1986; Wetherington et al. 1989). Balsano et al. (1981) studied the asexual-sexual mating complex of *P. formosa* with *P. mexicana* as sexual host species in the Soto La Marina drainage, Mexico. They found that bisexual organisms were more frequent in headwaters and unisexual numbers increased in downstream habitats.

Wright & Lowe (1968) adopted the botanical term “weed habitat” for those habitats (marginal, ecotone, extreme, perpetually disturbed) to which the unisexual species are restricted. They conclude that phenotypic plasticity of unisexual organisms allows comparison with such plants inhabiting “weed habitats”.

However, there is only little evidence for niche segregation in coexisting asexually and sexually reproducing vertebrates (Moore et al. 1970; Schultz 1971; Balsano et al. 1981; Schenck & Vrijenhoek 1986). There seems to be a tendency that asexuals are specially adapted to more extreme environmental conditions.

Therefore, to find an explanation for coexistence in mixed sexual-asexual populations, it seemed interesting to study – possibly fine-scaled – niche partitioning or niche segregation *via* the use of different microhabitats or temporal segregation.

Competition for shared resources leads to diversification and niche segregation, which results in character displacement in closely related coexisting and competing species (Brown & Wilson 1956; Fenchel 1975; Fenchel & Kofoed 1976; Connell 1980; Arthur 1982) (but see Cherill 1988). Ecological character displacement is difficult to show, and criteria upon which evidence is evaluated become increasingly stringent (Grant 1994; Robinson & Wilson 1994; Schluter 1994).

The aim of studying *P. formosa* complexes in the field (chapter 2) was to detect any parameter that might explain frequency of Amazons in mixed populations with *P. latipinna* in South and Central Texas, USA. Regional or temporal patterns of population ecology should be studied with focus on solving the paradox of sexually and asexually reproducing coexisting individuals in syntopy.

Frozen niche variation model

Individual clones tend to express less morphological variation and have more specialised niches than coexisting sexual relatives. This has been called the frozen phenotypic variation model (Jokela et al. 1997b) and is usually applied to multiclonal organisms. This model has been derived from the „frozen niche variation“ (FNV) model (Vrijenhoek 1979; Vrijenhoek 1984; Vrijenhoek 1989; Wetherington et al. 1989). The model was developed to account for coexistence of genetically related clones with one another and with sexual relatives (Vrijenhoek 1979; Vrijenhoek 1984). Accordingly, multiple origins of clones from genetically variable sexual ancestors produce a broad array of phenotypically diversified unisexual genotypes. Interclonal selection eliminates clones with substantial niche overlap. The result is a structured assemblage of clonal genotypes that exploit the breadth of available resources in heterogeneous environments. Thus, the success of natural unisexuals results from selection of clones from a broad spectrum of genotypes that arose via multiple clonal origins (Wetherington et al. 1989). Similar models based on interclonal resource partitioning have been explored by Bell (1982) and by Case & Taper (1986).

The frozen niche variation model considers both genetic and ecological characteristics of sexual species and asexual clones, and thus provides a tenable explanation for the persistence of mixed reproductive assemblages. The model assumes that distinct clones have independent origins from sexual ancestors. Cloning effectively “freezes” and faithfully replicates multilocus genotypes which may encode ecologically relevant differences already existing in the gene pool of the sexual progenitors (Schenck & Vrijenhoek 1986). Sexual ancestors must possess enough genetic variability for phenotypic characters that affect niche breadth (Roughgarden 1972).

Ecological differences among coexisting clones and their ancestors reduce competition and thereby facilitate coexistence. In an ecological context, unisexual Poeciliids are remarkably successful. They often coexist with, and in many localities outnumber the sexual lineages from which they arose (Vrijenhoek 1979; Vrijenhoek 1984; Schultz 1989).

Many studies have been carried out on the ecology of sexual-aseexual fish complexes with hybridogenesis as asexual reproductive mode testing the frozen niche variation hypothesis (Wetherington et al. 1989; Echelle & Echelle 1997; Vrijenhoek & Pfeiler 1997; Schlosser et al. 1998). In systems like *Poeciliopsis monacha lucida* (Vrijenhoek 1994) where asexuals (hemiclinal organisms) develop via hybridogenesis and asexuals evolved several times independently, frozen niche variation (Vrijenhoek 1979; Vrijenhoek 1984) is expected. Ecological studies on multiclonal unisexual taxa generally support FNV-model (Harshman & Futuyma 1985; Case & Taper 1986; Case et al. 1994; Dybdahl & Lively 1995; Echelle & Echelle 1997; Jokela et al. 1997b; Semlitsch et al. 1997; Vrijenhoek & Pfeiler 1997; Gray & Weeks 2001).

Alternatives to frozen niche

Without opportunity for independent origin of new clones, unisexual populations have only mutation and migration as sources of variation. These processes cannot generate sufficient phenotypic variation for ecological differentiation, and thus hamper the opportunity for the unisexual population to usurp a major proportion of the niche of the sexual ancestor (Vrijenhoek 1979; Vrijenhoek 1984).

GENERAL-PURPOSE GENOTYPE

While the frozen phenotypic variation model usually applies to multiclonal organisms, another model, that of a general-purpose genotype (Parker et al. 1977), is expected to be suited to monoclonal organisms (Lynch 1984), but those models are not mutually exclusive hypotheses.

The factors determining whether selection favours a clonal lineage with a specialised adaptation or ecological generalism appear to be a function of the long-term stability of environmental conditions (Schlosser et al. 1998). Lynch (1994) provided a plausible explanation of this relationship: Each surviving clone must have had a tolerance (positive fitness) to the full range of environmental conditions to which it has been exposed since its incipience. Relatively specialised clones will surely arise (perhaps frequently), but they will only survive as long as the narrow niche to which they are adapted remains available. Therefore, in the long term, clonal selection will promote the evolution of highly generalised (or general-purpose) genotypes, which are characterised by both broad tolerance ranges and low fitness variance for robust physical, chemical, and biotic gradients.

The geographic distribution pattern of different haplotypes of *P. formosa* reveals low (mitochondrial) genetic diversity in populations in Texas and Mexico. The ancestral haplotype of *P. formosa*, which is identical to that of its maternal ancestor, was present in all populations studied (Möller 2001). This is in agreement with the all-purpose genotype hypothesis.

Like other asexual fishes, the Amazon molly *P. formosa* is a sperm dependent hybrid species originating from sexual ancestors. The Amazon molly most likely originated from a single or very few hybridisation events (Möller 2001). Therefore, frozen niche variation might not be an explanation for coexistence in this system. That is why the mating complex of *P. formosa* is an ideal system to study ecological coexistence in a bisexual – sexual system of single origin.

Chapter 2: Population ecology in the mating complex of the unisexual Amazon molly *Poecilia formosa*.

Temporal and spatial patterns of coexistence of the *P. formosa* and its sexual host species *P. latipinna*

Introduction

Visiting natural habitats of the all-female Amazon molly *Poecilia formosa* and its associated bisexual host species, is an outstanding experience. It is especially puzzling how variable habitats are and how successful mollies are in populating even small and temporary water bodies in high densities and under – for vertebrates – harsh and fast changing environmental conditions. The huge difference between conditions mollies have to cope with in their natural environment, which are fundamentally different from conditions under which Poeciliids are kept in the laboratory, become immediately obvious.

Gaps in our knowledge

Snelson & Meffe (1989) consider basic natural history and community ecology the „gaps in our knowledge“ on ecology and evolution of livebearing fishes (Poeciliidae) since there is not much known besides the „tank ecology“ of guppies (*Poecilia reticulata*) and Mosquitofish (*Gambusia*). Only few authors have studied the situation in the field extensively (Meffe & Snelson 1989). They point out that while genetics of Poeciliids is generally well understood, basic aspects of ecology and natural history are often undocumented. This is even more true for bisexual-unisexual species complexes of Poeciliid fishes.

To my knowledge, this is the first ecological field study on an asexual vertebrate and its co-occurring sexually reproducing relatives that integrates seasonal and spatial variation in several populations and measures such a variety of parameters.

What explains the success of Amazons?

This study focuses on exploring factors that might explain frequency of the Amazons and the ecological coexistence of sexual females and their sperm dependent unisexual associates. Especially interesting seemed those biotic and abiotic parameters that might predict high or low frequency of Amazons and stability or instability in maintaining coexistence.

The two-fold advantage of asexual reproduction (Williams 1975; Maynard Smith 1978) due to avoiding cost of males (Maynard Smith 1978) and cost of meiosis (Williams 1975) derives from the fact that offspring from sexual females multiplies at twice the rate as the progeny descending from a sexual female, assuming all else being equal. This advantage of asexual reproduction predicts extremely high success and high densities of Amazon mollies in comparison to bisexual relatives. But since Amazons are gynogenetic and thus depend on sperm provided by its sexual host male to trigger embryogenesis, stable coexistence is a prerequisite for the persistence of *P. formosa*. If asexual *P. formosa* outcompeted the sperm donating species this would immediately lead to the extinction of *P. formosa* as well.

Besides the two-fold advantage of asexuality also a cost of reproduction would favour the asexual Amazon molly. Jokela et al. (1997) found evidence for this in the sexual / parthenogenetic syntopically coexisting freshwater snail *Potamopyrgus antipodarum*. In the laboratory, they found that population growth rate was different and thus cost of males was present. They also measured variation in life history traits among habitats and sampling localities and analysed life history traits of sexual *versus* asexual females suggesting that female size at maturity was affected by the female's reproductive mode and habitat. They conclude, there must be a genetic or ecological cost of sexual reproduction.

Heterogeneity and variation of habitat and fish community

To understand how stability and coexistence in this mating complex can be maintained, it is important to obtain some knowledge of the position of the Amazons in their community. Properties of the habitat, as stability and structure, species diversity, relative densities, predation risk, and physicochemical parameters might be important factors influencing occurrence and success of Amazons. How diverse or homogeneous are habitats in space and time and how high is within - habitat variation compared to between-habitat variation? This may be of importance to the coexistence of the two species. MacArthur (1965) studied general patterns of within - habitat diversity versus between - habitat diversity and found that population density was low due to disturbances that allow resources to remain unlimited. This would release competition among coexisting species.

The plankton paradoxon (Hutchinson 1961) deals with occurring coexistence when niche partitioning does not occur. Under these circumstances, that may apply to the mating complex of *P. formosa*, short lived, ephemeral microhabitats of unpredictably variable duration might account for coexistence. The stabilising effect of habitat heterogeneity could allow coexistence without niche partitioning. This heterogeneity can be spatial or temporal.

Temporal or spatial population patterns within the asexual / sexual mating complex

The study of variation and patterns within the bisexual – unisexual species complex definitely deserves a closer look. Do Amazons dominate mixed populations as expected by the two-fold cost of sexual reproduction? Is there any evidence for an advantage of asexuals in their natural context? Are there temporal or spatial patterns or cycles?

Coexistence of closely related competing species such as the sexual-parasite *P. formosa* and its sexual host species *P. latipinna* could be explained by niche partitioning (Roughgarden 1972; Tokeshi 1999). Ecological specialisation on limited spatial and trophic resources and subtle microhabitat partitioning allow unisexual - bisexual species assemblages of *Poeciliopsis* to coexist (Vrijenhoek 1978; Vrijenhoek 1984b; Schenck & Vrijenhoek 1986; Wetherington et al. 1989b) with unisexual species being adapted to more extreme environmental conditions.

Studying spatial and temporal patterns is important to detect any evidence for niche segregation. According to niche segregation - theories and findings of Balsano et al. (1981), Amazons should be more frequent in more disturbed, extreme, or downstream habitats.

Seasonal variation in frequencies might indicate presence of externally driven population cycles, which also contributes to coexistence in this mating complex.

Fluctuations or seasonal changes in frequency of Amazons need to be studied in the ecological context in which they occur. Therefore changes in proportion of juveniles, sex ratio, male mate choice behaviour, body sizes, species diversity, predation risk and abiotic parameters are important to relate with abundance of Amazons. This procedure may reveal any underlying frequency or density dependent relationships that might regulate abundance and coexistence or provide temporal or spatial niches in which Amazons persist (or succeed).

Frozen Niche Variation

For hybridogenetic or gynogenetic unisexual vertebrates with multiple origin as in the *Poeciliopsis* complex (Vrijenhoek 1994) the frozen niche variation model (FNV) (Vrijenhoek 1979; 1984a; 1989; Wetherington et al. 1989b) has been renowned to account for coexistence of genetically related clones with their sexual relatives (see chapter 1: general introduction).

If I assume frozen niche variation to apply, variation between populations must be extremely high since in every population Amazons are expected to be highly locally adapted opposed to the sexual host species. Like other asexual fishes, *P. formosa* is a sperm dependent hybrid species originating from sexual ancestors. Hubbs (1964) studied population ecology in allopatric and sympatric populations of *P. latipinna* and its gynogenetic associate *P. formosa*. In systems like *Poeciliopsis monacha lucida* (Vrijenhoek 1994) where asexuals (hemiclinal organisms) develop via hybridogenesis and asexuals evolved several times independently, frozen niche variation (Vrijenhoek 1979; Vrijenhoek 1984a) is expected. The Amazon molly most likely originated from a single or very few hybridisation events (Möller 2001) and therefore frozen niche variation is not necessarily expected to occur.

The stability may also be maintained by other causes and thus, coexistence between *P. formosa* and its sexual host species is an interesting model system to study.

The role of males

In this system, males provide sperm to both conspecific and asexual females. Their role in mixed populations is important. Besides behavioural aspects that are the main issues in the following chapters (chapter 3, 4, 5, 6), the role of males in natural populations needs special attention. *P. latipinna* males are more conspicuous than females due to coloration and courtship behaviour. This may cause them being more susceptible as targets of predators.

Fisher (1930) emphasised the importance of natural selection on sex ratios. Since then, several studies have been carried out on differential mortality (e.g. Krumholz 1963; Trexler et al. 1992; Reznick et al. 1996; Godin & McDonough 2003). It is well known that differential male mortality leads to female-skewed sex-ratios in Poeciliids (Snelson & Wetherington 1980; Wetherington et al. 1989a).

To study whether there is evidence for the behavioural regulation hypothesis, it is essential to integrate newly gained data on frequency of Amazons and its spatial and seasonal patterns into male mate choice experiments. Chapter 3 focuses on this aspect.

Long-term success of Amazons: disadvantages of asexual reproduction

The long-term success and thus persistence of Amazons is still under debate. Sexually reproducing *P. latipinna* and gynogenetic *P. formosa* have been coexisting in South Texas for more than 100.000 generations (Schartl et al. 1995; Möller 2001). According to Muller's ratchet (Muller 1964) sexually reproducing species should outcompete co-occurring closely related clonal organisms due to accumulation of deleterious mutations in the latter group (Crow & Kimura 1965). Asexual lineages should go extinct after approximately 10.000 – 100.000 generations (Lynch & Gabriel 1990). This seems not to be the case. Why are Amazons successful in maintaining a stable coexistence for such a long time?

Genetic models of asexual disadvantage (Muller 1964; Kondrashov 1988; Lynch & Gabriel 1990), namely Muller's ratchet (Muller 1964), describe stepwise accumulation of deleterious mutations in a population that cannot be reversed. This is because there is no genetic recombination (Muller 1964) and lower probability for beneficial mutations to become fixed in asexual populations (Crow & Kimura 1965; Maynard Smith 1978).

Ecological models on asexual disadvantages are based on the fact that rates of evolution are slower in unisexual organisms (Crow & Kimura 1965; Williams 1975; Maynard Smith 1978). Hence, in fast changing environments asexuals are expected to adapt not as quick and efficient as sexual species.

Presence of long-term disadvantages of *P. formosa* could be demonstrated by deviating fitness in comparison to sexual females. Whether or not reproducing, number of juveniles, and body condition or body size can be used as appropriate indicators of female fitness. It is known that larger females are more attractive to males and thus have higher mating success and carry more offspring (Reznick & Miles 1989b; Schlupp & Ryan 1997; Trexler 1997; Trexler et al. 1997).

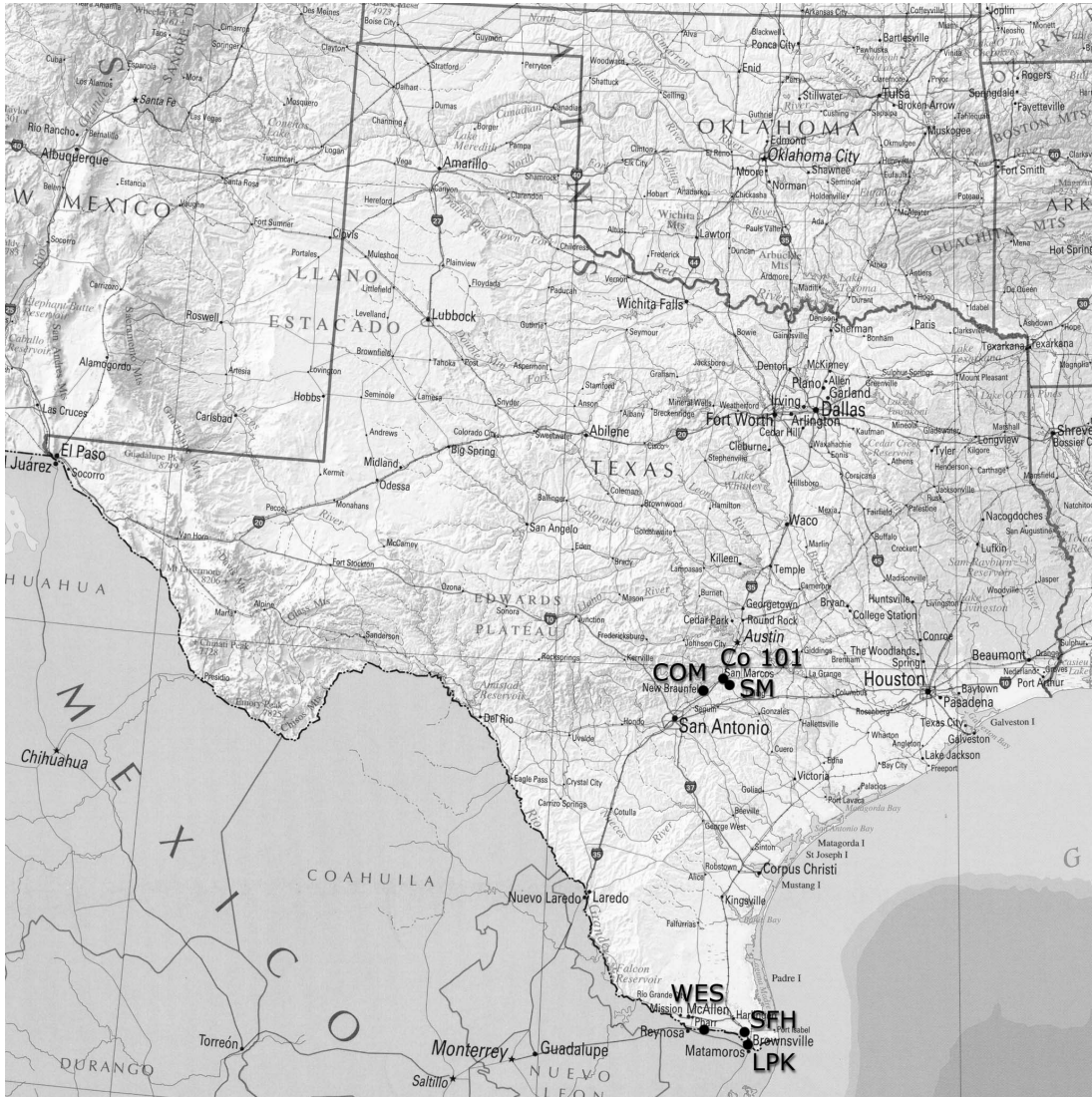
Abiotic parameters: a key to Amazons?

Among a variety of abiotic parameters, those seemed to be of interest, that are known to account for plasticity in Poeciliid life-history traits (reviewed in Trexler 1989a). For *P. latipinna*, temperature is known to affect male colouration (Angus 1983), interbrood interval (Snelson 1986), and age at maturity (Trexler 1989b). Temperature and pH are known to have an effect on sex determination in Poeciliids and thus sex ratios (Snelson 1989). Chlorophyll a concentration as a measure of phytoplankton biomass relates to primary production and thus reflects the trophic status of the habitat. It might be a parameter that influences communities.

Endler (1980; 1987; 1991) and Endler & Houde (1995) conducted a variety of excellent studies on Trinidad guppies highlighting the importance of the visual environment. Light conditions in natural habitats affect courtship behaviour, predation risk management, and visual communication. The same might apply to turbidity (Heubel & Schlupp submitted, chapter 3). Intuitively, turbidity affects ability to communicate visually with the opposite sex, competitors, members of the same sex or even other members of the community, such as predators (see chapter 3 and references therein).

Study area

The sexual-asexual mating complex of the Sailfin molly *Poecilia latipinna* and its gynogenetic associate, the Amazon molly *Poecilia formosa* occurs in the coastal plains of the Gulf of Mexico (Map 2.1). I studied the population biology in mixed *P. formosa* / *latipinna* populations in Central and South Texas (Tab. 2.1).



Map 2.1: Map of field sites in Central and South Texas (Source: National Atlas of the United States of America, General Reference MaP. U.S. Geological Survey, 2001 (University of Texas Online Map Collection).

Tab. 2.1: Field sites in Central and South Texas studied between February and September 2001.

site name	water body	river basin	code	latitude	longitude	altitude
Comal Landa Park New Braunfels	Springhead Comal River, spring lake	Guadalupe River	COM	29°42.758'	98°08.156'	187 m
San Marcos Co 101	San Marcos River	Guadalupe River	Co 101	29°51.433'	97°53.801'	162 m
San Marcos Martindale	San Marcos River creek, pond	Guadalupe River	SM	29°51.482'	97°51.846'	158 m
Weslaco Floodway Progreso	North Floodway Llano Grande, ditch	Nueces - Rio Grande	WES	26°07.201'	97°57.674'	21 m
Lincoln Park Brownsville	Oxbow lake (resaca)	Nueces - Rio Grande	LPK	25°53.978'	97°28.769'	6 m
State Fish Hatchery Olmito	Resaca del Rancho Viejo, ditch	Nueces - Rio Grande	SFH	25°59.192'	97°31.878'	11 m

INTRODUCED MOLLY POPULATIONS

Populations of *Poecilia* in Central Texas lie outside of the natural range of distribution of mollies. Sailfin mollies *P. latipinna* have been introduced into the San Marcos river drainage in 1938 from a population originating from Louisiana (Brown 1953). About three decades later, *P. formosa* has been introduced in 1958 (Drewry et al. 1958) originating from South Texas (State Fish hatchery at Olmito) (W.H. Brown pers. comm. cited in Hubbs (1964).

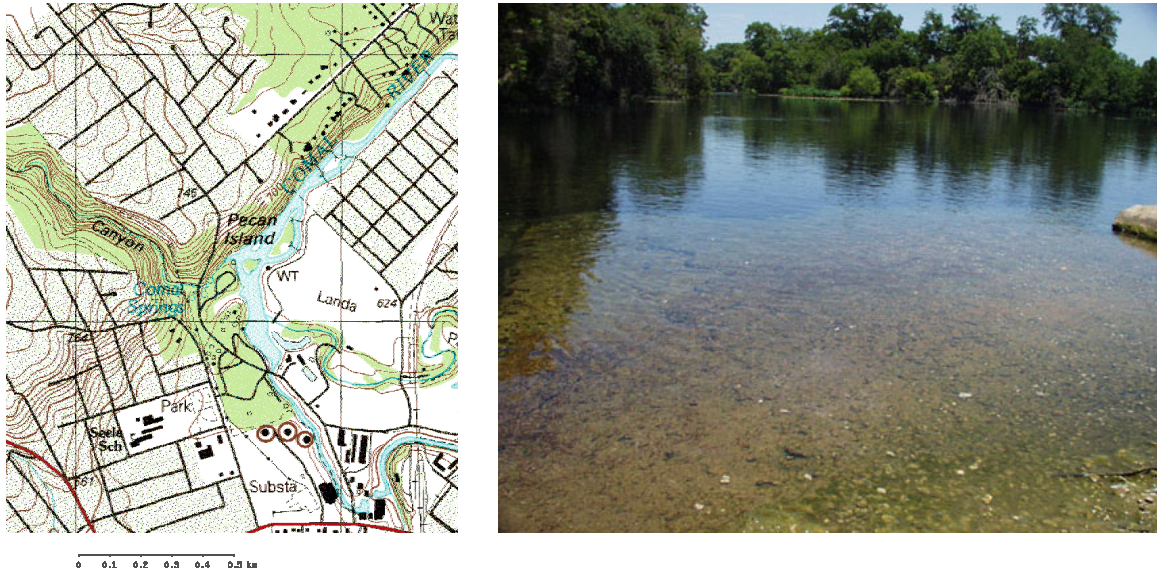
Central Texas:

Molly habitats in Central Texas are characterised by their geologic background. The interior coastal plains have an elevation of 100-250 m. Their topography consist of parallel ridges (questas) and valleys or low rolling terrain in the Backland Prairies. The geologic structure consists of beds tilted towards the Gulf with consolidated sands and muds as bedrock types (Wermund 1999a; Wermund 1999b; Spearing 1991). Land resources are expansive clay and mud, locally silty or calcareous in a flat to low hilly prairie. The land is commonly tilled. Geologically it belongs to the upper cretaceous Navarro and Taylor groups (Spearing 1991). In this region, precipitation typically reaches 750 – 1000 mm per year (Spearing 1991).

I studied three populations in Central Texas. All were situated in the Guadalupe River basin and belonged to the subcrop in the confined zone of the limestone Edwards aquifer. Therefore, less variation among habitats within the group of Central Texas' populations was expected as compared to variation between habitats from South Texas and Central Texas. In Tab. 2.2 presents water quality data from several years of monthly sampling at two stations in Central Texas and one station in South Texas. These data were collected by several monitoring projects on water quality in Texas (TWC 1990; Webster et al. 1998).

COMAL SPRINGS (COM)

This site is situated a few metres downstream of the springhead in the headwater section of the Comal River. It is located at recreational Landa Park, City of New Braunfels, Comal County, Texas, USA (Tab. 2.1). Comal Springs has as its source in the Edwards Aquifer.



Map 2.2: Topographical map of Comal Spring field site. Altitudes are in feet. Source: TopoZone.com © 1999-2003.

Fig.: 2.1: Photo field site Comal Spring, Gazebo Landa Park, New Braunfels.

All collections were made and all measurements were taken at the gazebo around a flat concrete ramp that provided a shallow section. Here, the channelled spring flows into the spring lake (Fig. 2.1, Map 2.2). A ramp and wall at this field site provide a low structured habitat with mixed substrate. This area served as a field site in several other studies on *Poecilia* (Witte & Ryan 1998; Gabor & Ryan 2001; Schlupp et al. 2002; Witte & Ryan 2002; Schlupp et al. submitted). It is also close to the EARDC Trinity aquifer research station at Comal Springs and the USGS / NAWQA station # 08169 Comal River (Bush et al. 2000) where data presented in Tab. 2.2 originated from (refer to appendix for abbreviations). In previous studies, this site has been considered as an allopatric population of Sailfin mollies (Gabor & Ryan 2001; Witte & Ryan 2002).

SAN MARCOS RIVER AT Co 101 (Co 101)

This site is a section of the San Marcos River a few kilometres downstream from the springhead Aquarena Springs at San Marcos. It is located in a rural area with farmland adjacent to the river at (Tab. 2.1) at the county line of Hays and Caldwell County, Texas, USA. A bridge crosses the 20 m wide river at this site. Water current is comparably strong for molly habitats. The habitat is highly structured. Water level is not managed. Occasional disturbances occur due to human recreational activities at the river (Map 2.3, Fig. 2.2).

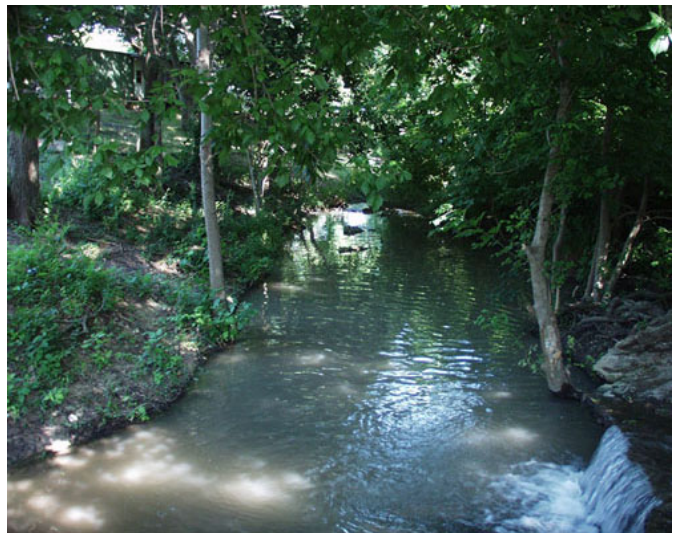
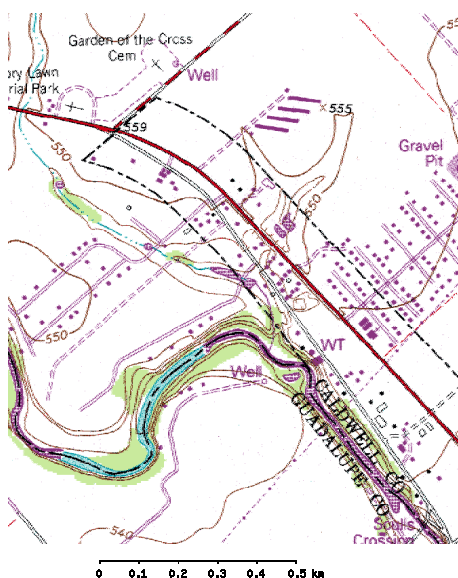


Map 2.3: Topographical map of San Marcos River, Co 101. Altitudes are in feet. Source: TopoZone.com © 1999-2003.

Fig.: 2.2: Photo field site of San Marcos River, Co 101. View from bridge.

SAN MARCOS RIVER AT MARTINDALE (SM)

This field site lies in a residential area of Martindale, Caldwell County, Texas, USA and is located just a few kilometres downstream from Co 101 (Tab. 2.1). This field site consists of a little pond dammed by a street. The pond drains across the street into a creek and later into a calm eddy of the San Marcos River (Tab. 2.2) with residential greens adjacent to the field site. Trees along the creek supply shade all day in the creek section. The upper pond section and the lower San Marcos River are exposed to sunlight most time of the day. This habitat has a high level of structuration and a highly diverse substrate (Map 2.4, Fig. 2.3).



Map 2.4: Topographical map of field site Martindale at San Marcos River, SM. Altitudes are in feet. Source: TopoZone.com © 1999-2003.

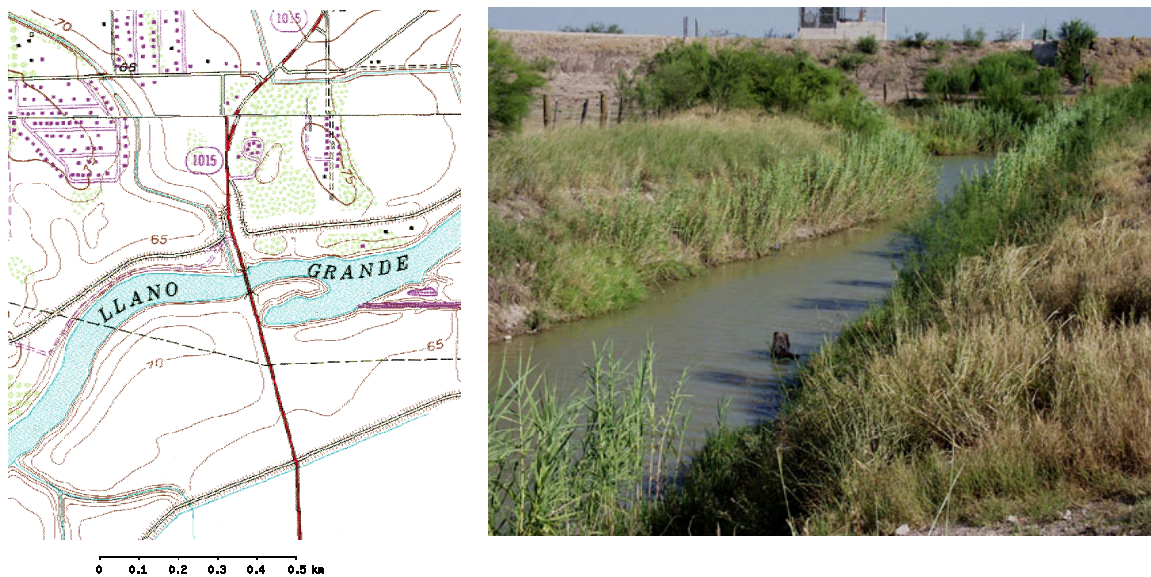
Fig.: 2.3: Photo Martindale creek (SM). View from street. The water flows from the upper pond into the creek.

South Texas

The three field sites in South Texas belong to the Nueces - Rio Grande River basin. This area is within the natural range of *P. latipinna* and *P. formosa* (Darnell & Abramoff 1968). All southern habitats lie in the coastal prairies with an elevation between 0-100 m. Its topography is characterised by a nearly flat prairie with deltaic sands and muds as bedrock type. Those young deltaic sands, silts, and clays eroded to nearly flat ranch- and farmland. Geologically, the area belongs to the quaternary Beaumont Formation. Typically, rainfall is between 500 – 750 mm per year (Spearing 1991). Due to irrigation of agricultural farmland, water level at southern field sites is regulated (Garza 1999; Garza & Long 1999). All studied habitats in South Texas form a natural group due to their common physical properties. Therefore, it is obvious that habitats from South Texas must generally differ from habitats in Central Texas due to differences in topography, geology, pedology, and climate.

WESLACO NORTH FLOODWAY (WES)

Located in the Progreso-area of Hidalgo County, Texas, USA (Tab. 2.1), this field site belongs to the “Llano Grande lake Arroyo Colorado”-watershed. It is part of the irrigation system and consists of the North floodway and a ditch. The field site is about 6 km north of the Rio Grande in an agricultural belt where numerous crops are grown year-round and where heavy pesticide applications are frequent (White et al. 1983; Webster et al. 1998; TNRCC 2001). Adjacent to the field is irrigated cropland. The habitat is structured with rocks, banks, bays, plants and irregular debris. The substrate is predominantly soft.



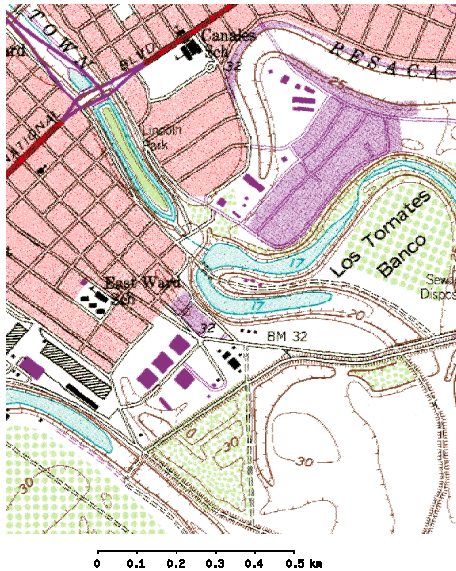
Map 2.5: Topographical map of field site Floodway Llano Grande near Weslaco (WES). Altitudes are in feet. Source: TopoZone.com © 1999-2003.

Fig.: 2.4: Photo Weslaco ditch.

For this field site, consumption advisories (in 1993) and consumption ban (in 1994) were issued (TNRCC 2001) suggesting, “not consuming any species of fish due to elevated levels of Chlordane, DDE, Toxophene in fish tissue” (TDH 1997; TNRCC 2001). Therefore, water quality has been intensively studied in this segment #2202 “Arroyo Colorado above tidal” (Arroyo Colorado upstream of the port of Harlingen including Llano Grande Lake and the main floodway by several agencies (TNRCC 2001) (Webster et al. 1998). (Tab. 2.2).

LINCOLN PARK BROWNSVILLE (LPK)

This field site is located in the city of Brownsville, Cameron County, Texas, USA, approximately 2 km north of the Rio Grande (Tab. 2.1). The water body is a “resaca” (oxbow lake), a part of the oxbow lake system of the Rio Grande. It is located directly underneath a newly constructed Express-Highway overpass close to a local sewage disposal. The area is heavily disturbed by construction work and irregular garbage disposal. Beside these structures the habitat is poorly structured with a soft substrate (Map 2.6, Fig. 2.5).



Map 2.6: Topographical map of field site Lincoln Park, Brownsville. Altitudes are in feet. The newly constructed highway is not shown. Source: TopoZone.com © 1999-2003.

Fig.: 2.5: Photo Lincoln Park, Brownsville at HWY 77.

STATE FISH HATCHERY AT OLMITO (SFH)

Map 2.7: Topographical map of field site State Fish Hatchery Olmito, Brownsville. Altitudes are in feet. Source: TopoZone.com © 1999-2003.

Fig.: 2.6: Photo ditch at State Fish Hatchery Olmito.

This site contains two ditches at the State Fish hatchery at Olmito, Cameron County, Texas, USA (Tab. 2.1) and is located approximately 8 km north of the Rio Grande. It belongs to the oxbow lake system “Resaca del Rancho Viejo”. This area is identical to “station 1” (“Lula B. Sams State Fish Hatchery at Olmito”) Hubbs (1964) studied in the 1960ies. The ditch bottom is a soft muddy substrate. At high water level, plants along the ditch provide cover and a medium level of habitat structuration (Map 2.7, Fig. 2.6). Mainly one ditch (Fig. 2.6) was sampled. When water level was too low or no mollies were present, a second ditch was sampled additionally (data marked with ‘II’ in appendix).

Tab. 2.2: Water quality (monthly sampling) at USGS and NAWQA stations in the Guadalupe River system and Nueces-Rio Grande River system. Data provided by Texas Water Commission and NAWQA.

Station name	#08169 Comal River, New Braunfels Central Texas		#081705 San Marcos River, San Marcos Central Texas		Arroyo Colorado Llano Grande South Texas	
in proximity to	COM		SM, Co 101		WES	
latitude, longitude	N29°42'21" E98°07'20"		N29°53'20" E97°56'02"		N26°10'24" E97°42'01"	
altitude	178 m		98 m		0 m	
physical data range	18/04/96-09/08/01		3/11/99 – 10/09/01		20/11/1986-18/9/2002	
chemical data range	96-98 (<i>n</i> = 25)		1996 (<i>n</i> = 4)		1986 - 2002 (<i>n</i> = 112)	
Parameter	Mean	SD	Mean	SD	Mean	SD
Temperature [°C]	23.0	2.23	21.9	1.01	24.9	3.9
Air pressure [hPa]	993	2.9	1012	10.2	1019	8.3
Discharge [m ³ /s]	7.0	1.7	4.9	1.5	6.9	2.6
Turbidity [NTU]					106	32
Spec. cond. [µS/cm]	538	10	586	17	4056	505
Diss. oxygen [mg/l]	8.2	0.4	7.8	1.0	7.9	1.1
pH	7.6	0.2	7.8	0.2	7.9	0.2
Ammonium [mg/l]	0.026	0.013			0.07	0.05
Nitrite + Nitrate [mg/l]	1.68	0.06			3.5	0.7
Calcium [mg/l]	76.9	1.9	85.8	1.9	201.3	26.5
Magnesium [mg/l]	16.0	0.2	16.3	0.4	80.5	11.5
Sodium [mg/l]	10.0	0.3	12.8	2.1	576.0	79.4
Potassium [mg/l]	1.4	0.1	1.5	0.2	10.7	1.4
Chloride [mg/l]	16.7	0.5	21.0	2.5	809.6	115.8
Sulphate [mg/l]	23.3	0.7	25.0	1.0	740.9	97.0

SD = standard deviation of mean

Materials and Methods

I studied six mixed populations of Amazon mollies *P. formosa* and Sailfin mollies *P. latipinna* in the Gulf Coastal Plains of Texas, USA. Three field sites were located in South-Central Texas, three in South Texas. Sampling of all six populations was scheduled approximately every 25 days. Order of sampling at those 6 populations was alternated within and between South and Central localities. During the period of February and September 2001, each site was visited nine times.

The on-site protocol consisted of a habitat assessment, measuring of physical and chemical parameters, sampling and assessment of fish community, estimation of relative densities and diversity of the fish community, processing of mollies, and release of fish back into the wild. Fish processing in the field included sampling, identifying, and enumeration of *Poecilia* species, measuring of standard length, and digital photographing of life individuals.

Habitat assessment integrated description of habitat, its surroundings, type of water body, development, disturbance and management.

At every field site, I noted date, time, geographical latitude and longitude, Temperature (air) [°C], and actual weather condition. I also noted the habitat properties like width [m], water colour, current, contact vegetation, cover, water level, management, disturbances, substrate, surrounding area, water course, structures, microhabitats, non-fish predatory animals (e.g. predatory birds, snakes, turtles), and other observations on site.

Fish sampling

Seining is a common technique used by fish ecologists (Bagenal 1978; Nielsen & Johnson 1983). It is a highly effective method for sampling small sized individuals (<10 cm total length (TL)) (Bayley & Herenden 2000).

The fish sampling protocol I developed for this study purpose, is adapted from similar protocols that describe methods for collecting a representative sample of the fish community for the selected sites (Meador et al. 1993; Walsh & Meador 1998; Moulton et al. 2002).

I standardised data by mean volume of water body sampled and / or mean area water surface sampled for every site. This correction factor describes the accessibility of the specific site.

I used a 6.4 mm standard mesh size 7.6 x 1.2 m standard minnow seine. To keep sampling effort comparable across sites and sampling sessions, seining was standardised. Depending on field conditions at least 6 hauls were taken, or until a minimum of $n = 100$ mollies caught, or up to 40 minutes -whichever came first. Every haul was classified and rated separately. The approximate area [m²] sampled was estimated per haul as well as minimum, maximum, and mean water depth in the seining area.

For all hauls combined, I separated juveniles and mature females, males and asexuals, and counted *Poecilia formosa*, *P. latipinna*, and unspecified *Poecilia*.

When field site conditions were inappropriate for seining (woody snags, irregular debris), I sampled mollies using minnow traps, a cast net, or a dip net. I standardised sampling conditions by keeping track on number of traps, throws, dips, proportion of successful catches, and time as catch per unit effort (CPUE) sampling rule.

COMMUNITY SAMPLING

After every haul, all individuals present in the net were identified and enumerated or rated. All aquatic vertebrates were classified to the most accurate taxa level possible with field methods. Fish abundance was rated in classes (Tab. 2.3). Presence of aquatic invertebrates and predatory birds and reptiles (snakes, turtles) was also noted. Apart from mollies and individuals donated to Texas Natural History Collection (TNHC), all individuals were released into the water immediately after identification.

Tab. 2.3: Abundance classes fish community

Abundance class	Proportion in community	code
absent	0%	-
one	1 individual	A1
rare	2-5 individuals; < 5%	A2
occasional	< 5%	A3
frequent	5-15%	B
common	15-25%	C
abundant	25-50%	D
super abundant	50-75%	E
extremely abundant	75-100%	F

Processing of *Poecilia*: length measurements, photographs, fin clips, preserved specimens

SORTING

Combining mollies caught in subsequent hauls, all *Poecilia* individuals were sorted for species, sex, and maturity. Males and females were recognised by field examination of anal fin morphology. I defined adult females as females with a standard length ≥ 30 mm, adult males as individuals with an intromittent organ, a gonopodium. Subadult males were defined as individuals with an already prolonged anal fin clearly in the process of developing a gonopodium within short time.

MEASURING

I measured standard length of 40 randomly selected adult *P. latipinna* males, females, and *P. formosa*. If fewer than 40 individuals were caught, I measured all available adult mollies. Standard length was measured of 40 adult *P. latipinna*. Standard length is defined as body length from the tip of the closed mouth to the posterior end of the fleshy caudal peduncle.

PHOTOGRAPHING

Digital photographs of both sides were taken from 20 living adult *Poecilia* of each sex (or as many as available). Pictures were made on site or immediately after returning to the laboratory on a laminated engineering sheet using an Olympus Camedia 2500L digital camera.

For each site and visit, a few fin clips were taken from *P. formosa* individuals as tissue samples for future research on genetic diversity and presence of triploid Amazons in this sexual-asexual mating complex.

OTHER FIELD AND POST-FIELD ACTIVITIES

For reference and future studies on parasite load, gonadosomal index, and genetic diversity, ten individuals of mature adult bisexual and unisexual mollies were preserved in 70% ethanol. Those samples were inventoried at the Texas Natural History Museum Collection (TNHC).

One individual of each new caught fish species (except possibly threatened or endangered species) was preserved in 70% ethanol for the voucher collection of the TNHC.

Mollies needed for behavioural experiments in the laboratory, were transported to the University of Texas at Austin, Section of Integrative Biology. Transportation took place in portable insulated and aerated containers. All other fishes were released to the habitat immediately after processing. Our sampling activities were designed not to affect population structure and densities.

Physical and chemical parameters of water quality

Using a Hydrolab™ multiprobe 4a (for specifications see appendix), I measured physical and chemical parameters of water quality of the field site. I measured water temperature [°C], ambient light intensity (PAR) [$\mu\text{E}/\text{s}/\text{m}^2$], pH, specific conductance [mS/cm], chlorophyll [$\mu\text{g}/\text{l}$], dissolved oxygen [% saturation and mg/l], and turbidity in nephelometric turbidity units [NTU]. All measurements are means from at least four readings: two readings were taken in low water areas or close to the surface, two readings in deeper water or close to the bottom. Ambient light intensity (photosynthetic active radiation PAR) was measured above and below the water surface. Wherever possible, turbidity and light intensity was measured six times throughout the water column.

Besides measurements taken from Hydrolab multiprobe readings, I noted air temperature [°C], salinity [ppt], time, substrate, depth and position of the probe, estimated shaded spots [%] and deployed an Onset StowAway™ light logger to log ambient light intensity at the same time as seining activities took place and Hydrolab readings were taken. In this study, I present and discuss only those parameters that turned out to have an effect on the abundance of Amazons and might affect stability of this asexual – sexual mating complex. Therefore, ambient light intensity (PAR) [$\mu\text{E}/\text{s}/\text{m}^2$], pH, air temperature [°C], and salinity [ppt] are only documented in the appendix, although they have been evaluated and were included in the analysis.

TEMPERATURE LOGGER

Underwater temperature loggers (Onset Optic StowAway™) were used to monitor water temperature at two field sites: one in South-Central Texas and one in South Texas. I deployed loggers at two field sites in session intervals between visits at SFH and SM. Temperature logger installed by other agencies (USGS, NAWQA, EARDC) (TNRCC 1994; Ulery & Brown 1995; Bush et al. 2000; TNRCC 2001) provided comparable data for COM, Co 101, and WES.

Data handling

LIGHT REDUCTION

I calculated light reduction, the relative decrease in light intensity in the water per total amount of light available at the field site as: $(PAR_{water} - PAR_{air}) / PAR_{air}$. Negative values towards -1 present total light reduction (for example due to turbidity, algae), values around 0 present no light reduction in the water column, and positive values towards +1 present data when more light was present under water than above water surface (this is only possible due to fluctuations in light intensity measured and must be an artefact).

DIVERSITY INDEX

Diversity was calculated as Brillouin - Index. This index is most sensitive to abundances of rare species in the community (Krebs 1999). Seining is a selective sampling method and not totally random. Different taxa are differently likely to be in the sample. Hence, use of Shannon index would be inappropriate (Krebs 1999). Brillouin - Index was calculated as

$$H_B = (\ln N! - \sum \ln n!) / N \text{ using Sterling - approximation with } n! \approx (2 \pi n (n/e)^n)^{-2} \text{ (Krebs 1999).}$$

N = total number of individuals in sample, n_i = number of individuals belonging to species i .

DEFINITION SEX RATIO

Sex-ratio was calculated for sexual species alone as well as for the complete sexual-asexual mating complex. Sex ratio of sexuals is defined as ratio of number of sexually active (= adult) males to number of adult males and females, and sex ratio total as ratio of number of sexually active (= adult) males to number of adult males and females and Amazons.

Catch Per Unit Effort sampling: Different parameters characterising catch per unit effort (CPUE) sampling were analysed. CPUE sampling can be performed appropriately by standardising samples by the number of hauls performed at each site.

All variables describing effort of sampling in the field did not correlate with the total number of fish sampled, number of Poeciliids sampled or number of species sampled at any given site and session. Therefore, these data were rather properties of the specific field sites and sampling date than due to biased sampling effort. I calculated the effort as the product of time spent seining and area seined.

There is a significant difference in the effort made at the six different studied populations ($\chi^2 = 17.668$, $p = 0.003$ $DF = 5$ Kruskal Wallis Test). This difference correlates with the different accessibility at the field sites. Therefore, CPUE is best performed by standardising samples by the number of hauls between field sites.

Number of hauls correlated significantly with area sampled per haul, minutes per haul, effort, time spent seining, and area sampled. It did not correlate with total number of fish sampled and total number of species sampled. Those parameters rather characterised different field sites than differences in sampling effort.

STATISTICAL ANALYSIS

All p -values are 2-tailed. Statistical analysis was conducted using Systat 10 SPSS Inc. 2000. Whenever post-hoc multiple comparisons were made, Bonferroni adjusted p -values were calculated using Dunn-Sidak Bonferroni corrections, unless stated otherwise.

Multiple regressions were performed stepwise (F to enter 4.0, F to remove 3.9) removing and entering variables both backwards and forwards to confirm results were not random due to the order by which variables entered the model. Plots of residuals against predicted values were consulted to confirm assumptions of normality, linearity, and homoscedasticity were not violated. Examination of scatterplots of residuals provide a test of assumptions of normality, linearity and homoscedasticity between predicted variables and errors of prediction (Tabachnick & Fidell 2001).

Principal component analysis was performed with varimax rotation ($\gamma = 1.0000$). This orthogonal rotation leads to uncorrelated factors, which is a prerequisite for a multiple regression on these factors. Oblique rotation on the other hand would lead to factors with a correlation of factors themselves (Tabachnick & Fidell 2001). Sizes of loadings reflect the extent of relationship between each observed variable and each factor. No problems with multicollinearity (variables are very highly correlated (>0.9)) or singularity (variables are redundant: one variable is combination of two or more other variables) occurred. From the loading matrix, only variables with loadings > 0.45 were interpreted. Tabachnick & Fidell (2001) considered those as fair loadings. Standardised factor scores were saved as a matrix of coefficients used in several regression –like equations to predict scores on factors from scores on observed variables for each individual.

Analyses of variances were designed as nested generalised models with temporal effects nested within populations. Thus, no interaction terms “session x population” were included into models (Tabachnick & Fidell 2001; Quinn & Keough 2002).

Percent variance explained by generalised models were calculated as proportions of sums of squares (SS) with $SS_{\text{effect}} / (SS_{\text{effect}} + SS_{\text{error}})$ (Jokela et al. 1997).

Normal distribution

Assessment of normal distribution of data was performed using Kolmogorov-Smirnov One Sample Test (Lilliefors probability 2-tailed) and graphical interpretation of probability plots and histograms.

To obtain normally distributed data, relative proportion of Amazons has been transformed using arcsine transformation.

To avoid violation of normality assumption, sex-ratio (within sexuals), sex-ratio (total), number of fish individuals and *Poecilia* sampled per minute, turbidity, specific conductance, and chlorophyll has been transformed using log-transformation; and relative proportion of Amazons sampled per haul were transformed using square root transformation.

Results

Community sampling at field sites

In total, approximately 50 000 fish individuals were sampled. Number of individuals was evenly distributed between South and Central Texas field sites (Tab. 2.4).

Ranking studied populations for fish abundance provided the following order: COM, LPK, WES, SFH, SM, and Co 101. Species richness in number of fish species detected followed the same pattern in opposite order. Overall, 39 fish species were sampled (Tab. 2.4).

Poeciliids predominated most samples (Fig. 2.7 and 2.8). Proportion of mollies was greatest in sampling session 8 (August) and session 1 (February 2001) and lowest in session 4 (May 2001). On the other hand, relative density of predatory fish was greatest in session 4 (May 2001) and lowest in session 7 (July 2001) (Fig. 2.8). At SFH no *P. latipinna* or *P. formosa* were caught during the first four visits.

Major predators in Central Texas were Sunfish species (*Lepomis* sp.), Mexican tetra (*Astyanax mexicanus*), and Largemouth bass (*Micropterus salmoides*). In South Texas, invasive Blue tilapia (*Oreochromis aureus*), Texas cichlid (*Cichlasoma cyanoguttatum*) and Largemouth bass (*Micropterus salmoides*) were the most frequent predators present in the seine (Tab. 2.4). High predation sites were SM (20% predators) and SFH (15% predators). Low predation sites were COM and LPK (Fig. 2.7).

At COM, *Gambusia geiseri* was extremely abundant (Fig. 2.7, Tab. 2.4).

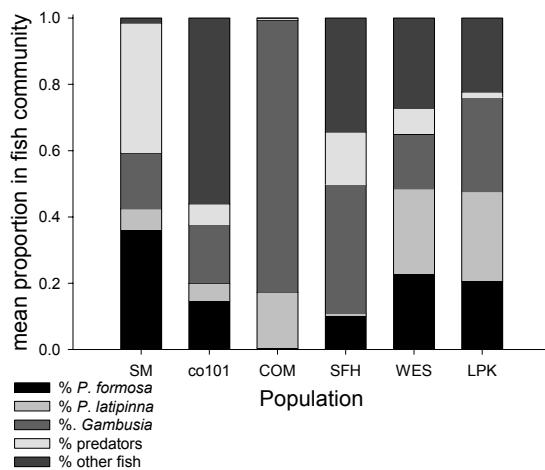


Fig. 2.7: Mean proportion of taxa in fish communities at six field sites in Texas.

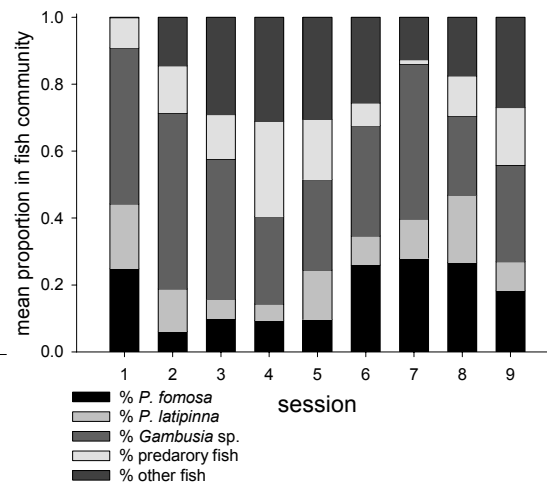


Fig. 2.8: Mean proportion of taxa in fish communities in three-weekly sampling sessions between February and September 2001.

Tab. 2.4: Fish community summary

Only species with a total of more than 5 individuals sampled are presented.

X: present; -: absent (0%); A1: one (1 individual); A2: rare (2-5 individuals; < 5%), A3: occasional (< 5%); B: frequent (5-15%); C: common (15-25%); D: abundant (25-50%); E: super abundant (50-75%); F: extremely abundant (75-100%). A comprehensive table is presented in the appendix (Tab. 8.6).

Population	n predatory species	n fish species	Poeciliidae															Centrarchidae				Cichlidae	Characidae	Clupeidae	Atherinidae	Cyprinodontidae	Catostrimidae	Percidae	Cyprinidae	total number fish	% <i>Poecilia</i> sp.	% Poeciliids	% predators	% other fish								
			<i>P. formosa</i>	<i>P. latipinna</i>	<i>Gambusia affinis/geiseri</i>	<i>Micropterus salmoides</i>	<i>Lepomis cyanellus</i>	<i>Lepomis macrochirus</i>	<i>Lepomis humilis</i>	<i>Lepomis gulosus</i>	<i>Cichlasoma cyanoguttatum</i>	<i>Oreochromis aureus</i>	<i>Astyanax mexicanus</i>	<i>Dorosoma cepedianum</i>	<i>Menidia beryllina</i>	<i>Cyprinodon variegatus</i>	<i>Etheostoma</i>	<i>Dionda episcopa</i>	<i>Campostoma anomalum</i>	<i>Cyprinus carpio</i>	<i>Cyprinella venusta</i>														<i>Notropis anabilis</i>	<i>Cyprinidae</i> indet						
SM	12	21	D	A3	B	A3	B	A2	A3	-	A3	A3	A3	-	A3	-	A2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2082	34	79	20	1	
Co 101	8	21	B	A3	B	A3	A3	A3	A3	-	A2	A3	A2	-	B	-	A2	A3	A3	A3	-	B	D	A1	-	-	-	-	-	-	-	-	-	-	-	-	1934	16	43	6	51	
COM	3	10	A3	B	F	-	-	A2	-	-	-	A2	A3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19312	7	100	0	0	
Σ central	12	28	A3	B	E	A3	A3	A3	A3	-	A3	A3	A3	-	A3	-	A3	A3	A3	A3	-	A3	A3	A2	-	-	-	-	-	-	-	-	-	-	-	-	23328	11	93	3	4	
SFH	6	17	A3	A3	D	B	A3	-	A3	A3	A1	A3	-	C	C	B	A1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4048	4	39	15	46
WES	5	15	B	B	B	A2	A2	-	-	-	A3	A3	A3	A3	C	A3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9072	30	73	5	22
LPK	3	12	B	C	C	-	-	-	-	-	A2	A3	-	A3	B	A3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13552	30	85	1	13
Σ south	8	23	B	B	C	A3	A2	-	A3	A3	A2	A3	A3	A3	B	A3	A1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	26672	26	74	5	21
Σ TEXAS	13	39	B	B	D	A3	A3	A3	A3	A3	A3	A3	A3	A3	B	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	A3	50000	19	83	4	13

A few fish species were predominating in the samples. Western mosquitofish (*Gambusia affinis*), Amazon molly (*Poecilia formosa*), Sailfin molly (*P. latipinna*), Inland silverside (*Menidia beryllina*), Sheepshead minnow (*Cyprinodon variegatus*), Mexican tetra (*Astyanax mexicanus*), Blue tilapia (*Oreochromis aureus*), Texas cichlid (*Cichlasoma cyanoguttatum*), Largemouth bass (*Micropterus salmoides*), Green sunfish (*Lepomis cyanellus*) occurred in most hauls.

Species occurring in all communities were: *Gambusia affinis*, *P. formosa*, *P. latipinna*, and *Oreochromis aureus* (Tab. 2.4).

In Central Texas, at only one field site occurring fish species were: Redbreast sunfish (*Lepomis auritus*), Longear sunfish (*L. megalotis*), and Golden shiner (*Notemigonus chrysoleucas*) at SM; Roundnose minnow (*Dionda episcopa*), Central stoneroller (*Campostoma anomalum*), and Orangethroat darter (*Etheostoma spectabile*) at Co 101. At field site COM exclusively sampled species were Largespring gambusia (*Poecilia geiseri*) and Fountain darter (*Etheostoma fonticola*), an endangered species that is endemic to the spring areas of Comal River and San Marcos River.

In South Texas exclusively sampled species were at SFH: Warmouth (*Lepomis gulosus*), *Fundulus zebrinus*, *Fundulus diaphanous*, and Red shiner (*Cyprinella lutrensis*); at WES: Common carp (*Cyprinus carpio*) and Clown goby (*Microgobius gulosus*).

Several individuals encountered in the samples were non-native and present due to introductions: *Oreochromis aureus* (in all populations), *Cyprinus carpio* (WES), *Lepomis auritus* (at SM), *Ambloplites rupestris* (at SM, Co 101). In Central Texas, *P. formosa*, *P. latipinna*, *Astyanax mexicanus*, *Cichlasoma cyanoguttatum*, *Notemigonus chrysoleucas* are introduced (Tab. 2.4).

Species diversity

39 out of the 247 fish species occurring in Texas (Hubbs et al. 1991) were sampled.

Species diversity (Brillouin – Index) was highly variable among populations (Fig. 2.9) and seasonal sampling sessions (Fig. 2.10), and ranged from 0.021 – 5.19 (mean \pm SE: 1.405 ± 0.127 , $n = 67$).

Highest diversity was reached in the period between April – June and lowest in February 2001 (Fig. 2.10). Among populations, COM had the lowest diversity indices and SFH highest (Fig. 2.9).

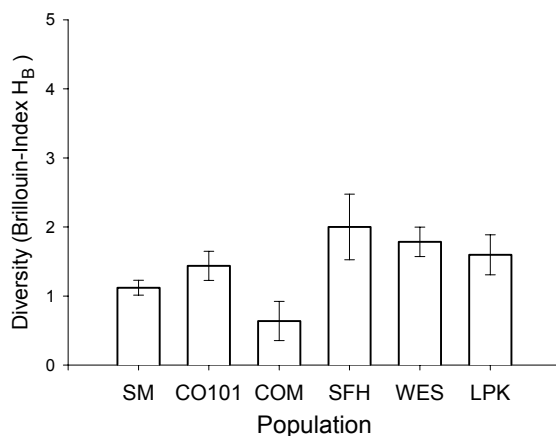


Fig. 2.9: Diversity of fish communities (Brillouin-Index) (mean \pm S.E.) in population.

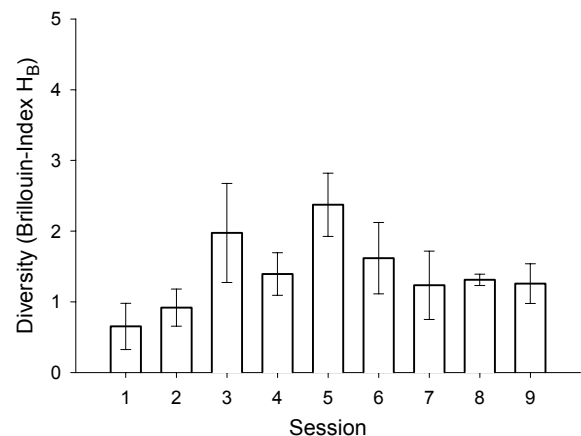


Fig. 2.10: Diversity of fish communities (Brillouin-Index) (mean \pm S.E.) in sessions.

Significance of *P. formosa* in the fish community

P. formosa's dominance status in its fish community was highly variable and ranged from 0-93.4% (mean \pm SE = 18.3 ± 2.8 , median = 9.2, $n = 67$).

Apart from COM, where Amazons always comprised $< 5\%$, *P. formosa* was dominating fish communities seasonally outside from springtime (March – June) (Fig. 2.11, appendix Tab. 8.3). Among populations, *P. formosa* was clearly the dominating species at SM (Fig. 2.12).

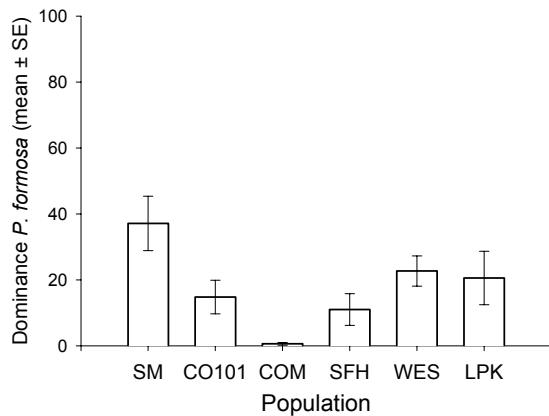


Fig. 2.11: Dominance of *P. formosa* within fish community in different populations.

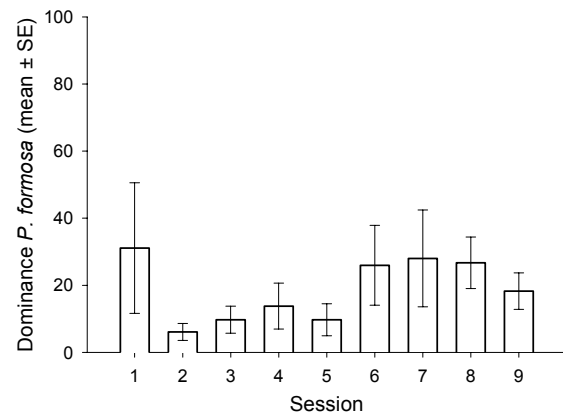


Fig. 2.12: Dominance of *P. formosa* within fish community in seasonal sessions.

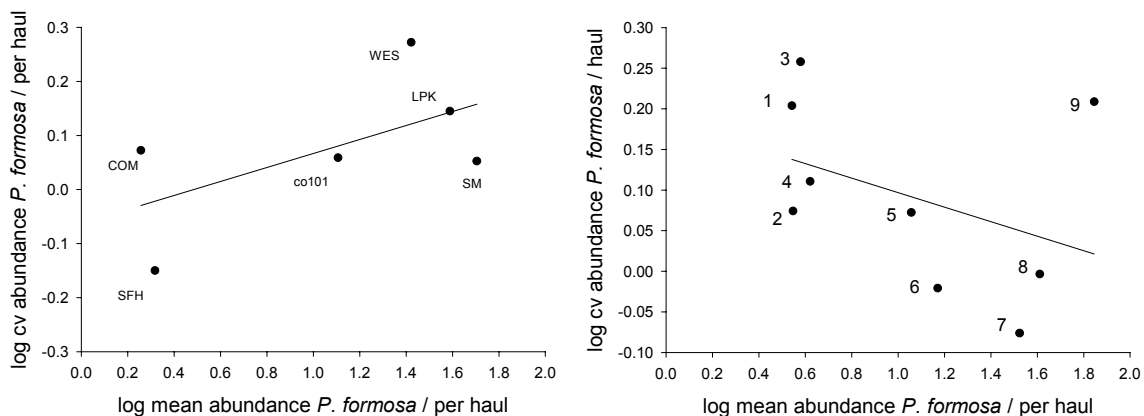


Fig. 2.13: a) Spatial and b) Temporal variability in the frequency of *P. formosa* within the community.

Taylor's power law (Taylor cited in Krebs 1999) is a useful way of summarising the structure of a sampling universe. It is a technique to describe count data from natural populations. If organisms have a random spatial pattern, then for each series of samples the variance will equal the mean, and the slope will be 1.0. Aggregated populations will have a slope > 1 .

According to Taylor's power law (Krebs 1999) there is a non-significant tendency that spatial variation in density of *P. formosa* in the community is greater at high relative Amazon-density

sites (slope $a = 0.13$, $r = 0.6$, $F_{1,4} = 2.2183$, $p = 0.2106$) (Fig. 2.13a) and seasonal variation greater at low relative Amazon-density sites (slope $a = 0.13$, $r = -0.09$, $F_{1,8} = 1.3378$, $p = 0.2854$) (Fig. 2.13b).

Therefore, spatial and temporal variation is not independent from population density and thus, the coefficient of variance is not a measure of population variability.

Comparing within-habitat variation versus between-habitat variation as well as within and between seasonal variation of the relative density of *P. formosa*, Amazon frequencies were more variable at those habitats that generally hosted relatively more *P. formosa* (Fig. 2.13a). In contrast, temporal variation in relative densities of *P. formosa* was higher at times with generally low proportions of Amazons (Fig. 2.13b).

A closer look at mollies: The sexual-asexual mating complex

Within the sexual-asexual mating complex, Amazons outnumbered their sexually reproducing females in all sampled populations beside field site COM (Fig. 2.14). The relative proportion of Amazons in the complex was high (above mean + 1 SD) in SM, Co 101 and SFH, intermediate in WES and LPK – where the host species was more abundant than *P. formosa* in most sampling sessions, and low in COM (below mean – 1 SD) (Fig. 2.16).

Seasonally, there was a tendency that the proportion of Amazons in the complex increased with seasonal progress (Fig. 2.17). In absolute numbers, Amazons reached its clear peak in sampling session 6 and 8 when Amazons clearly outnumbered their sexual host species females (Fig. 2.15). Only in session 2 and 9 sexual females were more abundant than Amazons (Fig. 2.15).

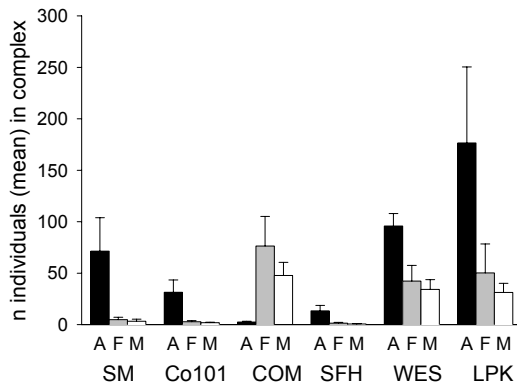


Fig. 2.14: Spatial variation of frequencies of *P. formosa* (A), *P. latipinna* females (F), *P. latipinna* males (M) in six different mixed populations.

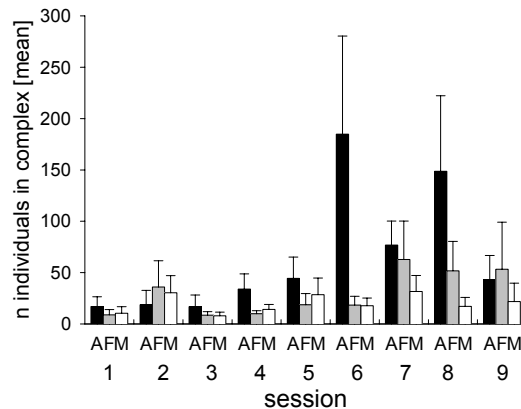


Fig. 2.15: Temporal variation of frequencies of *P. formosa* (A), *P. latipinna* females (F), *P. latipinna* males (M) in six different mixed populations.

PROPORTION OF UNISEXUALS IN THE COMPLEX

In a nested general linear model (GLM), I tested the relative proportion of Amazons within the complex per number of hauls (square root transformed) as response variable. As factors, ‘population’ and ‘session nested within population’ were included in the model. The proportion of Amazons was significantly different among populations (Tab. 2.5, Fig. 2.16). Population explained 97.2% of the total variation in this model. There was no significant temporal effect within populations (Tab. 2.5, Fig. 2.17).

In a post-hoc comparison, using model mean squares of errors (MSE) of 0.020 with 3 degrees of freedom (*DF*), the only significant difference among populations was between SM and COM (pairwise mean difference = 0.574, $p < 0.05$, Bonferroni adjusted) (Fig. 16).

Tab. 2.5: Analysis of Variance. Dependent variable: relative proportion of Amazons within the complex per number of hauls (square root transformed), (multiple $r^2 = 0.980$, $n = 59$).

Source	SS	DF	MS	F	p
Population	2.145	5	0.429	21.147	0.015
Session (Population)	0.967	50	0.019	0.954	0.621
Error	0.061	3	0.020		

SS = sums of squares, DF = degrees of freedom, MS = mean squares, F = F-ratio

To uncover any underlying seasonal effects on relative abundance of Amazons in the complex across all populations, I separately tested in an analysis of covariance (ANCOVA) the relative proportion of Amazons in the complex with population as factor and date (day number) as covariate. Population and sampling date had a significant effect (Tab. 2.6). Population explained 71.5% of the total variance. The seasonal effect on proportion of Amazons in the complex is also shown in Fig. 2.17.

Tab. 2.6: Analysis of Variance: Dependent variable relative proportion of Amazons within the complex per number of hauls (square root transformed), (multiple $r^2 = 0.735$, $n = 59$)

Source	SS	DF	MS	F	p
Population	2.059	5	0.412	26.047	0.000
Date	0.206	1	0.206	13.039	0.001
Error	0.822	52	0.016		

In a post-hoc comparison using model MSE (mean squares of error) of 0.016 with 52 *DF*, it turned out that COM is significantly different from all other populations and LPK is different from all Central Texan populations. All differences are presented in Tab. 2.7. (see also Fig. 2.16).

Tab. 2.7: Matrix of pairwise mean differences in relative proportion of Amazons within the mating complex.

	a	b	b	d	bc	cd
Population	COM	LPK	SFH	SM	WES	Co 101
COM	0.000					
LPK	0.203*	0.000				
SFH	0.368*	0.164	0.000			
SM	0.558*	0.355*	0.191*	0.000		
WES	0.291*	0.087	-0.077	-0.268*	0.000	
Co 101	0.431*	0.228*	0.064	-0.127	0.141	0.000

Significant pairwise comparison probabilities (Bonferroni adjusted) are marked with an asterisk. Populations that differ in frequencies of Amazons are marked with different letters.

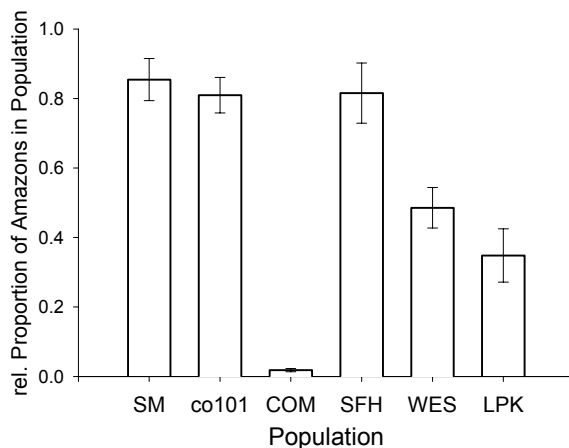


Fig. 2.16: Relative proportion of Amazons in the sexual-asexual mating complex in populations in South and Central Texas.

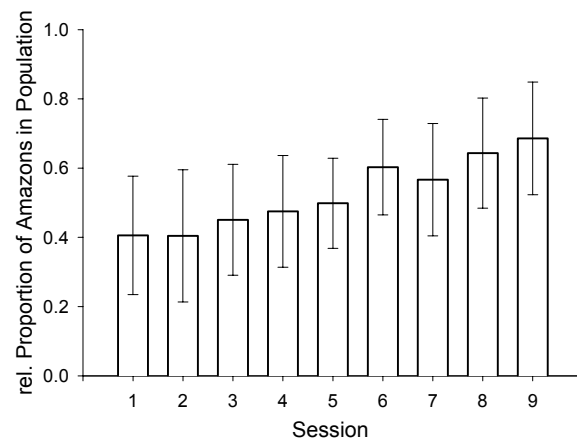


Fig. 2.17: Rel. proportion of Amazons in the sexual-asexual mating complex in different three-weekly sampling sessions (February – September 2001) throughout populations. ANCOVA: significant effect of temporal covariate: $F = 13.04$; $DF = 5,1$; $p = 0.001$.

JUVENILES

Relative proportion of juveniles was higher in South Texas populations than in central Texan populations with mainly adult individuals sampled. From the data, it appears that Central Texas populations only had one clearly dominating cohort of juveniles in summer (session 7 and 8) and a majority of adults throughout the rest of the study period. On the other hand, in South Texas as in all data combined, proportion of juveniles was fluctuating between subsequent sampling sessions with juveniles' frequencies alternating throughout the study period (February - September 2001) besides April (Fig. 2.18).

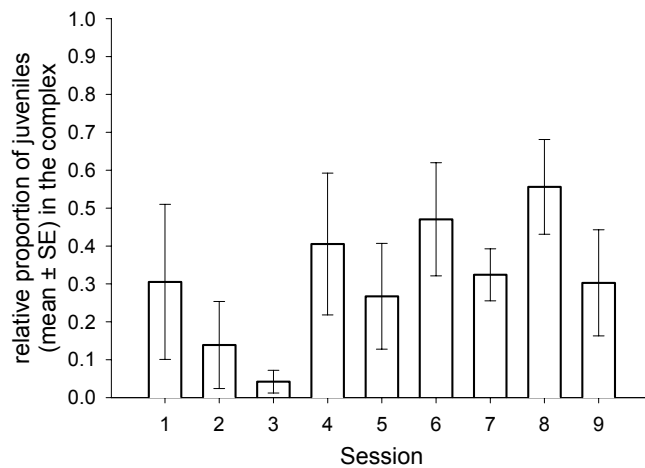


Fig. 2.18: Relative proportion of juveniles in the complex in three-weekly sampling sessions (February - September 2001) throughout populations.

SEX RATIO

Sex-ratios (n males / n males + n females) were biased towards females (Fig. 2.19 – 2.22). The sex-ratio becomes heavily biased towards females (Fig. 2.20 and 2.22) when analysing the sex-ratio for the whole mating complex with both types of females (*P. latipinna* and *P. formosa*). Males outnumbered sexual and gynogenetic females combined only in three samples at COM ($>$ mean + 1 SD), where hardly any Amazon mollies were present. In 20% of all samples, more males than sexual females were present. Besides the above-mentioned cases at COM this has been observed at SM, SFH, and LPK. There was a tendency of increasingly female-skewed bias in seasonal progress (Fig. 2.21 and 2.22).

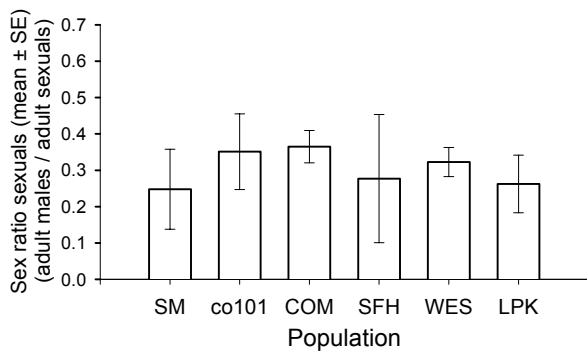


Fig. 2.19: Sex - ratio (males / males + sexual females) in *P. latipinna* in different populations.

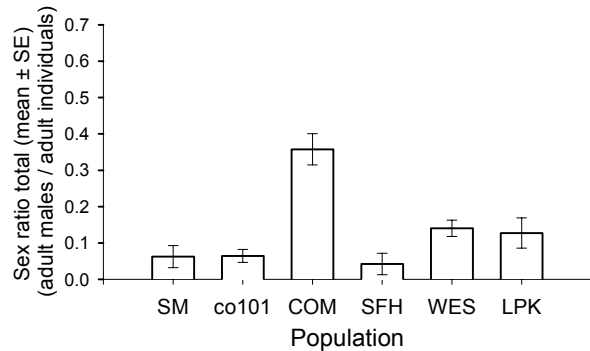


Fig. 2.20: Total sex - ratio (males / males + sexual females + asexual females) in the complex in different populations.

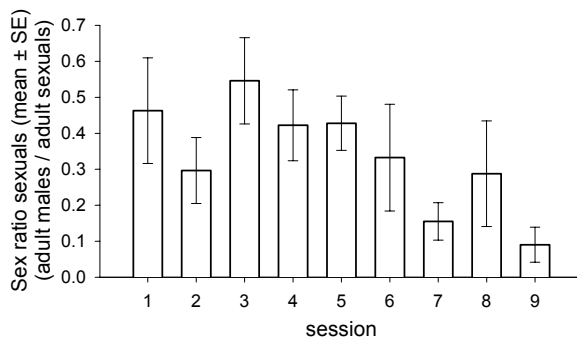


Fig. 2.21: Sex ratio (males / males + sexual females) in *P. latipinna* in three-weekly sampling sessions (February - September 2001).

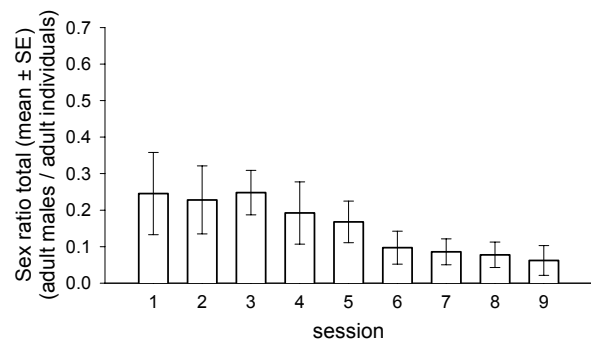


Fig. 2.22: Total sex ratio (males / males + sexual females + asexual females) in the complex in three-weekly sampling sessions (February - September 2001).

SIZES

Standard length of 935 males, 1016 sexual females, and 949 unisexuals were measured in total (Tab. 2.8). In general, asexual *P. formosa* females were larger (mean SL) than females of its sexual host species *P. latipinna* (Wilcoxon Signed Rank Test: $n = 42$, $z = -2.807$, $p = 0.0050$, Fig. 2.23). Not only were Amazons larger than their sexually reproducing female competitors, but variation was also larger. Male standard length ranged from 16 – 53 mm. Maximum size of Amazons was 67 mm, of *P. latipinna* females 61 mm.

I analysed 51 visits in either old (three populations in South Texas) or young sympatry (three populations in Central Texas). *P. latipinna* females and *P. formosa* mean standard length differed not significantly in relative size difference although there was a trend that females from Central Texas (the young sympatry) differed more than the females from South Texas (old sympatry) (Mann-Whitney U Test: $U = 227.5$, $U' = 416.5$, $z = -1.792$, $p = 0.0731$).

Tab. 2.8: Summary of descriptive statistics on standard length of adult mollies in the sexual-asexual mating complex of *P. formosa* from six populations studied in Texas, USA.

	Mean \pm SE	N	min.	max.	cv	median	IQR
male <i>P. latipinna</i>	28.2 \pm 0.2	935	16	53	0.20	27	8
female <i>P. latipinna</i>	37.2 \pm 5.8	1016	30	61	0.17	36	9
unisexual <i>P. formosa</i>	41.3 \pm 8.8	949	30	67	0.21	40	14

SE = Standard error of mean, cv = coefficient of variation, IQR = interquartile range

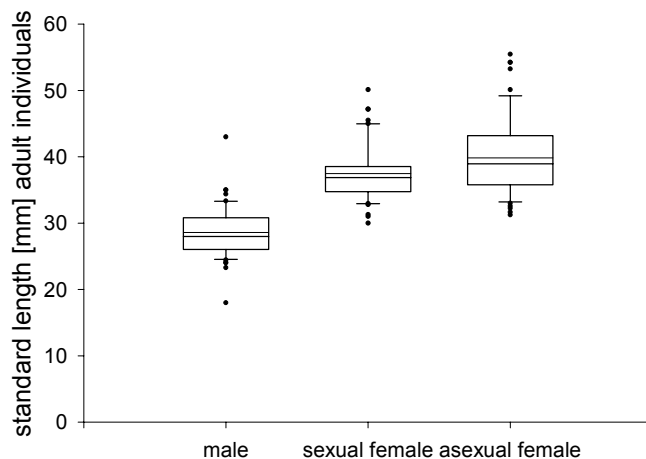


Fig. 2.23: Standard length from adult mollies originating from six populations in Texas sampled between February and September 2001. Box-plots: The lower boundary of the box indicates the 25th percentile and the upper boundary the 75th percentile, the solid line represents the median, and the mean is hairline. Whiskers indicate the 90th and 10th percentiles. All outlying data points are shown.

Male sizes

On average, smallest males occurred in population WES, LPK, and Co 101; and largest males at SFH, COM, and SM. In a nested generalised linear model (GLM) with ‘male standard length’ ($n = 779$) as response variable and ‘population’, ‘session’, and ‘session nested within population’ as factors, there was a significant effect of all factors (Tab. 2.9). The model explained 24.5% of the variance in male size. In Tukey tested multiple contrasts, using $MSE = 24.749$ with 738 DF , male sizes differed significantly between COM vs. LPK (mean difference $\bar{x} = -2.122$, $p = 0.002$), COM vs. WES ($\bar{x} = -2.092$, $p = 0.004$), LPK vs. SM ($\bar{x} = 6.130$, $p = 0.007$), and WES vs. SM ($\bar{x} = 6.099$, $p = 0.007$). No significant difference between pairs of sessions occurred.

In summary, males from Comal Springs (COM) and San Marcos River at Martindale (SM) in Central Texas were larger than males from Lincoln Park (LPK) and Weslaco Floodway (WES) in South Texas.

Tab. 2.9: ANOVA table (nested GLM) of male standard length.

Source	SS	DF	MS	F	p
Population	731.124	5	146.225	5.908	0.000
Session (Population)	4147.912	35	118.512	4.789	0.000
Session	2777.591	8	347.199	12.482	0.000
Combined Model	5930.487	40	148.262	5.991	0.000
Error	18264	738	24.749		

Female sizes:

Female type (sexual vs. asexual) had no effect on size in a partially nested GLM with standard length of females ($n = 1640$, multiple $r^2 = 0.469$) as dependent variable and ‘female type’, ‘population’, ‘session’, interaction of ‘female type x population’, and ‘female type x session nested within population’ as factors. There was a significant effect on population and session as well as on seasonal interaction with female type, but only a trend on an interaction effect of female type by population (Tab. 2.10). Population effect alone explained 10.3% of the variance in the model, ‘female type x session nested within populations’ explained 15% of female size variation (Fig. 2.25). As in males, sexual females and Amazons were also smaller in population LPK and larger in population SM and SFH (*P. latipinna*) or COM (*P. formosa*) respectively (Fig. 2.24).

Tab. 2.10: Analysis of Variance of mature female sizes in the *P. formosa* / *latipinna* complex.

Source	SS	DF	MS	F	p
Female type	56.497	1	56.497	1.733	0.188
Population	5913.222	5	1182.644	36.275	0.000
Session	602.398	8	75.300	2.310	0.018
Female type x Population	337.556	5	67.511	2.071	0.066
Female type x Session (Population)	9108.984	40	227.725	6.985	0.000
Error	51511.305	1580	32.602		

Pairwise multiple comparisons of female size between populations were tested using model MSE of 32.602 with 1580 *DF*. Female standard length of females originating from LPK and SM differed significantly from all other populations (Tab. 2.11). In Fig. 2.24, the mean size per sample is presented.

Pairwise Tukey HSD multiple comparisons of female size between sampling sessions were tested using model MSE = 32.602 with 1580 *DF*. Significant pairwise differences in female size occurred between session 5 (May / June) and session 4 (May), 6 (June / July), and 8 (August). Fig. 2.25 presents the mean female size per sampling location in different sessions.

Tab. 2.11: Matrix of pairwise mean differences of female standard length between populations.

	a	b	a	c	ac	d
Population	COM	LPK	SFH	WES	Co 101	SM
COM	0.000					
LPK	-4.900*	0.000				
SFH	0.734	5.634*	0.000			
WES	-2.866*	2.034*	-3.600*	0.000		
Co 101	-1.799	3.100*	-2.533	1.067	0.000	
SM	4.943*	9.843*	4.209*	7.810*	6.743*	0.000

Significant pairwise comparison probabilities (Tukey HSD Multiple Comparisons) marked with an asterisk and populations that differ in female size are marked with different letters.

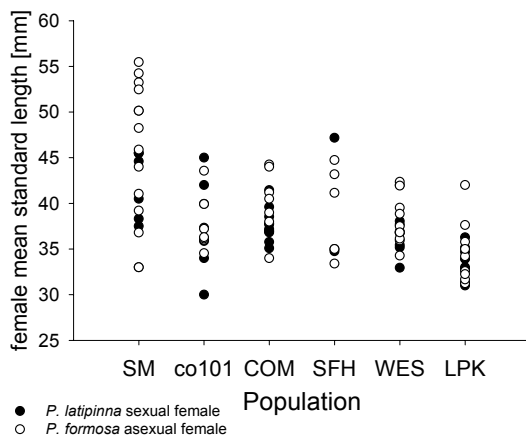


Fig. 2.24: Mean standard length of sexual (full circles) and asexual females (open circles) in the complex in sampling sessions between February and September 2001 in six different populations.

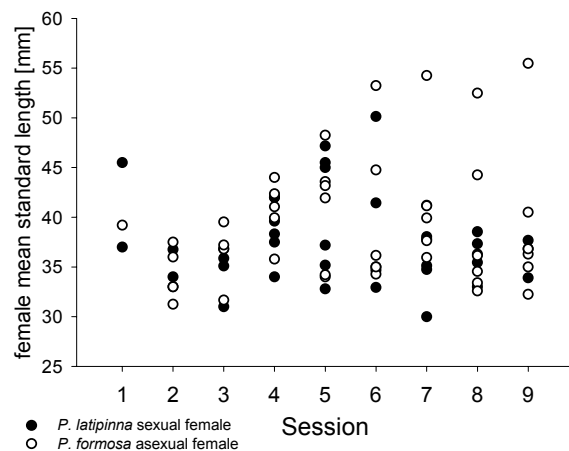


Fig. 2.25: Mean standard length of sexual (full circles) and asexual females (open circles) in the complex in six different populations sampled during nine visits in 2001.

Selected parameters of spatial and seasonal variation of water quality that affected frequency of *P. formosa*

MONITORING OF WATER TEMPERATURE

Logging water temperature revealed extreme changes in water temperatures in South and Central Texas. At SFH, water temperature varied between 14.1°C and 33.8°C, at SM it ranged from 10.2°C – 30.4 °C. At both sites, high daily amplitudes in winter and early spring were measured (Tab. 2.12). The opposite extreme was observed in the spring fed habitat. Here at COM, stable conditions with almost constant water temperatures of 23.6 ± 0.2 °C were monitored throughout the year (Tab. 2.13).

Tab. 2.12: Monitored water temperature (deployed data logger).

session-interval	Date	site	mean	±SD	min	max
1-2	18/02/01-08/03/01	SFH	21	2.4	15.9	26.1
2-3	08/03/01-11/04/01	SFH	22	2.6	17.3	27.9
3-4	11/04/01-05/05/01	SFH	25	1.5	21.5	28.2
4-5	05/05/01-30/05/01	SFH	26	1.0	24.3	29.7
5-6	30/05/01-26/06/01	SFH	29	1.0	26.8	33.8
6-7	26/06/01-18/07/01	SFH	28	0.9	26.4	31.2
7-8	18/07/01-15/08/01	SFH	28	1.4	25.4	32.7
8-9	15/08/01-12/09/01	SFH	28	0.7	25.4	29.3
9-winter	12/09/01-05/12/01	SFH	22	3.3	14.1	29.7
1-2	19/02/01-21/03/01	SM	18	3.1	12.0	30.0
2-3	21/03/01-06/04/01	SM	19	2.8	13.1	24.6
3-4	06/04/01-03/05/01	SM	22	2.1	15.5	26.4
4-5	03/05/01-12/06/01	SM	24	2.2	18.3	29.3
5-6	12/06/01-09/07/01	SM	26	1.9	22.2	30.0
7-8	27/06/01-23/08/01	SM	28	1.4	24.6	30.4
8-9	23/08/01-13/09/01	SM	26	1.5	23.2	30.4
9-winter	13/09/01-08/01/02	SM	20	3.8	10.2	29.3
winter	04/10/02-16/04/03	SM	19	2.8	11.6	27.5

Measuring interval was 10 minutes, except hourly measures in fall 2001 and 30 min intervals in winter 2002 / 2003.

Tab. 2.13: Monitored conditions at Comal Springs. Source: Database Trinity Aquifer research program <http://www.eardc.txstate.edu/trinity>

Daily (12:00 h)	Spec. cond. [$\mu\text{S} / \text{cm}$]		Temperature [$^{\circ}\text{C}$]	
	mean	± SD	mean	± SD
1999	507.4	59.9	23.5	0.1
2000	547.8	14.7	23.5	0.1
2001	551.1	3.5	23.7	0.1
2002	486.6	90.8	23.7	0.2
Total ($n = 1791$)	505.4	91.2	23.6	0.2
range	177 – 588		23.3 – 24.0	

WATER CONDITIONS AT FIELD SITES DURING SAMPLING VISITS

Water temperature

Variation among populations and seasonal changes of actual water temperature during the study are presented in Fig. 2.26. Again, water temperature at COM remained stable throughout the study, whereas all other populations showed typical seasonal changes. Extremely high water temperatures occurred from July – August, when at SFH the ditch was almost dry and hence the water body extremely small and shallow (Fig. 2.26). Water temperature correlated significantly with air temperature, specific conductance, and date (Tab. 2.14).

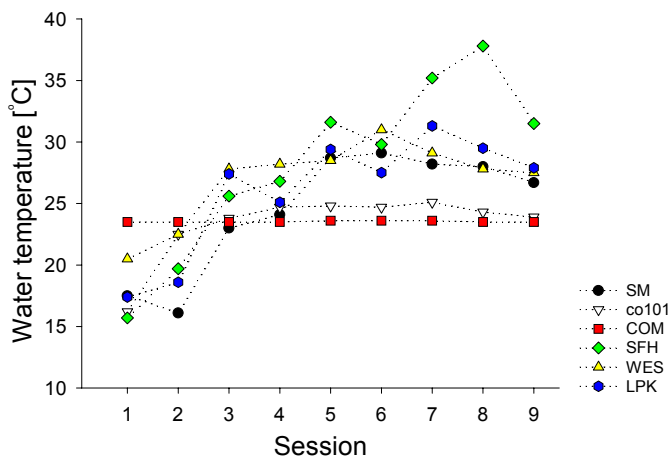


Fig. 2.26: Water temperature in sessions and populations.

Specific conductance

Central Texas field sites had stable low specific conductance throughout the study, WES remained on a high level during the study period. At this field site, up to 3% salinity was measured. All three southern populations had a peak in August when the water level was low at the end of a long dry period before the rainy season began in September (Fig. 2.27).

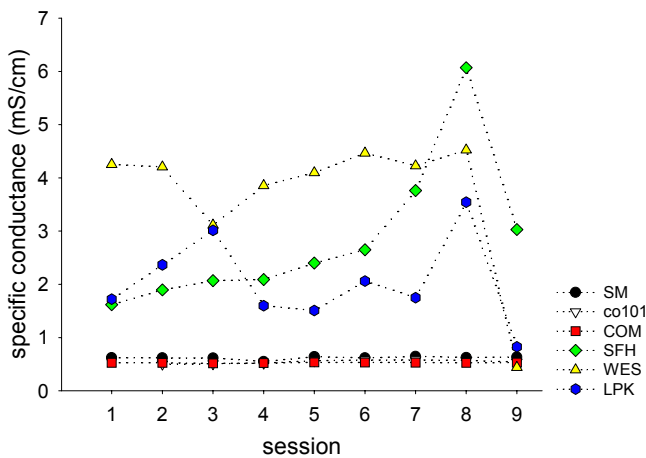


Fig. 2.27: Specific conductance in sessions and populations.

Turbidity

Mean turbidity was 137.2 ± 139 SD. Water was generally murkier at southern field sites. Central Texan field sites had comparably clear water conditions. At SFH, WES, and LPK, the southern populations, water clarity was variable but on a highly murky level (Fig. 2.28). The spring population COM had stable crystal clear water throughout the study. Turbidity levels at the field sites at San Marcos River (populations SM and Co 101) fluctuated on a lower level of turbidness (Fig. 2.29).

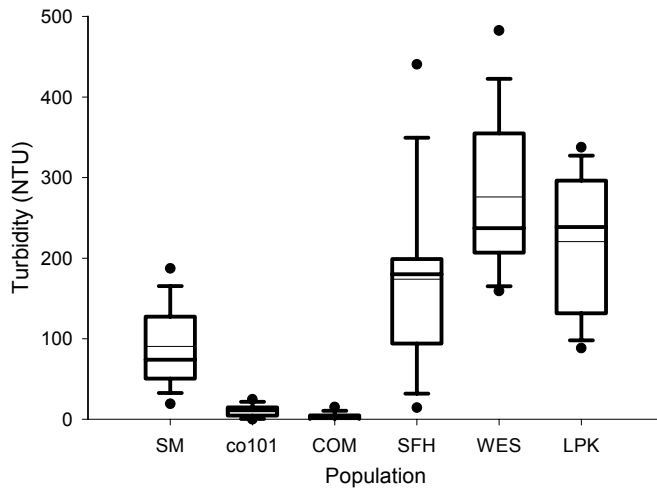


Fig. 2.28: Turbidity level in populations (for explanation of boxplots see Fig. 2.23).

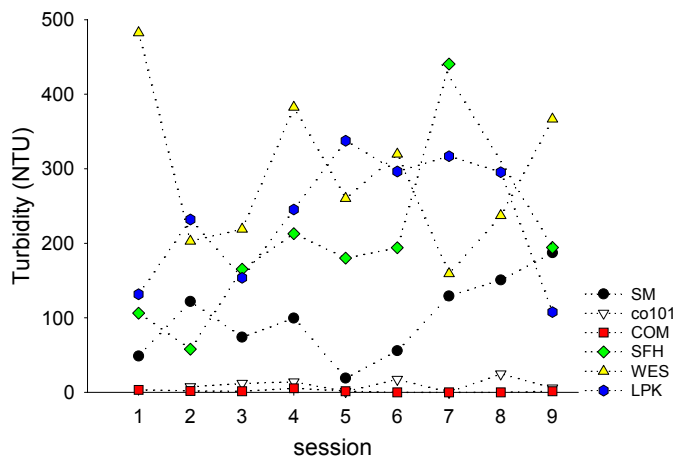


Fig. 2.29: Turbidity level in sessions and populations.

Chlorophyll

Chlorophyll α concentration as a measure of primary production decreased in the course of the study (Fig. 2.30). COM and Co 101, the two habitats with clearest water were also those with lowest chlorophyll concentrations throughout the study. At June and July, chlorophyll concentration reached its summer maximum – before ditches became dry.

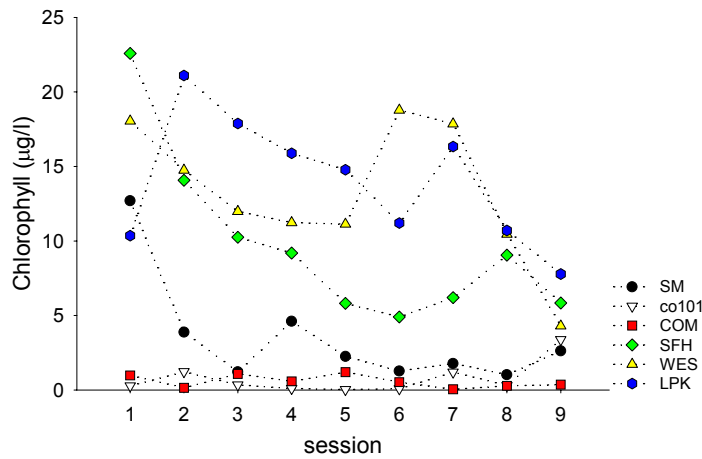


Fig. 2.30: Chlorophyll concentration in sessions and populations.

The same difference as in turbidity level between Central and South Texas (Fig. 2.28 & 2.29) was observed for variation in specific conductance (Fig. 2.27) and chlorophyll (Fig. 2.30). There was a significant correlation between these three parameters (Tab. 2.14).

Dissolved oxygen

Dissolved oxygen never reached levels below 50% saturation. Oversaturation occurred in many cases since water temperature increased rapidly at field sites during the day.

Absolute concentration of dissolved oxygen reached maximally possible values of > 13 mg / l (June at WES) and lowest oxygen concentrations of 3.8 mg / l (Fig. 2.31). On average, mean dissolved oxygen concentration in samples was 7.9 ± 0.3 ($n = 58$). Especially at the beginning and the end of the study, in February and March and again in September, dissolved oxygen concentrations were lowered (Fig. 2.32). Seasonal variation in the whole of all sampled population follows roughly the same pattern with generally lower levels of oxygen at COM and higher at the turbulent field site Co 101 (Fig. 2.31). In June (session 5 and 6), oxygen levels were highest. This peak occurred one sampling visit session before chlorophyll concentration reached its maximum. Measured dissolved oxygen concentration correlated with number of fish species caught at the field site (Tab. 2.14).

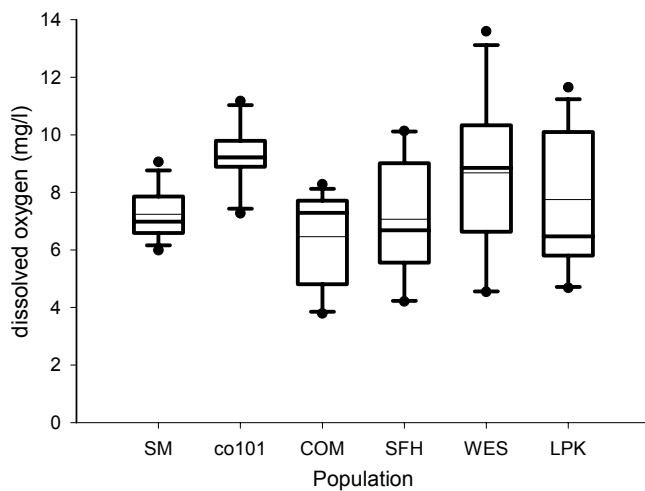


Fig. 2.31: Dissolved oxygen in populations (for explanation of boxplot see Fig. 2.23).

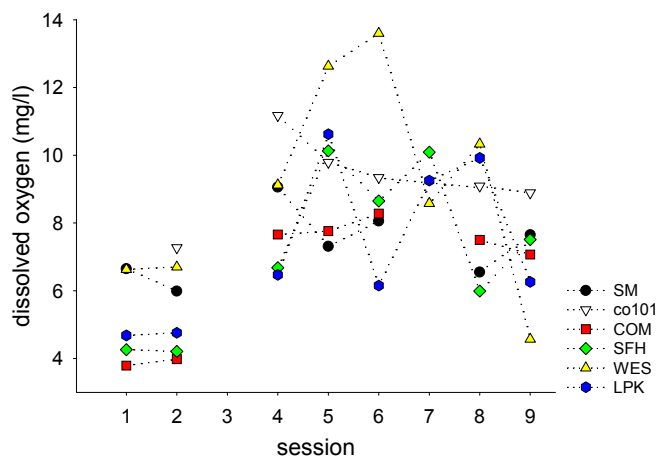


Fig. 2.32: Dissolved oxygen in sessions and populations.

RELATIONSHIPS BETWEEN PARAMETERS MEASURED AT FIELD SITES

Many parameters measured in the field correlated with each other (overall pearson listwise sig. correlation: Bartlett $\chi^2 = 752.752$, $DF = 300$, $p = 0.000$, $n = 29$). Pairwise correlations are presented in Tab. 2.14. In the focus of this study were specially the relationships between the frequency of Amazons and other biotic or abiotic parameters. Proportion of unisexuals among mollies correlated positively with relative abundance of predators at the site and negatively with sex-ratio in its sexual host species. Chlorophyll concentration as a measure of primary production in the habitat correlated positively with specific conductance and turbidity. Concentration of dissolved oxygen correlated positively with species richness at the field site. Relative fish density correlated negatively with proportion of predators and Amazons (Tab. 2.14).

Tab. 2.14: Significant pairwise correlations between measured parameters (using transformed data; $p < 0.05$ presented as *, $p < 0.01$ as **, p - values are Dunn-Sidak corrected).

Variables	pearson r	N
water temperature - date	0.573**	69
water temperature - specific conductance	0.523**	69
water temperature - % sat. dissolved oxygen	0.564**	57
specific conductance - chlorophyll	0.689**	69
specific conductance - salinity	0.797**	62
turbidity - specific conductance	0.555**	67
turbidity - pH	0.450*	67
turbidity - chlorophyll concentration	0.758**	67
dissolved oxygen - # fish species sampled	0.413*	58
relative fish density - proportion predators in community	-0.470*	66
relative fish density - rel. density <i>P. formosa</i> in community	-0.624**	59
proportion <i>P. formosa</i> in complex - sex-ratio within <i>P. latipinna</i>	-0.789**	62
proportion <i>P. formosa</i> in complex - proportion predators in community	0.486*	61

Population ecology in the complex: Integrating biotic and abiotic parameters to explain spatial and seasonal variation

WHICH PARAMETERS EXPLAIN FREQUENCY OF AMAZONS?

Sampling different mixed molly populations at different times of the year revealed many differences but also communalities throughout field sites. This raises the question what the differences are – besides the obvious and challenging variations in frequency of Amazons. To answer the question, which parameters explain variation in frequency of Amazons best, a stepwise multiple regression was conducted. I used relative proportion of asexuals per haul in the mating complex (square root transformed) as dependent variable ($n = 57$, multiple $r^2 = 0.657$, adjusted $r^2 = 0.631 \pm 0.142$), and 16 measured abiotic and biotic (transformed) parameters as variables. In a backward stepwise multiple regression, from the initial model removed were: date, spec. conductance, pH, light intensity (PAR) in the water, ambient light intensity reduction in the water column, dissolved oxygen, ratio of males per female mollies, sex-ratio of sexuals, species diversity, relative abundance of predators, mean male SL, and mean sexual female SL.

In the model remained: **water temperature, turbidity, chlorophyll, and fish density in the community** (Tab. 2.15). The final regression model explains 65.6% of variation in relative abundance of *P. formosa* in the complex.

Tab. 2.15: Multiple stepwise backward regression model. Dependent variable: relative proportion of asexuals per haul in the mating complex.

Effect	Coefficient	SE	Std Coef	Tolerance	t	p
Constant	0.168	0.123	0.000	.	1.374	0.175
Water temperature	0.021	0.006	0.363	0.676	3.671	0.001
Turbidity (log)	0.063	0.020	0.518	0.238	3.113	0.003
Chlorophyll (log)	-0.146	0.034	-0.644	0.301	-4.349	0.000
N Fish / time (log)	-0.141	0.021	-0.627	0.725	-6.569	0.000

Analysis of Variance

Source	SS	DF	MS	F	p
Regression	2.011	4	0.503	24.907	0.000
Residual	1.050	52	0.020		

Case 33: leverage = 0.314, Durbin-Watson D statistic 1.473, First order autocorrelation 0.252.

FINDING COMMUNALITIES AND REDUCING THE NUMBER OF VARIABLES: PRINCIPAL COMPONENT ANALYSIS

To reduce the number of parameters responsible for the general overall variation among populations and sessions – regardless of variation due to frequency of Amazons – a principal component analysis was conducted. To keep factors independent from influences of Amazons for a multiple regression on factors, no variables containing any data on frequency of asexual mollies were included in this analysis. In total, 18 variables were included. The eigenvalues varied from 3.522 – 0.006.

Consultation of scree plot revealed a considerable drop of eigenvalue loading and therefore no need for selection of a different number of components, seven principal components with eigenvalues greater than 1 were selected (Tab. 2.16).

Tab. 2.16: Factors from principal component analysis.

Factor	1	2	3	4	5	6	7
Label	abiotic	Community	season	habitat	Light	Male mollies	size / habitat
Description	physical properties of habitat	fish community	seasonal influence	habitat quality	light environment	Male mollies and pH	molly size and habitat structure
variance explained by rotated components	2.958	2.434	2.085	2.005	1.753	1.527	1.940
% of total variance explained	16.433	13.520	11.584	11.136	9.737	8.481	10.775
major variables: (stand. factor scores)	chlorophyll (0.321) ***	n fish/time (0.382) ***	date (0.434) ***	n species (0.448) ***	PAR water (0.538) ***	% males (-0.574) ***	female SL (-0.484) ***
	spec. cond. (0.326) ***	Poecilia/time (0.345) ***	water temp (0.428) ***	diss. O₂ (0.366) ***	light reduction (0.441) ***	pH (0.313)	male SL (-0.302) *
	turbidity (0.303) ***	% predators (-0.236) **	(area/haul)	(area/haul)	(turbidity)	male/female (0.284)	area/haul (-0.342) *
	pH (0.132) *	male/female (-0.263) *	(male/female (% predators))			(male SL)	(pH)
	(water temp)						
	(male SL)						

*** excellent (> 0.71), ** very good (> 0.63), * good (> 0.55) loadings in varimax-rotated loading matrix reflecting extent of relationship between each observed variable and each factor (Tabachnick & Fidell 2001). Variables in parentheses were not interpreted (loading < 0.45).

All seven components contributed approximately the same amount of explained variance. Among factors, percent of variance explained varied from 16.4% to 8.5%. Only the abiotic component (factor 1) explained slightly more variance than expected from uniform distribution (14.3%) (Tab. 2.16). Habitats are approximately evenly characterised by entities of all seven factors obtained from the PCA. However, abiotic properties (factor 1: Chlorophyll, conductance, turbidity, pH) explain more of the variation among samples. Fish community data (factor 2: fish density, *Poecilia* density, % predators, male/female-ratio) explain slightly less (Tab. 2.16).

WHICH FACTORS EXPLAIN ABUNDANCE OF ASEXUALS? - MULTIPLE REGRESSION ON FACTORS

A multiple regression on factors drawn from principal component analysis – again with relative proportion of asexuals per haul in the mating complex (square root transformed) as dependent variable ($n = 31$, multiple $r^2 = 0.326$, adjusted $r^2 = 0.278 \pm 0.184$) - was performed. The community component (factor 2) and the molly-size / habitat component (factor 7) remained in the model (Tab. 2.17). This model explains 32.6% of the variance.

Tab. 2.17: Multiple regression (stepwise backward) on factors from PCA.

Effect	Coefficient	Std Error	Std Coeff.	Tolerance	t	p
Constant	0.414	0.036	0.000	.	11.628	0.000
Factor (2)	-0.105	0.036	-0.451	0.999	-2.903	0.007
Factor (7)	-0.078	0.034	-0.363	0.999	-2.337	0.027

Analysis of Variance

Source	SS	DF	MS	F	p
Regression	0.456	2	0.228	6.772	0.004
Residual	0.944	28	0.034		

Case 59 is an outlier (Studentised Residual = 3.107), Durbin-Watson D Statistic 1.352.
First Order Autocorrelation: 0.322.

As presented in Tab. 2.17, the proportion of Amazons within the asexual / sexual mating complex of *P. formosa* is explained best by two factors:

- (1.) Factor 2: fish density, *Poecilia* density, % predators, male/female-ratio).
- (2.) Factor 7: female size, male size and area sampled per haul. The area sampled per haul is a measure of how accessible and thus heterogeneous structured the habitat was.

Discussion

This field study on the spatial and temporal variation of coexistence of the asexual Amazon molly *Poecilia formosa* and the sexual host species *P. latipinna* provides an immense amount of data. It shows how highly variable molly habitats in general are. Additionally, it reveals insight into the status of the unisexual Amazon molly in its community and the dynamic patterns of sexual-aseexual coexistence within the mating complex of *P. formosa*, and suggests biotic and abiotic parameters that may affect the stability of this system.

Community and the success of Amazons

Ranked order of field sites after relative fish density is inverse to species diversity. High densities in habitats go along with low species diversity in contrast to lower densities in habitats with more species present. This order also reflects habitat diversity of the field sites.

Proportion of mollies is greatest when lowest relative densities are sampled. Relatively few mollies are in those samples, which have the maximum species diversity and the maximum relative densities. Samples with more predators contain lower absolute numbers of fish.

MacArthur (1965) and MacArthur & Lewins (1967), studied within-habitat diversity versus between-habitat diversity and found that population density was low due to disturbances that allow resources to remain unlimited and thus, would release competition among coexisting species. Comparing within-habitat variation versus between-habitat variation as well as within and between seasonal variation of the relative density of Amazons, frequencies of *P. formosa* were more variable in those habitats but not at those times that generally hosted relatively more *P. formosa*. This finding supports MacArthur's (1965) competition release hypothesis, assuming that higher variation in relative densities provides heterogeneity preferably at those sites but not at those times with extremely high abundances of Amazons.

Representativeness and validity in comparison to other studies

Community samples seem to be representative. Other studies obtained similar species lists and frequencies (Hubbs 1964; Whiteside & McNatt 1972; Bush et al. 2000; McNeely & Wade 2003). Sampling data from Guadalupe River spring branch (Bush et al. 2000) where the situation is similar to San Marcos River because it belongs to the same river system, show comparable species lists and abundances except for the fact that this study reports fewer Poeciliids and more Centrarchidae (Tab. 2.18). This might be due to the use of a different sampling technique as they conducted electro-fishing sampling (Bush et al. 2000; Moulton et al. 2002).

Tab. 2.18: Data from NAWQA fish samplings at Guadalupe River (N 29.8605°, W 98.3836°) (Bush et al. 2000).

Date / rank	1.	2.	3.	4.
11.7.1996 (n = 224)	<i>Lepomis megalotis</i> (23%)	<i>Cyprinella venusta</i> (17%)	<i>Campostoma anomalum</i> (11%)	
14.10.1997 (n = 34)	<i>Cyprinella venusta</i> (21%)	<i>Mircropterus salmoides</i> (12%)	<i>Gambusia affinis</i> (12%)	
4.08.1998 (n = 194)	<i>Mircropterus treculi</i> (24%)	<i>Lepomis megalotis</i> (22%)	<i>Lepomis cyanellus</i> (15%)	<i>Cyprinella venusta</i> (13%)

In Brownsville, McNeely & Wade (2003) recently carried out a study on fish composition and frequency of Amazons in winter 1998 / 1999. They sampled a total of $n = 1505$ individuals at a field site in the neighbourhood of Lincoln Park (LPK). Mollies comprised 51%, and 3% were individuals from predatory species. Ranked abundances were: *Poecilia latipinna* (43%), *Cyprinodon variegatus* 23,5%), *Menidia beryllina* (14%), *P. formosa* (7.5%), *Gambusia affinis* (7.4%), *Oreochromis aureus* (2%), *Cichlasoma cyanoguttatum* (1%). In general, McNeely & Wade (2003) sampled the same species pattern with smaller proportions of *Gambusia affinis*, and higher proportions of *P. latipinna* and *Cyprinodon variegatus* as I did in my present study in 2001. These minor differences can be easily explained by seasonal variation and disturbances due to highway construction.

However, composition within the mixed mating complex was different. The situation in Brownsville in winter 1998 / 1999 with *P. latipinna* 654 (85.3%) and *P. formosa* 113 (14.7%) (McNeely & Wade 2003) was far less biased towards Amazons than a few months later, when Amazons comprised 70% of adult mollies.

Hubbs (1964) sampled $n = 1030$ *P. formosa* (80.8%) and $n = 244$ *P. latipinna* between February and May 1960 at SFH. Amazons comprised 66 – 80% in subsequent samples of that year.

In the same year, he sampled at another field site in Brownsville (Central Avenue ditch) 1381 *P. formosa* (89.7%) and 150 *P. latipinna*. In general, Hubbs' data (Hubbs 1964) are very similar to the situation encountered almost 40 years later.

Mollies and their natural enemies: the role of predators in the community

Predation seems to be a real threat to the abundance of mollies. The abundance of *Poecilia* decreases with increasing relative densities of predators. The major predatory fish species is *Micropterus salmoides*. According to Paine (1969) this species is a keystone predator. *Micropterus* prefers prey fish of 1/3 of its own body size (Werner & Hall 1988), which fits size of adult mollies sampled in this study.

As in the present study, Hubbs (1964) considered SFH as high predation site, and classified *Micropterus salmoides* as major predator of mollies at this site. *Oreochromis aureus*, the most abundant fish predator in my recent study, had not yet been introduced then.

A special case of species competition for resources is competition for the resource of “predation – free space” (Holt 1977; 1985). Under the threat of predation, in mixed populations, *P. latipinna* and *P. formosa* also have to cope with the risk of predation and might compete for refugia with lower risks of predation. Interestingly, *P. formosa* seems to be less sensitive or more successful in dealing with predators than *P. latipinna*. Proportion of unisexuals increased when more predators were present. It is impossible to disentangle cause and effect without conducting carefully designed experiments. Increased relative abundances of Amazons may possibly be a result of males being less discriminating between the asexual and sexual females they encounter under higher predation risk. In Trinidad guppies, weaker discrimination has been shown for female mate choice behaviour (Breden 1987; Godin & Briggs 1996). This aspect of predation-risk sensitive male mating behaviour and thus predation risk dependent regulation of coexistence in this bisexual – unisexual species complex needs further investigation. If this were true, males originating from low-predation sites as COM and LPK should be more discriminating than males from the high-predation sites SM and SFH. At least in general, this seems not to be the case, since there were no general differences in male mate preferences

among populations (chapter 3, Fig. 3.1). However, this needs to be studied carefully, since predation risk - dependent differences in male behaviour may be obstructed by the remaining ecological context. Additionally, males may react to the perceived predator-free laboratory environment and change their discriminative behaviour. Male mating behaviour may be influenced by differences in frequencies, evolutionary background, experience, presence of other males (Schlupp et al. submitted), season (as I show in chapter 3), or environmental conditions e.g. turbidity (as I show in chapter 4, Heubel & Schlupp submitted).

As discussed in Hubbs (1964), relatively higher proportions of Amazons in mixed populations under higher predation risk could also be due to differential predation on visually more conspicuous males. This could also explain the observed more female biased sex-ratios at high-predation sites suggesting that sex-selective predation risk seems to play an important role in this system. In Trinidad guppies (*Poecilia reticulata*), effects of varying predation risk have been studied intensively. Sex-selective predation affects female-skewed sex ratios (Garcia et al. 1998; Godin & McDonough 2003). Male guppies switch from courtship to forced copulations (Godin 1995; Dill et al. 1999). Sperm competition is higher at low risk sites (Evans & Magurran 1999). Females are more likely to imitate mate preferences of other females (Briggs et al. 1996). Females are less choosy (Breden 1987; Godin & Briggs 1996) or reverse their sexual preference towards duller and less conspicuous males (Gong & Gibson 1996; Gong 1997). Male-male agonistic behaviour is lowered at high predation risk (Kelly 2001).

Properties of habitats and environmental fluctuation

Generally, species diversity decreases under abiotic stress, like toxicity, or extreme temperatures and oxygen concentrations (Krebs 1994). However, in this study diversity seems highest in variable habitats. This can be explained by the intermediate disturbance hypothesis (Connell 1978), which predicts maximum diversity at habitats with a medium degree of disturbance. In this study, for practical reasons, only field sites where conditions promised permanent presence of *Poecilia* were included. Other, definitively more extremely disturbed, ephemeral and unreliably fluctuating habitats are common. And there, lower diversity is expected.

Comal Springs – an exceptional population

Comal Springs is an extremely unusual habitat for mollies. It is a spring with remarkably stable environmental conditions throughout the year. Ranking all six populations, Comal has the highest abundance of *Gambusia*, the highest relative density of fish, most males, the clearest water, the fewest Amazons, the lowest number of predators, the lowest diversity, and the lowest dissolved oxygen concentration, water level amplitude, specific conductance, and temperature, and also the smallest proportion of Amazons in the complex.

Generally, higher relative fish densities correlate with lower abundances of *P. formosa*. This can be an artefact caused by extremely high frequencies of *Gambusia* sp. in the almost *P. formosa*-free population at Comal Springs. Previous studies considered this population as allopatric (Gabor & Ryan 2001; Witte & Ryan 2002) but now Amazons are present on a stable low-frequency level (Heubel pers. obs., Schlupp et al. 2002). The low success of Amazons in this headwater habitat would support the niche segregation hypothesis favouring bisexual species in headwater and unisexuals in downstream habitats (Balsano et al. 1981). But only if frequency of Amazons was also lower at Co 101, which it is not.

In contrast, at the field site San Marcos River at Co 101 has the highest levels of species richness, dissolved oxygen, light intensity, and water current; and the least relative density of fish and Poeciliids sampled.

Highest diversity has been measured at Olmito State Fish Hatchery (SFH), where water temperature is highest, as well as variation in temperature, water level, and number of predators. Poeciliids comprise the smallest proportion within in the fish community. At this site, the ditch dried out completely in August.

In conclusion, environmental fluctuations were highest at SFH. Nevertheless, field conditions are still comparable to that of 40 years ago (Hubbs 1964), when mollies also disappeared eventually after dredging activities in June 1960 and again in September 1961 after heavy rainfall. Within the sexual host species *P. latipinna*, sex ratio was 22.3% in 1960, 20.27% in 1961, and 27.77% in 2001. Gynogens comprised 87% in the present study, which is slightly higher than 50-81% *P. formosa* within the complex reported for 1960-61 (Hubbs 1964).

A closer look: dynamics and patterns within the complex

Proportion of Amazons within the complex varies strongly among sites. Seasonal variation within populations is less important. Nevertheless, there was an overall significant increase of Amazons in the complex during the season. In conclusion, frequency of gynogens in a specific population seems to depend mainly upon local conditions.

Within the sexual-asexual mating complex, Amazons outnumber their sexual host species. More than 50% of all adult mollies sampled were *P. formosa*. On average, at the San Marcos River at Martindale (SM) the highest proportions of gynogens occurred: 90% of all adult *Poecilia* were unisexuals. Sexual *P. latipinna* females comprised < 10%, and sexual host males less than 5% of adult individuals in the complex ($n = 1112$).

LONG-TERM SUCCESS OF AMAZONS

This result does not reflect the average long-term situation at this site. Previous data from 24 visits (between 1993 – 1999) from the same field site using the same sampling method (Schlupp, unpublished data) show that composition within the *P. latipinna* / *P. formosa* complex has changed remarkably. Abundance of Amazons obviously increased (Tab. 2.19). Nevertheless, Amazons used to be more frequent than sexual host females, although the situation was more balanced. Interestingly, the sex ratio within *P. latipinna* remained the same.

Tab. 2.19: Martindale, San Marcos River field data from 1993-1999. (I. Schlupp and co-workers: unpublished data).

SM	<i>P. latipinna</i>	<i>P. formosa</i>	<i>P. latipinna</i>
1993-1999	female		male
percentages	33.7%	55.2%	11.1%
<i>N</i>	471	771	155

Schlupp and co-workers (unpublished data) sampled a total of $n = 1397$ individuals from the mixed complex at San Marcos River at Martindale (SM) (Tab. 2.20). In this long-term data set, sex-ratio within sexually reproducing *P. latipinna* alone was the same as in the present study. But since, the proportion of *P. formosa* within the complex increased drastically. This is due to decrease in relative densities of *P. latipinna* at this field site. Hence, the total sex-ratio of the complex is now heavily biased towards females.

Tab. 2.20: Martindale population ecology data from previous years (1993-1999, $n = 24$ samples)

	sex-ratio (sexuals)	sex-ratio (total)	sex. females/ all females	Temperature air [°C]	Temperature water [°C]
mean	0.31	0.19	0.45	30.1	26.2
sd	0.20	0.19	0.26	3.9	3.0
range	0.04 - 0.80	0.01 - 0.73	0.07 - 0.91		

The observed pattern of high variation within and among sites is comparable with data presented by Balsano et al. (1989) suggesting that random fluctuations between seasons and between microhabitats are so high that any pattern is obscured during a given year.

In South Texas, in mixed populations in the Rio Grande drainages in the Brownsville area, Rasch & Balsano (1989) found that Amazons comprised 17 – 60% of females and report a long-term average of 37% between 1964-1982.

Advantage of asexuals

In mixed populations, unisexuals avoid the cost of males (Maynard Smith 1978) and theoretically produce twice as many female offspring per generation as sexually reproducing females. Case & Taper (1986) discuss that actual reproduction rates of unisexuals can be much less than two-fold. Even with lower fecundity in Amazons (Hubbs 1964), gynogens still maintain a higher population growth rate than *P. latipinna*.

As predicted, Amazons successfully dominated over sexually reproducing *P. latipinna* females in most populations and at most times. The generally rather high proportions of Amazons and the increasing numbers throughout the season support hypotheses of the advantage of asexual reproduction and contradicts hypotheses of the long-term genetic disadvantages of unisexuals *sensu* Muller's ratchet (Muller 1964): Amazons were not less abundant in South Texan populations of old sympatry. This also contradicts proposed ecological disadvantages of asexual reproduction due to slower adaptation (Bell 1982; Maynard Smith 1978; Williams 1975; Crow & Kimura 1965). On the contrary, asexuals were less abundant in habitats (considering only native habitats with old sympatry) with stable conditions than in habitats with high ecological perturbations. This contradicts models that assume the opposite, assuming that asexuals are not able to adapt fast enough to ecological changes.

Life history patterns in the complex

SEASONAL PATTERNS OF REPRODUCTION

Populations in Central Texas had only one clearly dominating cohort of juveniles in summer (session 7 and 8) and a majority of adults throughout the rest of the study period. In South Texas, frequencies of juveniles were fluctuating on a monthly cycle, suggesting several cohorts throughout the season. This pattern is similar to other findings from populations in South Texas by Hubbs (1964), suggesting two to three generations per year. *P. latipinna* has a mean inter-brood interval of 34.8 days (Reznick & Miles 1989b; Reznick & Miles 1989a). This suits the observed alternating higher and lower relative frequencies of juveniles in subsequent sampling visit sessions.

TEMPORAL AND SPATIAL VARIATION OF SEX RATIOS

Live-bearing fishes of the family Poeciliidae are widely known to exhibit female-biased sex-ratios (Geiser 1924; Haskins et al. 1961; Krumholz 1963; Snelson & Wetherington 1980; Snelson 1989). It is well known that differential male mortality leads to female-skewed sex ratios in Poeciliids. Snelson & Wetherington (1980) found no correlation of *P. latipinna* adult sex ratios and a variety of chemical, physical, and biological parameters measured monthly at two sites. They also found no biologically meaningful relationships timewise; and no monthly pattern in variation of sex ratios either within or between sites, and also environmental disturbances had no effect.

Female biased sex ratios are a well-known phenomenon in the system. Hubbs (1964) measured sex ratios (of adult fish) in allopatric *P. latipinna* populations and mixed populations with *P. formosa*. In an allopatric population at Rockport, Texas, he sampled 38.8% males ($n = 4934$) – a situation comparable to data for *P. latipinna* from COM and Co 101. From two mixed populations in Brownsville, he collected 26.37% males ($n = 1839$). This percentage is similar to *P. latipinna* sex ratios we sampled in the same area.

At SFH, males comprised 22.3% ($n = 305$) of sexuals in 1960, 20.3% ($n = 74$) in 1961 (Hubbs 1964), and 27.8% ($n = 18$) forty years later in this study. Apparently, the absolute abundance of *P. latipinna* decreased remarkably and proportion of Amazons remained stable or increased slightly from 50-81% in the 1960ies (Hubbs 1964) to 87% of all adults in the complex sampled at SFH ($n = 138$) in 2001. Hubbs (1964) argued that occasional disturbances like dredging activities evened the sexual-asexual ratio at SFH.

In highly fluctuating dry season pools, males comprised only 13% (Barus et al. 1980), which is similar to many sex-ratios measured in this study – especially in September samples.

There was a tendency of increasingly female-skewed bias in seasonal progress. At least for the total sex ratio, this could be a consequence of the increase of the relative proportion of Amazons. But also the sex ratio within the bisexual species alone decreased slightly, which might be due to males dying earlier throughout the season.

Another explanation for female biased sex-ratios in Poeciliids is delayed maturation of juvenile males in response to social competition (Krumholz 1963; Borowsky 1973; Sohn 1977). This has been shown to be a factor producing female-biased sex ratios in *Poecilia gillii* and other species (Chapman et al. 1991). However, in *P. latipinna*, social interactions between males do not influence size or age at maturity (Farr & Travis 1989). In addition, our data do not indicate that

this is the case at the sampled field sites. Larger (from COM and SM) and smaller males (LPK, WES) come from populations that do not appear to differ generally in male densities, predation risk, and competition.

Unfortunately, I was unable to discriminate sexual and asexual juveniles and measure primary sex ratio using field methods. But see Snelson & Wetherington (1980) and references herein for data suggesting 1:1 sex-ratio at birth and differential male mortality in males.

VARIATION OF BODY SIZE IN MIXED POPULATIONS WITH P. FORMOSA

Variation in male size

Variation in **male size** was higher between than within habitats. This is different from other findings by Trexler (1989a;b). He found that temporal variation in male body size in *P. latipinna* was marginal and that 20% of male size variation could be explained by differences among local populations. He found no North - South cline in size variation. He suggested a differential survival of size genotypes in nature due to size selective predation (e.g. Trexler et al. 1994).

However, in my study, field sites with larger *versus* smaller males differ in biogeographic origin (Brown 1953). The different biogeographic origin and thus genetic background seems to have an impact on male sizes. But these differences could also be an effect of underlying differences of the environment. Parameters as temperature, specific conductance, chlorophyll concentration, dissolved oxygen, and turbidity differed widely among populations and could also be responsible for differences in male body size. Interestingly, the multiple regression on factors showed that body sizes of either sex of the sexual host species explained variance in relative proportion of Amazons in a negative relationship. However, it is impossible to draw conclusions on what specific parameter might cause this effect.

Sizes of asexual and sexual females

Body length of sexually reproducing *P. latipinna* females and gynogenetic *P. formosa* differed more among population and over time than generally between species. But Amazons are larger in some populations and also in certain sampling sessions within populations. We might expect character displacement in closely related coexisting and competing species (Brown & Wilson 1956; Fenchel 1975; Fenchel & Kofoed 1976; Connell 1980; Arthur 1982) (but see Cherill 1988). At least for body size, character displacement seems not to play a role. Otherwise, females from young sympatry in Central Texas were expected to differ less than those from old sympatry in South Texas. Since Amazons are sperm-dependent sexual-parasites, there may exist a local adaptation to their particular host population. This might be the case, since there was a trend that females originating from populations in young sympatry differed more than those from old sympatry. This result could also be due to general environmental or genetic differences among populations (Möller 2001). While in Central Texas introduced *P. formosa* originated from Brownsville (Brown pers. comm. in Hubbs (1964)), *P. latipinna* was introduced from Louisiana (Brown 1953). *P. formosa* is larger in Central Texas (mean 45.7 mm SL) than in its original area (mean 37.5). *P. latipinna* females in Central Texas (mean 37.3) are also significantly larger than in South Texas (mean 36.1), but they seem to have the same size in

Central Texas as in its original area in Louisiana (37.5 mm SL). Mean female sizes from *P. latipinna* from Louisiana were kindly provided by Dr. Robert Cashner, New Orleans.

Morphological niche breadth and character displacement between biotypes needs to be studied in more detail (compare Schlosser et al. 1998).

A temporal niche? The success of *P. formosa*

At the end of the season, **Amazons were larger and more abundant** than their sexual congeners, and **sex ratio** was even stronger biased towards females (Fig. 2.22). Therefore, *P. formosa* is probably more successful obtaining matings at the end of the season. Males generally have a sexual preference for larger females (Ptacek & Travis 1997; Schlupp & Ryan 1997; Gabor 1999). This preference might represent a conflicting difference to the general underlying preference for conspecific females (Schlupp et al. 1991; Ryan et al. 1996; Schlupp & Ryan 1997; Gabor & Ryan 2001; Niemeitz et al. 2002), but see chapter 3 and 4 (Heubel & Schlupp submitted) for discussion. The aspect of seasonally influenced mating preferences in males has been studied in chapter 3.

But size does not necessarily reflect fitness of females. Large old Amazons dominating at the end of the season might be senescent and thus without functioning gonads (Reznick & Miles 1989b).

On average, Amazons measured in populations at the end of the season were considerably larger. On average, sexual females were smaller. This pattern could be caused by the fact that sexual female populations most likely consisted mainly of (small) recruits from the spring. This phenomenon could be explained with Amazons postponing their reproduction relative to sexual females. But this hypothesis based on female sizes should be handled carefully since there is no clear relationship between size and age in Poeciliids (Snelson 1989; Morris 1990) although many other authors routinely draw conclusions on age from body size (e.g. Dugatkin 1992; Dugatkin & Godin 1993). Size distributions among sexual and asexual females in late summer after the major breeding season suggest that Amazons have had less offspring during the spring than sexual females. This might be a sign of lowered fitness of asexually reproducing females and thus supports hypotheses of long-term disadvantages of asexual reproduction in this system.

Hubbs (1964) provides support to the hypothesis on different reproductive seasons in *P. latipinna* and *P. formosa*. Data on reproductive status and brood size from sexual and asexual females at different times of the year showed that Amazons were pregnant later than sexual females and suggested that males mated with Amazons mainly when sexual females were already pregnant. He also showed that sexual females were more fertile as there existed higher percentages of ovulated females with embryos (Hubbs 1964).

Parker (1979) pointed out that phenotypic responses to fluctuating environmental conditions might be fundamentally different for sexual versus clonal genotypes.

As discussed with similar results on niche relationships in the sexual-asexual complex of *Phoxinus eos-neogaeus* (Schlosser et al. 1998), environment-genotype interactions can produce significant effects on growth rate under different laboratory conditions of diet and temperature (Schultz & Fielding 1989; Wetherington et al. 1989a; Wetherington et al. 1989b).

Population ecology in the complex: Integrating biotic and abiotic parameters to explain spatial and seasonal variation of the habitat

Oxygen level was normal to high compared to other habitats of Poeciliids that are able to cope with hypoxic conditions. Vrijenhoek & Pfeiler (1997) observed stress reactions - surface skimming with aquatic surface respiration (ASR) (Kramer & Mehegan 1981) - when dissolved oxygen concentration was below 2 mg/l, and individuals died at 1.2 mg/l.

This situation applies also to mollies. I observed ASR behaviour at the Weslaco field site. In September 2002, 22 allopatric sexual or sympatric sexual-asexual populations with either *P. latipinna* or *P. mexicana* as sexual host species (see appendix Tab. 8.7) were sampled and dissolved oxygen concentrations were measured. Dissolved oxygen ranged from 1.08 mg/l to 11.65 mg/l. Dramatically low concentrations were measured at a hot sulphur spring (Banos de San Ignacio, Linares, Nuevo Leon, Mexico) and the (also sulphurous) cave area at the Cueva del Azufre (PS XIII, PSX, PS0, Tapijulapa, Tabasco, Mexico (Parzefall 2001)). In both areas, mollies were present (K. Heubel, M. Plath & I. Schlupp unpublished data, see appendix).

McKinsey & Chapman (1998) measured only 0.2 – 1.81 mg / l along a spring gradient with low seasonal variation at Singing Springs, Florida. The description of the field site resembles that of Comal Springs, Texas. Oversaturated dissolved oxygen levels as they occurred several times throughout the study are common in shallow water or close to surface. In summer, saturation often reaches 150% (Lampert & Sommer 1993). Extremely high oxygen concentrations at WES in June must be explained by locally and short-term elevated concentrations. However, at night, when plants dissimilate, oxygen concentrations may drop drastically.

High turbidity levels and their variation has been literally overlooked so far in their ecological relevance in the context of coexistence and population ecology, with few exceptions (Seehausen et al. 1997; Franck et al. 2001; Heubel & Schlupp submitted), (see chapter 4 and references therein). Nevertheless, the role of turbidity in aquatic habitats has been studied in predator-prey interactions and in applied aquacultural aspects (see chapter 4 and references therein).

Which parameters explain frequency of Amazons?

Relative proportions of Amazons within the sexual-asexual mating complex correlate positively with species richness and relative densities of predators; and negatively with fish densities at the site.

More turbid water, higher water temperature, lower concentrations of chlorophyll and thus lower primary production, and lower relative fish densities explain proportion of *P. formosa* in a multiple regression model.

The general underlying variation among field sites and sampling sessions could be broken down to seven components that contribute equally to the overall variation. These components are physical and ecological properties of the habitat, fish community, seasonal influence, habitat quality, light environment, male mollies and pH, and molly sizes and habitat structure. Of these factors, “fish community” and “molly sizes / habitat structure” combined explain most variation in abundance of *P. formosa* within the complex.

Interestingly, the factor explaining most variance of the data, which is that of “physical properties of the habitat” (e.g. chlorophyll concentration, specific conductance, turbidity, and pH), does not contribute to the variation of the proportion of Amazons. However, this factor consists of several parameters that explain variation of *P. formosa* in the multiple regression model. It is more conservative to draw conclusions from the multiple regression model on variables than from that of factors, since the first is more robust and explains 65.6% of variance. Whereas principal component analysis (PCA) did not reveal any factors that contribute more than average to the general variation and multiple regression on factors explains overall variation insufficiently (32.6%).

Apparently, the multiple regression suggesting **water temperature, turbidity, chlorophyll, fish density** on the one hand, and PCA favouring **fish community and sexual host species population parameters** as predictors on the other hand, seem contradicting – but: both can be true and thus both should be taken seriously.

The multiple regression analysis approaches the major question of what explains frequency of Amazons in general by integrating all measured variables. The PCA with a multiple regression on factors reveals components responsible for the underlying general spatial and temporal variation among and within habitats – and asks then, which out of these factors, explains frequency of Amazons. Both approaches are important and not interchangeable. The PCA rather shows general patterns, and evaluates relative importance of factors.

Although abiotic parameters derived from a multiple regression model explained abundance of Amazons better, much of this variation might be due to general underlying variation in habitats (e.g. COM had low abundance of Amazons, clear water). One should also consider the fact that e.g. turbidity and chlorophyll concentration have also excellent loadings of standardised factor scores in factor 1. This factor explained most of the general variance among samples in the PCA.

In contrast, a multiple regression on factors derived from a PCA, controls for that and suggests that within varying molly habitats, rather habitat structure as well as biotic and social components (predation risk, sex ratio, fish densities, size of mature *P. latipinna*) may explain abundance of Amazons. This model does not imply any causes or effects: it is not known whether high frequencies of Amazons are responsible for a skewed sex ratio within its host species, or are favoured by it.

In **conclusion**, the relative abundance of Amazons mainly depends on the typical properties of the habitat and its temporal heterogeneity. Abiotic variables (e.g. temperature, turbidity, chlorophyll concentration, specific conductance, pH) that might explain abundance of Amazons, simultaneously explain general temporal and spatial variation. Therefore, these parameters most likely explain the general ecological situation mollies have to cope with. Hence, this might explain long-term perspectives for *P. formosa* to persist ecologically in a habitat. Life history traits of the sexual host species and spatial heterogeneity of the habitat are more likely to affect the success of *P. formosa* within its mating complex.

Evolutionary stability caused by ecological instability?

How can bisexuals and unisexuals coexist in mixed populations? An important factor are **environmental fluctuations**. Occasional occurring serious flooding events and droughts wipe out populations locally – without discriminating between sexuals and asexuals. For example, at the State Fish Hatchery at Olmito (SFH) high frequencies of *P. formosa* were present in November 2000 and no mollies present from February until late spring when recolonisation of sexuals and asexuals began. Flooding events allow migration of individuals among locally scattered habitats. Local extinctions and recolonisation after ecological disturbances contribute to the long-term stable ecological coexistence of host and sexual-parasite. Locally occurring absolute high proportions of Amazons – up to all-gynogenetic populations – alternate with low-density recolonisation phases of sexual host species and *P. formosa* that follow ecological disturbances during which all mollies present disappeared. An interesting exception is the population at Comal Springs (COM). Here, environmental conditions are stable, the water is clear and the proportion of Amazons is exceptionally low. There are two possible explanations:

1.) Until very recently (probably as late as 1999), this population was allopatric and Amazons just began to invade the population (Schlupp et al. 2002). Coexistence in Central Texas has been maintained for approximately roughly 100 –150 generations (Brown 1953; Drewry et al. 1958; Hubbs 1964), but sympatry at Comal Spring might have been established just ten generations ago. Therefore, rapid increase in proportion of Amazons is expected to occur within the next generations. Such an invasion could only be restricted by physical properties (temperature, pH, CO₂, or too stable conditions) of this spring habitat *sensu* niche segregation reported by Balsano et al. (1981).

2.) Water clarity allows sexual males to discriminate effectively between sexual females and Amazons, maintaining stable low proportions of unisexual females. This hypothesis has been tested in chapter 4 (Heubel & Schlupp submitted) where predicted preferences have not been found.

Southwood (1977) classified **habitats** with regard to properties in time and space. Time-wise, habitats could be constant, predictably variable, unpredictable, ephemeral, or spatial. He categorised habitats as continuous, mosaic, or isolated. Comal Springs (COM) belongs to the group of constant and continuous habitats. All others should be rather categorised as more or less unpredictable mosaics. In nature, many molly habitats are ephemeral mosaics – “weedy habitats” *sensu* Wright & Lowe (1968) but such were not included in this study for practical reasons.

The stabilising effect of heterogeneity (Hutchinson 1961) can also be caused by disturbances. The **mosaic cycle concept** (Pickett & White 1985; Yodzis 1986) is based on disturbances as regulating mechanisms in open systems. Molly habitats are open patchy environments. Hence, the observed disturbances due to flooding events or droughts, may explain coexistence in this system of Amazons and its sexual host as a mosaic cycle. Thus, phenotypic plasticity and all-purpose genotypes are prerequisites for a long-term success of the Amazon molly.

The stabilising effect of temporal heterogeneity (Hutchinson 1961) and the above mentioned mosaic cycle concept of regulation of coexistence via instability caused by disturbances in a patchy open environment perfectly suit the situation of molly populations. Bisexual and unisexual species of this complex eventually disappear locally. After the habitat re-establishes

(after flooding, heavy rainfall, cold snaps in winter, droughts, human disturbances), both types of mollies reinvade the habitat. As long as perturbations occur often enough, coexistence of bisexual and unisexual species in this mating complex of *P. formosa* can be maintained.

Chapter 3: Males are choosy when it matters

Flexible male mating preferences in *P. latipinna* within the asexual / sexual mating complex of *P. formosa*

Abstract

In mixed populations of *P. latipinna* and *P. formosa*, males encounter two types of potential mates: conspecific sexual females and gynogenetic sexual-parasitic Amazon mollies. The latter is an all-female species that produces clonal offspring via gynogenesis. Gynogenetic species need sperm from sexual host males, in this case *P. latipinna* to trigger embryogenesis. But the male genes do not enter the genome. Because *P. latipinna* males do not benefit from matings with *P. formosa* they should avoid mating with them. Mate choice might become crucial in this context, especially when asexuals become abundant in mixed shoals or seasonally influenced at times of enhanced female fecundity.

The major question in this study was to test frequency dependent or seasonally influenced behavioural plasticity in male mating preferences in natural mixed *P. formosa* / *P. latipinna* populations that may contribute to the maintenance of stability in this asexual / sexual mating complex.

I studied male mate preferences in *P. latipinna* originating from several populations in South and Central Texas. Association time of males with syntopic adult females of *P. latipinna* or *P. formosa* was measured in a standard visual simultaneous dual choice set-up.

There was no general preference for conspecific sexual females in any population. Within populations, there was a high seasonal variation in male association patterns. There was no difference among mixed populations with different relative densities of Amazons. Male mating preferences were seasonally influenced. Males spend less time with asexual *P. formosa* during spring. Male body size and relative proportion of Amazons in the habitats males originated from did not influence male preferences. I discuss how plasticity in male mate choice preferences might contribute to the maintenance of the stability in this asexual / sexual mating complex. I also discuss potential causes of the lack of a sexual preference for conspecific females and whether non-discriminating male mating behaviour can be adaptive in this complex.

Introduction

Male mate choice and sexual preferences have been far less intensively studied than female mate choice. Nevertheless, male mating decisions become worth studying in most systems as soon as male parental investment increases or differences in female quality occur, leading to situations with choosy males (Kraak & Bakker 1998; Berglund & Rosenqvist 2001).

One system in which male mate choice behaviour becomes crucial and especially interesting to study, is in the context of the stability and maintenance of the asexual / sexual mating complex of the Amazon molly *P. formosa* (Ryan et al. 1996; Marler et al. 1997; Marler & Ryan 1997; Körner et al. 1999; Landmann et al. 1999; Schlupp et al. 1999; Gabor & Ryan 2001).

The asexual Amazon molly *P. formosa* is an ovoviviparous all-female fish of the live-bearing family Poeciliidae (Hubbs & Hubbs 1932). It ameiotically produces offspring via gynogenesis, a special form of parthenogenesis. Asexually reproducing females rely on sperm of males from other closely related host species as a physiological stimulus to trigger embryogenesis. Sperm is normally not incorporated into the genome of the offspring (Schlupp et al. 1998). Therefore, Amazon mollies can be considered as a sexual-parasite of their sexual hosts with which they co-occur in mixed populations. In South and Central Texas, Sailfin mollies *P. latipinna* serves as natural host species (Hubbs & Hubbs 1932; Darnell & Abramoff 1968; Schlupp et al. 1998; Schlupp et al. 2002). The Amazon molly is derived from a single hybridisation event of a *P. mexicana* female and a *P. latipinna* - like male ancestor (Turner 1982; Avise et al. 1991; Schartl et al. 1995; Möller 2001).

Males should be choosy in this asexual / sexual mating complex of *P. formosa* for several reasons. In *P. latipinna*, male courtship behaviour is elaborate (Parzefall 1969; Travis & Woodward 1989). Courtship makes males more conspicuous to potential predators leading to risk-sensitive alternative mating strategies (Endler 1987; Godin 1995; Evans & Magurran 1999; Evans et al. 2003; Godin & McDonough 2003). Heavily female-biased sex-ratios are a common phenomenon in these populations (Hubbs 1964; Snelson & Wetherington 1980; Balsano et al. 1985) (chapter 2). Skewed sex-ratios are discussed as a result of differential predation risk due to courtship behaviour (Evans et al. 2003; Godin & McDonough 2003). Courting and mating with *P. formosa* has no immediate fitness benefits because there is no male genetic contribution to offspring of Amazons. Thus mating with Amazons might incur a cost of enhanced risk of predation without benefit of genetic contribution to offspring. Additionally, while interacting and mating with Amazons, males might miss opportunities to mate with conspecifics. Another cost of indiscriminately mating with both types of females depends on sperm availability. In Poeciliids, sperm is not an unlimited resource (Monaco et al. 1981; Pilastro & Bisazza 1999). Sperm depletion can be a problem for males in mixed asexual / sexual shoals of *P. formosa* and its sexual host species. Hubbs (1964) showed that Amazons in South Texas were often partially pregnant and carried many unfertilised eggs in broods. He discussed that apparently skewed sex-ratio and patterns of male mate selection led to unfertilised Amazons. An identical situation was found in another complex of bisexual – unisexual species of *Poeciliopsis* (Poeciliidae) (McKay 1971; Moore & McKay 1971).

As predicted, several studies found that sexual males have a strong preference for conspecific females (Hubbs 1964; Woodhead & Armstrong 1985; Schlupp et al. 1991; Ryan et al. 1996; Schlupp & Ryan 1997; Gabor & Ryan 2001; Niemeitz et al. 2002).

Although these studies suggest a general existing pattern of male preferences for conspecific females, it is interesting to consider carefully under which circumstances males actually had preferences for conspecific females. Studies carried out by Hubbs (1964) and Woodhead & Armstrong (1985) were based on a very small sample size. Ryan et al. (1996) only included those data into the analysis of male mating preferences, where males were highly motivated to copulate with females. Woodhead & Armstrong (1985) and Schlupp et al. (1991) presented contradicting results, depending on the method used, size, and experience of males. Schlupp & Ryan (1997) showed that the male's initial preference for conspecific females could be altered by the presence of another male (due to male mate-copying behaviour). Gabor & Ryan (2001) showed male mating preferences for conspecific females only in sympatric populations with *P. formosa*.

Most studies had been carried out with either laboratory populations or natural populations that had been kept in tanks for at least several months before testing, during which males were not exposed to *P. formosa*. In general, studies did not report at what time of the year experiments had been carried out.

Some other studies present and discuss controversial results (Balsano et al. 1981; Balsano et al. 1985; Woodhead & Armstrong 1985; Balsano et al. 1989; Schlupp et al. 1991; Heubel & Schlupp submitted; Schlupp et al. submitted) (see chapter 4). Mate discrimination may change with male size, age, or experience (Woodhead & Armstrong 1985). In a laboratory population, males showed preferences in visual preference tests, but not when full body interaction was allowed (Schlupp 1991). As I present in chapter 4, wild-caught males did not prefer conspecific females in sequential visual preference tests (Heubel & Schlupp submitted). Wild-caught males (tested within five days after collection) from a population with extremely low frequencies of Amazons (COM, see chapter 2) did not prefer conspecific females in simultaneous visual tests. This study showed, that male preferences could be altered by the presence of another male as audience.

Therefore, it seems interesting to review above-mentioned studies presenting positive results with the objective to find circumstances under which males actually had preferences for conspecific females. Independent from the method used, as well in visual preference tests as in full-contact mate choice tests, negative and positive results had been reported.

In the mixed Amazon complex with *P. mexicana* as sexual host species in Mexico, no preference for conspecific females was found (Balsano et al. 1981; Balsano et al. 1985; Balsano et al. 1989). Those authors were the first that discussed a possible behavioural plasticity of male mating preferences depending on female receptive status. They state that asynchronous receptivity in females led to seasonal variation in male mating preferences.

These apparently contradicting results lead to the question whether males should always discriminate between conspecific sexual and heterospecific asexual females. Schlupp et al (1994) discovered heterospecific mate-copying in this mating complex. Mating with Amazons is potentially adaptive since this behaviour increases a male's attractiveness to conspecific females that observe those heterospecific matings, leading to increased potential future fitness. The role of mate copying in this complex is studied in chapter 5 (Heubel et al. submitted). Female mate-copying behaviour might counterbalance male association preferences. Male copulation attempts and courtship behaviour patterns signal a male's property and ability to mate (Heubel et al. submitted). I hereby disagree with (Farr 1989) who stated "gonopodial thrusting cannot be considered a form of display".

In mixed shoals, Sailfin molly males regularly encounter two types of females as potential mates: conspecific sexually reproducing *P. latipinna*, or asexual gynogenetic Amazon mollies. It is still unanswered how asexual - sexual coexistence can be maintained in this mating complex. Analytical models suggest some form of density or frequency dependent mating success as a requirement for stable coexistence between a sperm-dependent parasite and its sexual host (Moore 1976; Stenseth et al. 1985).

This study deals with differences among male sexual preferences to associate with both types of females among populations and in the course of the season. Maintenance of asexual / sexual coexistence might be size or dominance status dependent due to social competition among

males (McKay 1971; Moore & McKay 1971), or seasonally influenced by an asynchronous initiation of reproductive activity (Monaco et al. 1978).

The behavioural regulating hypothesis was expressed to explain stability of the hybridogenetic asexual / sexual complexes in *Poeciliopsis* (McKay 1971; Moore & McKay 1971). The authors state that males generally have a mating preference for conspecific females, but males are socially structured in dominance hierarchies, with subordinate males mating predominantly with *P. formosa*. During heightened sexual activity, subordinate males become indiscriminate and mate with asexuals. Such matings would be inversely proportional to the frequency of sexual females. In addition, mate preferences are, in part, a learned behaviour and immature males may err during learning (Balsano et al. 1989).

Also in bisexual species of the mating complex of the gynogenetic unisexual Amazon molly, dominance hierarchies exist among males of *P. latipinna* (Baird 1968) and *P. mexicana* (Parzefall 1969; Balsano et al. 1985), but in both species, dominance hierarchies among males do not restrict access to females.

Male mating behaviour might be highly affected by body size. Small subordinate males might be more likely to rely on alternative mating strategies such as coercion and sexual harassment (Schlupp et al. 2001; Plath et al. 2003) and thus males frequently mate with any female present non-discriminatively and thereby enhancing its attractiveness via mate-copying.

Assuming frequency dependent behavioural plasticity in this mating complex, one would expect differences among populations and seasonal patterns of male sexual preferences. In allopatric populations or mixed populations of very young sympatry (<150 generations) and low frequency of Amazons in Central Texas (chapter 2) males should be less discriminating than in populations where sexual host species and Amazons have been coexisting for more than 100.000 generations in South Texas (Avisé et al. 1991; Schartl et al. 1995; Möller 2001). Such reproductive character displacement has been shown in allopatric versus sympatric populations (Gabor & Ryan 2001). Males from allopatric populations and from young sympatry with *P. formosa* are naïve and thus not discriminating whereas males originating from old sympatry discriminate between sexual and asexual females.

Seasonal patterns of male's association preferences should reflect variable pay-off matrices of costs and benefits of male preferences for conspecific females at different times of the year. I expected a seasonal pattern with males mating predominantly with conspecific females prior to peak reproductive periods, a few weeks before number of juveniles peak in spring (see chapter 2) and less discriminative preferences for any type of female at other times of the year when reproduction ceases (e.g. in autumn). Thus, male mating preferences contribute to stability of this asexual / sexual mating complex.

I tested the hypothesis that male mating behaviour contributes to the stability of this mating complex. I expect a seasonal pattern of mate choice discrimination with more discriminating males that exhibit preferences for sexual females during mating season (before juvenile number increases in spring), and less discriminating males at times when reproduction slows down – early and late during the year. Male size might affect the extent of preference.

I also hypothesised frequency (and density) dependent male mate choice behaviour with males discriminating more when the probability to encounter the wrong type of female and to mate with Amazons is high.

Materials and Methods:

Male *P. latipinna* were tested with live conspecific and heterospecific females in a simultaneous visual preference test. Male association time with female stimuli was measured.

TEST SETUP

A standard preference testing setup for simultaneous dual choice visual preference tests had been used.

The test tank (120 x 30 x 52 cm) was identical to that in chapter 4 and 5 (Heubel et al. submitted; Heubel & Schlupp submitted). The test tank was divided into five equal zones. The two outer compartments were separated from the three inner remaining sections by clear Plexiglas dividers. The three inner zones were virtually divided by vertically drawn pen markings at the front side of the tank. The central compartment was defined as neutral zone. The test male was able to move freely among the three inner sections.

Illumination was provided by two fluorescent 40W tubes, which emit visible light plus UV. The short ends and the rear long ends of the tank were covered with grey Teflon release sheet that reflects light of all wavelengths equally (K. Lunau pers. comm.). All dividers and the cylinder (10 x 10 cm) for acclimatisation were made of UV translucent Plexiglas. The dividers were fit tightly to reduce flow of water and chemical cues between the compartments. Water level and temperature in the test tank were stable during the experiment.

Measurement of standard length (snout to caudal peduncle) was taken from females prior to testing to match size of stimuli, and from males after testing to avoid any stressful handling of focus animals. To avoid inadvertent use of immature males instead of females as stimuli, only adult females with a body size of standard length (SL) > 28 mm were used.

Preference tests were initiated by introducing a test male into a clear cylinder in the centre of the neutral zone. A conspecific sexual *P. latipinna* female and the sexual-parasite *P. formosa* matching in sizes were selected (mean size difference 0.2 ± 1.4 mm SD). Both originated from the same population. These stimuli were introduced into randomly assigned outer stimulus compartments. After five minutes acclimatisation, the cylinder was gently raised and the time the male spent in each of the three sections was recorded for five minutes. Then the positions of the stimulus females were swapped and the experiment was repeated to detect a potential side bias.

FISH

Fish were collected a few days prior to testing at selected field sites in Texas, USA in the wild between February and September 2001 and again, September and October 2002 (chapter 2). Fish originated from six mixed *P. latipinna* and *P. formosa* populations that have been regularly sampled in South and Central Texas (Tab. 2.1 (chapter 2)). The populations were Comal Springs (COM), San Marcos River at Co101 (Co101), and San Marcos River at Martindale (SM) in the Guadalupe Rives Basin in Central Texas, and Weslaco North Floodway (WES), Lincoln Park Brownsville (LPK), and State Fish Hatchery at Olmito (SFH) in the Nueces-Rio Grande River Basin in South Texas. A detailed description of field sites, population ecology and sampling procedure are given in chapter 2. From each sampled population, approximately every 25 days, 20 randomly selected adult males, females and asexuals each (or as many as caught) were brought into the laboratory and maintained at UT Austin, Section of Integrative Biology.

In the laboratory, all fish were maintained in 20-200 l tanks at 25-26° C on a 12/12 h illumination cycle. All fishes were fed daily with commercially available flake food. All fish were released into large outdoor breeding tanks at Brackenridge Field Laboratory of the University of Texas at Austin after completing the experiments.

Individuals were allowed to acclimate to laboratory conditions. I separated species and sexes for five days before testing. Test males and stimulus females originated from the same population, whenever possible. Males from Comal Spring (COM, chapter 2) were tested with adult female pairs of Sailfin and Amazon mollies originating from San Marcos River (SM and Co101, chapter 2) since Comal Springs is a population with very low relative densities of *P. formosa* (Tab. 2.4, chapter 2).

Tab. 3.1: Relative abundance of asexuals in mixed populations tested males originated from, and standard length of individuals used in the experiment (mean \pm SE).

Population	Comal	San Marcos	Lincoln	Weslaco
Relative proportion of <i>P. formosa</i> in complex	0.02 \pm 0.001	0.78 \pm 0.05	0.11 \pm 0.02	0.48 \pm 0.04
Size <i>P. formosa</i> mean \pm SE [mm SL]	40.9 \pm 0.8	40.8 \pm 2.6	37.4 \pm 1.3	39.4 \pm 1.2
Size <i>P. latipinna</i> male mean \pm SE [mm SL]	31.2 \pm 0.8	28.6 \pm 1.8	32.2 \pm 2.0	29.7 \pm 0.9
Size <i>P. latipinna</i> female mean \pm SE [mm SL]	40.6 \pm 0.7	40.4 \pm 2.8	36.91 \pm 1.2	39.4 \pm 1.1

STATISTICAL ANALYSIS

The time spent with female stimuli in the two test parts combined (before and after swapping sides to control for side bias) was analysed. To compare male preferences among populations and sessions, the relative time males spent with *P. formosa* was calculated as proportion of time male spent in the compartment adjacent to the asexual female and response time males spent with either female. It was a priori defined that a side bias occurred when a male spent more than 80% of its time on the same side of the tank after swapping stimuli. Those trials were excluded from further analysis.

As a measure of male general responsiveness to the stimuli, the response index was calculated as relative time males spent outside the neutral zone. Trials with males spending most of their time in the neutral zone in the centre of the aquarium showing no response to any stimulus were excluded from further analysis (Schlüter et al. 1998).

Data were analysed using Systat 10 (SPSS inc. 2000). All *p*-values are 2-tailed. For planned pairwise comparisons, non-parametric tests were used. When testing parametrically, relative time spent associated with stimulus was arcsine-transformed (Tabachnick & Fidell 2001). In a generalised linear model (GLM), population origin and sampling visit session were tested as factors and male size as covariate. Graphical evaluation of probability plots revealed no severe divergence from normal distribution, thus I relied on robustness of GLM (Quinn & Keough 2002).

Results

A total of 337 simultaneous visual choice tests have been conducted (158 COM, 114 WES, 33 LPK, 14 SM, 16 Co101, 2 SFH). 26 were excluded due to insufficient reaction index ($RI < 0.5$), 165 trials were side biased and therefore excluded from further analysis. The two trials with fish originating from SFH were excluded due to insufficient data basis. Both populations from San Marcos River (SM Martindale and SM Co101) were pooled as San Marcos (SM). Therefore, a total of 144 trials remained in the data set for further analysis.

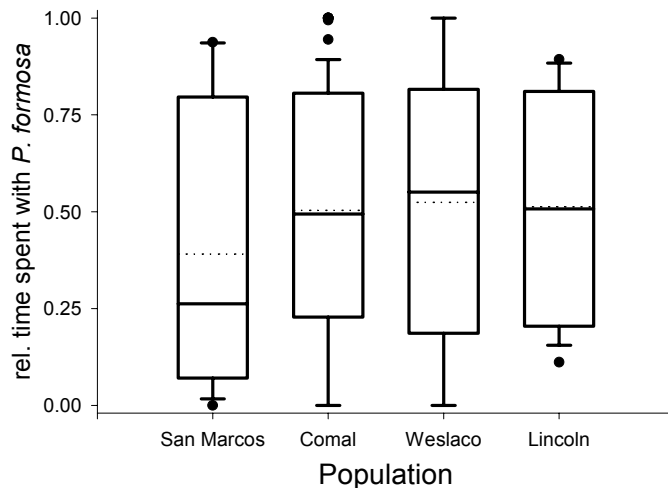


Fig. 3.1: relative association time males from different populations spent with *P. formosa* in simultaneous preference tests. (San Marcos $n = 11$, Comal $n = 79$, Weslaco $n = 43$, Lincoln $n = 11$). Kruskal Wallis Anova on ranks: $DF = 3$, $H = 1.045$, $p = 0.7904$.

In most sessions and populations, males did not show a clear preference to associate with conspecific females (Fig. 3.1). In general, males did not show a preference for conspecific females in any population (Tab. 3.2).

Tab. 3.2: Association time of *P. latipinna* males with *P. formosa* in simultaneous visual preference tests. Wilcoxon test statistics are presented.

Population	Mean [s]	\pm SE	CV	n	Median [s]	IQR	z	p
Total	261	15.1	0.7	146	243	318.0		
COM	263	19.5	0.66	79	245	290.75	-0.08	0.94
LPK	225	36.4	0.54	11	229	223.0	-0.18	0.86
SFH	297			2	296.5	593.0		
SM	219	63.0	0.95	11	147	395.0	-1.07	0.29
WES	276	30.6	0.73	43	255	352.5	-0.46	0.65

SE = Standard Error, CV = coefficient of variation, IQR = inter-quartile range.

Comparing males' behaviour at different times of the season, males showed a tendency to spend more time with conspecific females in April 2001 (Wilcoxon Test, $n = 12$, $z = -1.65$, $p = 0.084$) and a significant preference for conspecific females in May 2001 (Wilcoxon Test, $n = 8$, $z = -2.100$, $p = 0.036$) (Fig. 3.2). Males originating from Weslaco again preferred to associate with sexual *P. latipinna* females in July 2001 (Sign Test, $n=5$, $p < 0.04$), whereas males from Comal Springs significantly preferred asexual *P. formosa* in March 2001 (Wilcoxon Test: $n = 6$, $z = -1.992$, $p = 0.046$) (Fig. 3.2).

There was no difference among populations (COM, LPK, SM, WES) in relative association time males spent with *P. formosa* (Kruskal-Wallis ANOVA on ranks: $DF = 3$, $H = 1.045$, $p = 0.7904$) (Fig. 3.1).

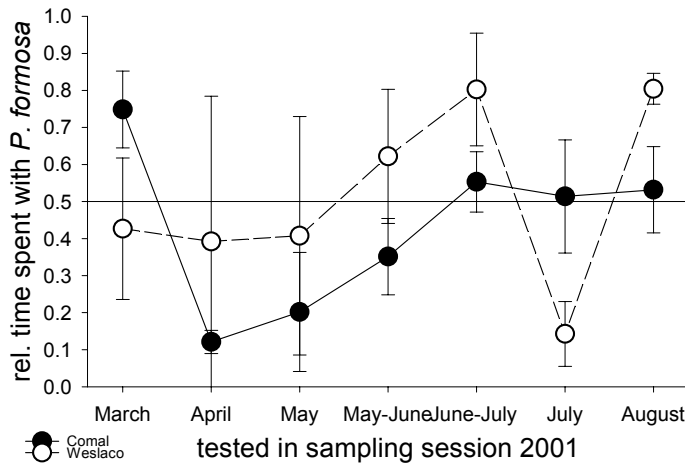


Fig. 3.2: relative association time (mean \pm SE) males originating from Comal Springs ($n = 52$, black circles) or Weslaco ($n = 28$, open circles) from different seasonal samples spent with *P. formosa* in simultaneous preference tests. There was a significant seasonal effect ($F_{6, 65} = 2.696$; $p = 0.021$, see also Tab. 3.3).

Tab. 3.3: In a generalised linear model (GLM) using relative association time as response variable, population origin and sampling visit session were tested as factors and male size as covariate.

Source	SS	DF	MS	F	p
Session	1.815	6	0.303	2.696	0.021
Population	0.058	1	0.058	0.516	0.475
Session*Population	1.155	6	0.192	1.715	0.132
Male size	0.214	1	0.214	1.903	0.173
Error	7.295	65	0.112		

There was no relationship of male body size and mating preference (Spearman rank correlation: $z = -0.211$, $p = 0.833$, $r = -0.018$, $n = 144$). Larger males did not tend to spend more time with conspecific females than smaller males.

There was no relationship between relative proportions of Amazons in the asexual / sexual complex and male association time with Amazons in experiments (Spearman rank correlation: $z = 1.108$, $p = 0.268$, $n = 130$). Males did not discriminate stronger between asexual heterospecific and sexual conspecific females when Amazons were more abundant within the asexual / sexual mating complex.

At two mixed populations, Comal Springs and Weslaco, males were tested after every sampling session and thus the data basis sufficient for a more detailed analysis. In a GLM (Tab. 3.3) with male size as a covariate, season has a significant effect on male preference for females (Fig. 3.2). There was no difference between populations COM and WES (Fig. 3.1), no significant interactions between spatial and temporal effects, and no effect of male body size (Tab. 3.3). During spring, males spent less time with heterospecific gynogenetic sexual-parasites. As in all other tests, using absolute time spent with Amazons instead of relative times did not change the result.

Discussion

I studied male visual mate choice preferences of *P. latipinna* originating from sympatric populations with *P. formosa* in South (old sympatry) and Central (young sympatry) Texas.

Males did not prefer their own conspecific sexual females. The high number of side-biases indicates that males might not always have clear consistent preferences for either one of the two females presented.

There was no clear frequency dependent pattern in male mate choice preferences and no difference in male association time among populations.

There was also no effect of male body size on male mate choice preferences. Smaller males were not less choosy than larger males. In general, males did not prefer conspecific females. One could argue that this result might be due to biased use of predominantly small males. However, I doubt this because the full size range of males present in the samples of the studied populations was tested.

The lack of frequency dependent preferences and no effect of male body size suggest that stable coexistence in this asexual / sexual mating complex is not maintained due to behavioural regulation *sensu* Balsano et al (1989), McKay (1971), and Moore & McKay (1971).

As predicted, male choosiness varied seasonally. Males significantly preferred their own sexual females when being choosy was most beneficial. Males visually preferred conspecific females in spring – approximately one month before the first cohort of juveniles occurred in spring. At Weslaco, juveniles comprised 0% in April, 79% at the beginning of May, and 43% at the end of May. At Comal, juveniles were absent in April and May and comprised 25% in June. Males from the southern population (Weslaco) showed a second period of clear conspecific mate preference in July – again one month prior to another peak of numbers of juveniles in the population (46% juveniles in August) (Fig. 2.18 (chapter 2), see also appendix).

Although it is not known which factor actually causes this relationship, it remains as an intriguing pattern.

I was unable to find a general male preference for conspecific females. Several other studies have reported such preferences (see introduction). A few other studies could not find such a male preference (Balsano et al. 1981; Balsano et al. 1985; Woodhead & Armstrong 1985; Balsano et al. 1989; Schlupp et al. 1991; Heubel & Schlupp submitted; Schlupp et al. submitted) (chapter 4).

There are two different reasons for obtaining negative results. Firstly, absence of preferences could occur due to methodological reasons, small sample size, or low statistical power. Secondly, negative results may occur due to real absence of male preferences. At least for recent studies based on large sample sizes, one should start to consider alternative explanations for the lack of preferences for conspecific females.

Body size, age, status, receptivity, experience, and population origin (sympatric or allopatric) had been discussed as factors affecting male mating preferences so far (see introduction), but it seems that those factors do not generally influence male mating preferences. This is the first study on the impact of seasonality to male mating preferences.

The phenomenon of absence of male sexual preferences for conspecific males might have been underestimated during the last decades, and needs more attention. There are several potential

explanations for the lack of a preference for conspecific females. In this study, by limiting mate choice to visual cues, important information (chemical or tactile cues) may not have been available for male mate assessment. Multiple cues may be important for species discrimination (Hankison & Morris 2003) and direct contact might be necessary.

However, previous studies on male preferences used two different techniques to study mating preferences: chooser and stimuli were either separated by dividers (Schlupp & Ryan 1997, Schlupp et al. 1991), or could freely interact (Gabor & Ryan 2001, Ryan et al. 1996, Schlupp et al. 1991). Both types of methods provided positive and negative results.

Attractiveness of females is highly influenced by the females' sexual cycle (Parzefall 1973; Schlupp et al. 1991). Females are receptive only for a few days during each monthly cycle (Parzefall 1973). Therefore, only a small proportion of females are fertile at any given time. Under those circumstances, males may be selected not to forsake any potential matings – given the high costs of missed opportunities.

The proportion of receptive females in a population may change seasonally due to breeding seasons or synchronisation of sexual cycles in females. This would alter the operational sex ratio and thus male search costs for mates and likelihood of missed opportunities of mating with sexual females may underlie seasonal variation.

Additionally, in this host-parasite system, asexuals might be highly adapted to their hosts and thus mate discrimination might be so costly (especially time consuming) that males will do better by indiscriminately mating with every female. Schlupp et al. (1991) showed that females that were sexually receptive were more attractive to males, independent of species. *P. formosa* might be locally adapted to its sexual host and thereby chemically or visually highly effective in mimicking sexual females, leading to situations where males are unable to distinguish Amazons effectively from conspecific females before an actual mating attempt. This has been shown in sperm dependent hybridogenetic all-female lineages of *Poeciliopsis*, another asexual / sexual mating complex of Poeciliids (Lima et al. 1996).

The present study focussed only on visual preferences of males to associate with either type of females, actual matings or mating success has not been studied. Males might be able to discriminate and thus treat both types of females differently and allocate sperm expenditure respectively. This aspect needs further examination since males could exploit females' tendency to imitate each others mating decisions. As I discuss more detailed in chapter 5, by interacting with Amazons, males might enhance their attractiveness to conspecific females via mate-copying and potential signal value of gonopodial thrusts (Heubel et al. submitted) without investing large amounts of sperm in “wrong” matings.

Male preferences for large females (Ptacek & Travis 1997) might be conflicting with a preference for conspecific females, especially at times when the sexual-parasite *P. formosa* is larger than sexual females (chapter 2). Males might have an underlying preference for conspecific females, but this can be overrun by its even stronger preference for larger females at the end of the season (J. Gumm & C. Gabor pers. comm. 2003).

Another explanation for absence of male mate preferences might be an ecological constraint. Males might be less able to discriminate visually or discrimination between sexual and asexual females becomes too costly when water conditions were turbid. At Weslaco, a population with relatively high frequencies of Amazons and turbid water throughout the year, males visually

preferred to associate more with Amazons when water became more turbid. This aspect needs further attention (chapter 4, Heubel & Schlupp submitted).

The results of this study raise the question under what circumstances it is beneficial for males not to discriminate, or when it does pay off to distinguish and forsake potential matings. This study clearly stresses one major result: there is a seasonal effect supporting the hypothesis of asynchronous initiation of reproductive activity (Monaco et al. 1978). The seasonal plasticity of male preferences indicate that male mating decisions are highly flexible and males might be able to consider carefully whether or not being choosy is beneficial under the given circumstances. This study also shows that male size, frequency of Amazons, or different population origin per se does not affect male mate preference patterns. Taking into account the predominating lack of a conspecific preference, this leads to the central question: when does it pay off to discriminate?

This question should be dealt with using an asymmetric game theoretical approach (Maynard Smith 1979, 1982; Parker 1990; Beaugrand 1997). Hereby, frequency dependent and environmentally or genetically constrained costs and benefits of both strategies can be incorporated into a model, including probability and extend of mate-copying behaviour and density or frequency of sexual and asexual females (see chapter 6).

Chapter 4:

Turbidity affects association behaviour in male Sailfin mollies (*Poecilia latipinna*)

Abstract

In nature, communication always occurs in an ecological context. When signalling, individuals have to cope with environmental background noise. Turbid water interferes with visual communication in Poeciliids. We studied male mate preferences in the asexual / sexual mating complex of the gynogenetic Amazon molly *Poecilia formosa* in clear and turbid environments. The sexual-parasite *P. formosa* “seduces” other closely related males to obtain sperm to trigger embryogenesis but the male genome is excluded from producing clonal all-female offspring. In mixed populations, males mate with conspecific sexual females and heterospecific asexual females. In South and Central Texas, *P. formosa* lives syntopically with *Poecilia latipinna* as its sexual host species. We sequentially measured association time of *P. latipinna* males with conspecific sexual and heterospecific asexual females in clear and turbid water. We found that turbidity has an influence on male mate choice behaviour. Males spent less time with any kind of female stimulus in turbid water. Interestingly, there was no preference for conspecific sexual females – neither in turbid water nor under clear conditions. Also, origin of males and acclimatization to turbid water had no effect. We discuss how turbidity as a source of visual noise might affect communication among individuals and how this environmental factor might contribute to the stability of this sexual-asexual mating complex in nature.

Introduction

Signalling interactions always take place in a specific ecological context and signals are adapted to constraints imposed by the environment (Bradbury and Vehrencamp, 1998; Endler, 1992).

Many naturally occurring fish habitats are considerably turbid throughout the year and others underlie high seasonal variation in turbidity. Especially in species with visual communication, turbidity can affect communicative behaviour by attenuating and masking signals and cues. So far, turbidity and its role in mate choice was explicitly studied only by Seehausen et al. (1997): This study discussed the impact of turbidity – caused by eutrophication – on sexual selection and reproductive isolation in Lake Victoria Cichlids. The authors experimentally showed that recently increased turbidity levels impair colour vision in fish, thereby interfering with mate preferences. The impaired mate recognition inhibits reproductive isolation and thus leads to a decline in cichlid diversity.

Most other studies on fish behaviour and turbidity focused on predator-prey interactions (Abrahams and Kattenfeld, 1997; Beauchamp et al., 1999; Gregory, 1993; Gregory and Levings, 1998; Gregory and Northcote, 1993; Hartman and Abrahams, 2000; Jepsen et al., 2001; Johnson and Hines, 1999; Mayama, 1998; Reid et al., 1999; Rowe and Dean, 1998; Sweka and Hartman, 2001a; Sweka and Hartman, 2001b; Utne, 1997; Utne-Palm, 1999; van Eerden and Voslamber, 1995; Vogel and Beauchamp, 1999). Turbid water can also influence intraspecific interactions of Poeciliids in a social context. Franck et al (2001) showed that schooling preferences in females changed in turbid water.

Visual communication and mate preferences have been intensively studied in Poeciliids. Several studies have established the importance of visual signals and cues in male mate choice in Poeciliids (Abrahams, 1993; Bisazza, 1989; Gabor and Ryan, 2001; Long and Rosenqvist, 1998; Moore and McKay, 1971; Ptacek and Travis, 1997; Ryan et al., 1996; Schlupp et al., 1991; Schlupp and Ryan, 1997; Smith et al., 2002).

Male mate choice preferences are especially interesting to study in the context of the stability and maintenance of the asexual / sexual mating complex of the Amazon molly *P. formosa* (Gabor and Ryan, 2001; Körner et al., 1999; Landmann et al., 1999; Marler et al., 1997; Marler and Ryan, 1997; Ryan et al., 1996; Schlupp et al., 1999). *P. formosa* is an all-female, gynogenetic species. Despite their clonal reproduction, females need to copulate with males of closely related species to obtain sperm they need to trigger embryogenesis (Hubbs and Hubbs, 1932; Schlupp et al., 1998). In Texas and North Mexico, several populations of the Sailfin molly *Poecilia latipinna* co-occur with the Amazon molly, *P. formosa*, and are sexually parasitised by it (Schlupp et al., 2002). In these populations, males are confronted with a choice between conspecific and heterospecific females. In such a mating complex, male mate choice should be crucial because matings with the sexual-parasite *P. formosa* do not incur any direct fitness benefits. As predicted, males have a strong preference for conspecific sexual females (Gabor and Ryan, 2001; Hubbs, 1964; Niemeitz et al., 2002; Ryan et al., 1996; Schlupp et al., 1998; Schlupp et al., 1991; Schlupp and Ryan, 1997; Woodhead and Armstrong, 1985) but some studies present and discuss controversial results (Balsano et al., 1981; Balsano et al., 1985; Schlupp et al., 1991; Schlupp et al., submitted; Woodhead and Armstrong, 1985).

Non-discriminating male mating behaviour in this sexual-aseexual mating complex could be explained by heterospecific mate-copying. Males gain an indirect benefit of increased attractiveness to conspecific females observing those heterospecific matings with Amazon mollies (see chapter 5, Heubel et al., submitted; Schlupp et al., 1994).

Previous studies were always conducted under clear water conditions. Two different experimental techniques were used: visual preference tests or mate choice experiments allowing full interaction. In visual preference tests, chooser and stimuli were separated by dividers and association time with the stimulus was measured (Schlupp et al., 1991; Schlupp and Ryan, 1997; Woodhead and Armstrong, 1985). In experimental designs allowing free interactions of chooser and stimuli, actual mating attempts were counted (Gabor and Ryan, 2001; Ryan et al., 1996; Schlupp et al., 1991; Woodhead and Armstrong, 1985).

Both types of experiments can be conducted as simultaneous tests with a choice between different stimuli, or as sequential tests with a serial presentation of different stimuli.

The availability of visual information changes substantially with visibility in the water e.g. by limiting the range or bandwidth of signals and cues. Here we argue that it is important to include turbidity as an environmental factor into experiments studying preferences in fishes.

In the specific case we address here, turbidity might affect male mate preferences or impair mate-choice, thereby increasing the cost of mate assessment. Consequently, this may be lowering the threshold of mating with the 'wrong' females, the sexual-parasites. Specifically, we ask how turbidity affects male association preferences and what the potential impact of this might be on the stability and maintenance of this asexual / sexual species complex.

Materials and Methods

FISH

We conducted two sets of experiments. In the first set, we tested individuals from a population in South Texas “Weslaco” (this field site is identical population “WES” in chapter 2 and 3), originating from the Rio Grande river system drainage (Hidalgo county, Texas, USA) (Gabor and Ryan, 2001). In this population, the frequency of Amazons – the sexual-parasite – has always been high during the last years and also turbidity levels had been high (Tab. 4.1).

In the second set, we tested *P. latipinna* males originating from a population in Central Texas (Comal River, New Braunfels, Texas, USA) (this field site is identical population “COM” in chapter 2 and 3) (Witte and Ryan, 2002). This population has a very low frequency of *P. formosa* and clear water throughout the year (Tab. 4.1). We used *P. latipinna* females and *P. formosa* originating from the same population and a nearby population (San Marcos River near Martindale, Texas, USA) (Schlupp et al., 1994) (this field site is identical population “SM” in chapter 2 and 3) (Tab. 4.1). Detailed descriptions of the habitat, fish community and population ecology are presented in chapter 2).

Tab. 4.1: Field observations (mean \pm SE) of turbidity and population parameters in 2001/2002.

Population Samples	South Texas	Central Texas	
	Weslaco 12	Comal 11	Martindale 11
Turbidity (NTU)	273 \pm 28.0	3 \pm 1.4	89 \pm 15.6
Proportion of <i>P. formosa</i>	0.49 \pm 0.06	0.02 \pm 0.01	0.87 \pm 0.05
Female asexual / sexual – ratio	2.07 \pm 0.39	0.03 \pm 0.01	11.14 \pm 4.84
<i>n</i> adult <i>Poecilia</i> sampled	1303	1628	662

Turbidity was tested as nephelometric turbidity units (NTU) with a shuttered turbidity (ISO 7027) nephelometer with 880 nm LED in a Hydrolab® Data Sonde 4 water quality multiprobe.

Proportion of *P. formosa* in mixed populations with *P. latipinna* is the ratio of numbers of adult Amazons to all adult *Poecilia* combined. Female asexual / sexual - ratio is the ratio of adult *P. formosa* to sexual adult *P. latipinna* females.

All fish were collected in the field up to one month before testing. In the laboratory (Section of Integrative Biology, Austin), all fish were maintained in 20-60 l tanks at 25°C on a 12/12h artificial illumination cycle. All fishes were fed daily with commercially available flake food. Prior to testing, males and females were kept visually separated in different tanks.

We used females with a minimum size of 30 mm standard length to prevent inadvertent use of immature males instead of females as stimuli. After completing the experiments, all fish were released into large outdoor breeding tanks at Brackenridge Field Laboratory at the University of Texas at Austin.

TURBIDITY

We created turbid water in the test tank by adding argillaceous earth powder (3.6 g Edasil® bentonite dissolved in 50 ml water and poured in 80 l). The same method had been used before (Abrahams and Kattenfeld, 1997; Franck et al., 2001; Hartman and Abrahams, 2000). After every water change, we added 1.8 g dissolved bentonite to maintain the same level of turbidity. In turbid tanks, turbidity was kept at 25 nephelometric turbidity units (NTU). In clear water

tanks, turbidity was kept under 5 NTU. Turbidity was measured before every series of trials as well as before and after every water change using the same shuttered turbidity sensor (ISO 7027) nephelometer with 880 nm LED in a Hydrolab® Data Sonde 4 water quality multiprobe as used in the field. *In situ* turbidity levels in the tested populations are shown in Tab. 4.1. We measured 90 NTU as overall mean turbidity level in 23 populations throughout Texas and Mexico, in September 2002.

EXPERIMENTAL SETUP

Trials were carried out in two identical test tanks (120*30*52 cm). One tank contained clear water, the other one turbid water. Both tanks had Teflon sheets as background and sides cover as a neutral gray background and a layer of gravel on the bottom. Turbidity, water level, and temperature were kept stable during the experiment. Before the start of an experiment, we stirred the water in both tanks. Each test tank was divided into five equal compartments: The two outer (stimuli: female/empty) compartments were separated by transparent dividers. The three inner compartments were only virtually divided by pen markings on the front of the tank. Thus, the test male could swim freely within these three inner compartments. The middle compartment was a neutral zone. The time a male spent in this zone was not counted. The two zones close to the dividers were the preference zones. Having two preference zones, one adjacent to the female stimulus and one at the opposite end of the tank next to the empty compartment, allowed us to test not only preferences for presented stimuli, but also to detect avoidance behaviour.

Every *P. latipinna* male was sequentially presented with four different female stimuli in randomised order: (1) (conspecific sexual female, clear water), (2) (sexual-parasite *P. formosa*, clear water), (3) conspecific sexual female, turbid water), (4) sexual-parasite *P. formosa*, turbid water). We recorded the time males spent in association with the female stimulus as the response variable.

P. latipinna and *P. formosa* females were matched for size and originated from the same population. Each test male was placed in a clear cylinder in the centre of the neutral zone. After a five-minute acclimatisation phase, we gently removed the cylinder and started the trial.

Using two stopwatches, we counted for five minutes the time the male spent in either the right or the left preference zone.

CONTROL EXPERIMENT

To control for habituation to the different turbidity levels in the two habitats the males originated from, we kept males under two different treatments. Males from the 'clear water' population (Comal) were kept in clear or turbid water in 25 – 100 l tanks for at least five days prior to testing and then individuals from both treatments were tested under clear and turbid conditions.

DATA ANALYSIS

For this split-plot repeated measures experimental design, we performed a partly nested fixed factors repeated measurement ANOVA using generalized linear models (GLM). We investigated the effect of female species (conspecific *versus* heterospecific) and turbidity level (clear *versus* turbid) as two crossed within subject factors and male population origin as

between subject factor on association time a male spent with the stimulus female as response variable.

We *a priori* excluded those data from further analysis with males having generally insufficient low response indices ($RI < 0.5$) (Schlüter et al., 1998). In those cases, males spent most of the observed time in the neutral zone in all four sequential trials.

To obtain normally distributed data, we transformed seconds spent with stimulus females using reflection and square root transformation. Thereby, $x' = \text{square root}(K - x)$ and $K = \text{constant}$ from which each score is subtracted so that the smallest score is 1 (Tabachnick and Fidell, 2001). Variances did not significantly differ (Bartlett-Box- F -test for homoscedasticity). All transformed variables did not significantly differ from a normal distribution (Kolmogorov-Smirnov One Sample test for normality with Lilliefors corrected probabilities). We used Greenhouse-Geisser corrected degrees of freedom testing within-subject effects. All p -values are two-tailed. Unless stated otherwise, averages are presented as mean \pm S.E. The data were analysed using SPSS 11.5. (SPSS Inc.).

Results

We conducted a total of 77 trials. We excluded eight trials from further analysis due to insufficient response indices. However, we conducted an exploratory analysis including these data and found that this did not change the results.

Males showed a strong response to female stimuli opposed to the empty compartment (Wilcoxon-Test, $z = -6.864$, $p < 0.0001$, $n = 69$). No avoidance of female stimuli occurred.

Under clear water conditions, *P. latipinna* males spent 208.2 ± 9.0 s in association time with conspecific females, and 212.2 ± 10.2 s with the sexual-parasite *P. formosa* (Fig. 4.1). Under turbid conditions, they in general spent less time in association with the female stimuli. Males spent on average 162.0 ± 12.0 s with sexual females, and 183.2 ± 11.6 s with the sexual-parasite (Fig. 4.1). We tested the effect of stimulus females' species and turbidity level as crossed within subject factors and male population origin as between subject factor on male association time with females in a repeated measure ANOVA (reflected square root transformed data). Under clear water conditions, males spent significantly more time with the stimulus female than under turbid conditions (Fig. 4.1) ($F_{1, 42} = 7.933$, MSE 19.561, $p = 0.007$). However, they did not spend more time with conspecific (*P. latipinna*) than sexually parasitising females (*P. formosa*) ($F_{1, 42} = 2.159$, MSE 27.427, $p = 0.149$). Population origin (Comal vs. Weslaco) did not affect mate choice preferences ($F_{1, 42} = 0.683$, MSE 26.897, $p = 0.413$). There was no significant effect of any interaction involving turbidity level, female stimulus species or population ($F_{1, 42} < 1.2$, $p > 0.28$).

We thus found that turbidity level alone had an effect on the time, males spent with the stimulus females – independent of the species of stimulus female or the population origin of the male.

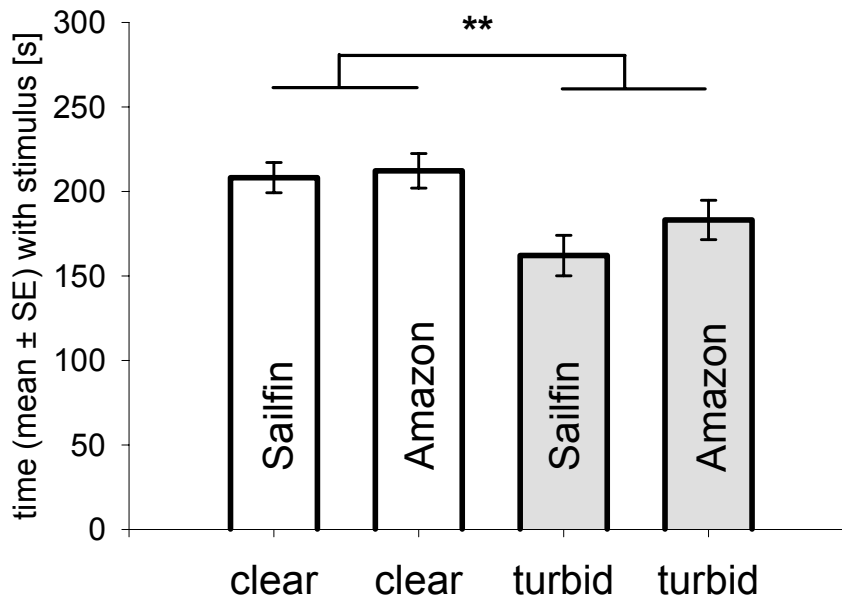


Fig. 4.1: Association time (mean \pm S.E.) of *P. latipinna* males ($n = 69$) spent in clear (< 5 NTU) or turbid (> 22 NTU) water with different female stimuli. Females were either conspecific Sailfin mollies (*P. latipinna*) or unisexual Amazon mollies (*P. formosa*). Trials were sequential visual preference tests.

To control for acclimatization to turbidity, we additionally tested fish originating from the clear water environment (Comal) that were acclimatized for five days to either turbid ($n = 25$) or clear conditions ($n = 22$). Acclimatization did not significantly affect the time males spent with the stimulus females ($F_{1, 45} = 1.558$, $MSE = 27.784$, $p = 0.218$), regardless of stimulus females' species and test turbidity levels ($F_{2.5, 113.2} = 0.172$, $MSE = 17.449$, $p = 0.886$).

Discussion

We found that males spent less time with any kind of female stimulus in turbid water. Clearly, turbidity has an influence on male mate choice behaviour. Interestingly, there was no preference for conspecific sexual females – neither in turbid water nor under clear conditions. Also, origin of males and acclimatization to turbid water had no effect.

EFFECTS OF TURBIDITY

Turbidity generally decreases the overall amount of ambient light in the water column. In addition, depending on the source that causes turbidity, it also affects other properties of light. Light in turbid water is more scattered and depending on the colour of the particles will change its colour (Bradbury and Vehrencamp, 1998; Endler, 1990; Heavens and Ditchburn, 1991)

In the specific case of turbidity in the natural habitats of the mollies of the Gulf coastal plains of South and Central Texas, clay particles are the main source of turbidity. Clay consists of layered silicate minerals causing scattering of light. Clay particles have sizes similar to the wavelength of visual light and thus predominantly cause Mie scattering by which smaller wavelengths – especially UV – are relatively more scattered than longer wavelengths (Bradbury and

Vehrencamp, 1998; Heavens and Ditchburn, 1991; Losey et al., 1999). This scattering of light can be viewed as “noise” in visual communication.

The bentonite we used to create turbidity in our experiments produces turbidity comparable to the situation in the field. There are linear relationships between dissolved bentonite concentration, NTU measures, and settleable solids in natural creeks (Duchrow and Everhart, 1971).

Natural habitats of mollies differ widely in the turbidity measured (pers. obs.), but clearly the more typical and common habitats are turbid. The single clear water population (Comal) forms an exception: the water is clear because it is only a few meters downstream from a springhead. Here both species were recently introduced, *P. latipinna* in the 1930ies (Brown, 1953) and *P. formosa* in the 1950ies (Hubbs, 1953). To what extent variability in turbidity is correlated with signals and/or signalling behaviour needs further examination.

CONSEQUENCES FOR SIGNAL DESIGN

It is well documented that environmental conditions influence signal design and signalling behaviour (Endler, 1992; Endler, 1993; Halliday and Slater, 1983; Wiley and Richards, 1982). Great tits e.g. shift to higher maximum frequencies of their songs in a noisy, urban environment (Slabbekoorn and Peet, 2003). Other examples include motion patterns in lizards and background movements (Fleishman, 1992), noise dependent adjustment of song amplitude in nightingales (Brumm and Todt, 2002), colour morphs under different light environments in Bluefin killifish (Fuller, 2002), and acoustic communication under changing weather conditions in penguins (Lengagne et al., 1999) and Tawny owls (Lengagne and Slater, 2002). Turbidity might have a comparable effect on visual signals in mollies. Behavioural adaptations to turbid conditions might be comparable to those adaptations to different light environments studied in Guppies. Adaptations to changing light conditions include increase of courtship frequency (Long and Houde, 1989; Long and Rosenqvist, 1998), redundancy and repetition of signals or a shift towards a different sensory mode (Endler, 1992). As a sensory compensation for decreased visual detection of a predator, fathead minnows (*Pimephales promelas*) were more sensitive to chemical alarm cues in turbid water (Hartman and Abrahams, 2000).

To cope with changing turbidity, sexes may establish conventions on when and where to meet – such as specific sites and times, courting close to surface, where water is comparably clear improves effectiveness of visual signals (Endler, 1992).

Turbidity does not only affect the range of a signal (or cue) by attenuation but also its properties. Because shorter wavelengths are affected relatively stronger by the small clay particles, the colour spectrum of the signal changes over distance. Our finding that males spent less time with stimulus females under turbid conditions can be explained by the fact that males had more difficulties to detect or recognize females when vision was impaired by turbidity.

Mollies are UV-sensitive (Körner et al., 1999). In *P. mexicana*, a close relative of the Sailfin molly and the maternal ancestor of *P. formosa*, UV vision is not used for mate choice (Waschulewski et al. in prep). Like the Sailfin mollies studied here, *P. mexicana* lives in mostly turbid habitats and therefore UV vision might not play a role. Swordtails of the genus *Xiphophorus* (Ryan and Rosenthal, 2001) for which a role of UV vision has been demonstrated (Cummings et al., 2003) live mainly in clear water habitats (Ryan and Rosenthal, 2001). If long-range visual detection of mating partners is limited, short-range communication should be

relatively more important. In mollies, chemical communication only plays a role in very close contact. The role of the lateral line in this context has not been studied so far. This would also mean that short-range communication in turbid conditions is likely to be unobserved by third-party individuals as an audience, or private (Losey et al., 1999). Individuals are not only visually less conspicuous to potential mates but also to predators. Males might perform courtship displays in close range to females without the threat of predation in the relative safety of turbid water. It might also cause privacy that protects visual communication from illegitimate receivers (McGregor, 1993; McGregor and Peake, 2000).

ABSENCE OF MALE PREFERENCE

We were unable to find male preferences for conspecific females. Several other studies have reported such preferences (see introduction) using roughly the same sample sizes, but a few others studies could not find such a male preference (Balsano et al., 1981; Balsano et al., 1985; Schlupp et al., 1991; Schlupp et al., submitted; Woodhead and Armstrong, 1985). Schlupp et al. (1991) provided an explanation for the lack of preference: females that were receptive to males were more attractive to males, independent of species. Generally, the preferences seem less strong when testing association time, allowing only visual signals. Testing sequentially rather than simultaneously may also have contributed to the absence of a male preference reported here.

There are several potential explanations for the lack of a preference for conspecific females. In our experiment, important information may not have been available, although we do not know what exactly this may have been. A fundamental difference may have been the sequential presentation of stimuli. Under the given circumstances, males may have perceived it to be less costly for them not to prefer conspecific females. A potential mechanism may be influenced by the females' sexual cycle (Parzefall, 1973): females are receptive only for a few days during each monthly cycle. Therefore, only a small proportion of females are fertile at any given time. Males may spend more time with a female that is presented without an alternative because there is no alternative and males may be selected not to forsake any potential matings (Schlupp and Ryan, 1997). Alternatively, mate choice under turbid conditions might become so costly – especially time consuming - that males will do better by indiscriminately mating with every female (see chapter 6). Additionally, a benefit to males via mate-copying (see chapter 5) Heubel et al., submitted; Schlupp et al., 1994) might further reduce the costs of 'wrong' matings but this applies only to situations in which the interactions can actually be perceived.

In conclusion, our data indicate that visual preferences in mollies are influenced by environmental noise. Turbidity is a very common source for visual noise. Our study highlights that mate choice is dependent on environmental conditions. Further behavioural experiments in the laboratory should pay more attention to environmental variables that might affect individuals' behaviour and ability to communicate in nature.

Chapter 5: Geographic variation in female mate-copying in the species complex of a unisexual fish, *Poecilia formosa*

Abstract

The Amazon Molly *P. formosa* is a gynogenetic all-female fish. Its unique mating system relies on heterospecific matings with males of two closely related sexual host species. In mixed populations, males mate with conspecific sexual females and heterospecific asexual females. Such matings are not isolated dyadic interactions but rather elements of a social network. Conspecific and heterospecific females can observe these interactions as an audience. This is the only known case of mate-copying between species, and thus a system in which the potential for mate copying could be influenced by the presence or absence of *P. formosa*. Here we show that mate-copying is exhibited by the sexual host species *P. mexicana* (Atlantic molly) and *P. latipinna* (Sailfin molly), and the asexual *P. formosa*. In both systems, sexual and asexual females copy each other's mate choice decisions in sympatry, but heterospecific mate-copying seems to be absent in allopatry. Males benefit from heterospecific matings with Amazon mollies because these increase their attractiveness to the conspecific sexual females. In mixed shoals, mate-copying potentially imposes a cost as it also increases a male's attractiveness to heterospecific females. We argue that the net-effect of mate-copying is beneficial to males because the relative strength of mate-copying is lower in Amazon mollies. Furthermore, males can choose to reject matings with Amazon mollies. We hypothesize that an added benefit to males lies in the signal value of copulations.

Introduction

Mate choice is often influenced by the social environment. Mate-copying is one such example of socially influenced mate-choice in which individuals copy the mate choice of others (Losey et al. 1986; Brooks 1998; Westneat et al. 2000). Studies on mate-copying place mate choice in a social context rather than viewing it as isolated events (Emlen & Oring 1977; Gibson & Höglund 1992; Pruett-Jones 1992; Andersson 1994; Höglund & Alatalo 1995; Dugatkin 1996; Galef & White 2000). Mate-copying is especially prevalent in fishes, where females copy conspecific females (Dugatkin & Godin 1992; Briggs et al. 1996; Witte & Ryan 1998; Witte & Ryan 2002), males copy males (Schlupp & Ryan 1997), and sneaker-males copy females (Gonçalves et al. 2003).

Although mate-copying typically occurs among conspecifics, there is a system in which it mediates heterospecific matings - the complex of unisexual mollies (*Poecilia formosa*) and their sexual counterparts. In this system, in nature, the gynogenetic *P. formosa* must obtain sperm from one of their close relatives, either *P. latipinna* or *P. mexicana*. Schlupp et al. (1994) showed that heterospecific mate-copying may contribute to the maintenance of this system because male *P. latipinna* increase their attractiveness to conspecific females by mating with the gynogenetic female *P. formosa*.

THE SYSTEM

Amazon mollies, *P. formosa*, are all-female gynogenetic fish of the live-bearing family Poeciliidae (Hubbs & Hubbs 1932). Gynogenesis is a special form of parthenogenesis in which sperm of a host species serve as a physiological stimulus to trigger embryogenesis. This sperm normally is not incorporated into the genome of the offspring (Schlupp et al. 1998). In the case of *P. formosa*, sperm is usually provided by males of one of two species, *P. mexicana* or *P. latipinna* (Hubbs & Hubbs 1932; Schlupp et al. 1998). The Amazon molly is probably derived from a single hybridisation event of a *P. mexicana* female and a *P. latipinna* - like male (Turner 1982; Avise et al. 1991; Scharl et al. 1995). Amazon mollies range from southeast Texas to northeast Mexico. *P. formosa* is sympatric with *P. latipinna* in Texas and a few areas in northeast Mexico, while it is sympatric with *P. mexicana* in Mexico (Darnell & Abramoff 1968; Schlupp et al. 2002).

SCENARIOS OF MATE-COPYING

To study mate-copying in this species complex, we took advantage of a natural experiment in Central Texas, USA. In the 1930's *P. latipinna* was introduced from Louisiana (Brown 1953) into the San Marcos River. Twenty years later *P. formosa* was introduced (Hubbs 1953). Thus the duration of sympatry for those populations can be dated exactly. The first documentation of heterospecific mate-copying by Schlupp et al. (1994) occurred not more than four decades after the introduction of Amazon mollies into the drainage. Assuming two to three generations per year (Hubbs 1964), there is a maximum of 80-100 generations of sympatry and hence opportunity for heterospecific mate-copying to arise in the San Marcos River drainage. Thus, if mate copying is absent in allopatry but present in sympatry this population offers some insight into the time scale over which this behaviour evolved.

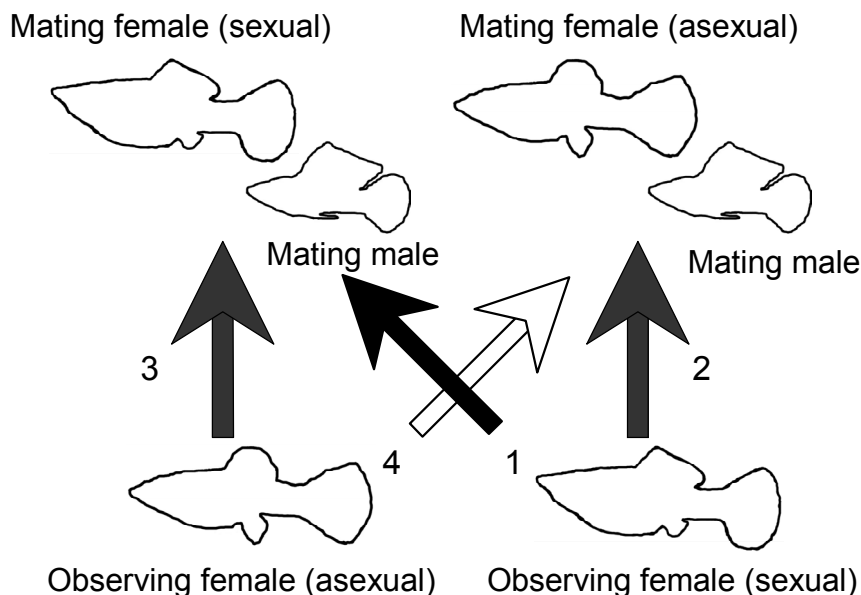


Fig. 5.1: The four different possible situations of male - female interactions with different net-benefits to males. (1) A sexual female observing a sexual female mating with a male, (2) a sexual female observing an asexual female mating with a male, (3) an asexual female observing a sexual female mating with a male, and (4) an asexual female observing an asexual female mating with a male.

Schlupp et al. (1994) argued that males gain an advantage by mating with Amazon mollies through heterospecific mate-copying. Their study provided the first evidence that it might be adaptive for males to serve as sperm donors for heterospecific females: *P. latipinna* males became more attractive to females when the *P. latipinna* female has had an opportunity to observe the male sexually interacting with *P. formosa*. The full complexity of potential interactions in the natural situation, however, is more complicated. Groups of these fishes in sympatry always comprise males, sexual females and asexual females (Schlupp & Ryan 1996).

Thus, any male / female interaction can be observed by either of the two species of females, leading to four possible situations with different net-benefits to males: (1) a sexual female observing a sexual female; (2) a sexual female observing an asexual female; (3) an asexual female observing a sexual female; and, (4) an asexual female observing an asexual female (Fig. 5. 1). While the first scenario of conspecific mate-copying in sexuals is obviously the most beneficial to males, the heterospecific situations provide only half of the opportunities for sexual reproduction to males. In the last scenario of Amazons copying Amazons, males only increase their attractiveness to other asexuals. In this case, males do not gain any benefit from female mate-copying.

P. formosa has two main host species: *P. latipinna* serves as sperm donor in the northern part of its biogeographic range, *P. mexicana* in the southern part. Several studies on mate-choice indicate that *P. mexicana* is less discriminating than *P. latipinna* (Balsano et al. 1985; Schlupp et al. 1991; Ryan et al. 1996). Therefore it is crucial to differentiate between these two different systems within the Amazon molly mating complex (Schlupp et al. 2002), and address the four possible behavioural interactions for the two mating systems. Furthermore, to understand the pattern of heterospecific mate-copying, it is important also to include populations that are allopatric with *P. formosa* (Tab. 5.2). Allopatric populations resemble the situation before introduction of Amazon mollies (Gabor & Ryan 2001).

For the present paper, we combined data from several studies investigating mate-copying, using both live stimuli and video-playback. We tested for presence of heterospecific mate-copying behaviour in both sexual host species of *P. formosa* and measured its relative strength in an allopatric and a sympatric population.

Materials and Methods

STUDY ORGANISMS

We used fishes from populations in which the sexual species *P. latipinna* and *P. mexicana* were either sympatric or allopatric with the asexual *P. formosa* (Schlupp et al. 2002) (Tab. 5.1).

All fish used in experiments 1a, 3a, 4, 5, and 6 originated from randomly outbred laboratory populations (Schlupp et al. 1991; Schlüter et al. 1998) and were maintained under standard aquarium conditions at the University of Hamburg, Germany. The founder fishes of these stocks were collected in 1993, 1995, and 1996 from San Marcos River, Texas, USA, from the Rio Purificacion, Nuevo Leon, Mexico, from water bodies near Tampico, Tamaulipas, Mexico, and Arroyo de Solpho, Tapijulapa, Tabasco, Mexico (Tab. 5.1). The Mexican government issued collecting permits no. 210 696 – 213 – 03 and DOO 750 - 1576 to collect the fishes. All animals used in these experiments were returned to stock tanks at the University of Hamburg at the end of the study. All fish used in experiments 1b, 2, and 3b were collected in the field from populations in Central Texas, USA (Comal River, San Marcos River) (Tab. 5.1). They were maintained at the University of Texas at Austin in large stock tanks in the laboratory or in large outdoor breeding tanks at Brackenridge Field Laboratory at University of Texas in Austin. Animals were cared for following Animal Protocol 10960202 and transferred to large stock tanks at the Brackenridge Field Laboratory at the end of the study.

In the laboratory, all fish were maintained in 25-600 l tanks at 24-29°C on a 14-12h artificial illumination cycle. All fishes were fed daily with commercially available flake food and *Artemia* nauplii, *Daphnia*, or *Tubifex* worms as occasional supplementary food. Measurements of standard length (snout–caudal peduncle) were taken from all individuals after testing.

GENERAL EXPERIMENTAL PROCEDURE

We used a standard preference-testing paradigm: each test tank was divided into three equal zones by lines drawn vertically on the front side as visual markings. The central compartment was defined as a neutral zone, the two side-sections as preference zones. The test female was able to move freely among the three zones. On the right and the left end of the experimental tank, adjacent to the preference zones we visually displayed the respective stimuli. In experiments using video-playback (Oliveira et al. 2000), we placed two video-monitors as close as possible next to the preference zones, so that the choosing females could view the displayed video images. This technique has been successfully used before in this species complex (Körner et al. 1999; Landmann et al. 1999; Gonçalves et al. 2000). In experiments with live stimuli we utilized a test tank with two outer compartments separated by clear Plexiglas dividers from the preference zones (Schlupp et al. 1994). The dividers were fit tightly to reduce flow of water and chemical cues between the compartments.

Females were separated from males prior to testing for at least one day. Unless stated otherwise, all fishes had prior experience with the opposite sex. Test females and stimulus males never originated from the same tank to exclude individual familiarity. Only adult females with a body size of > 28 mm standard length were used in the experiments and most females displayed a gravity spot. This procedure makes it unlikely that late maturing males

were inadvertently tested as females (Parzefall 1969). Water level and temperature in the test tank were stable during the experiments. The bottom of the tank was covered with gravel. The back and the sides of the tank were covered with light blue cardboard or grey Teflon foil (unless we used monitors for playback) as a neutral homogenous background.

Each test consisted of three different phases: (1) an initial preference test that determined which male a focal female preferred; (2) a presentation in which the focal female had the opportunity to observe the initially less preferred male interacting with another (model) female; and finally, (3) a second preference test in which the focal female's preference was again measured. Mate copying took place if in this final test the female increased her preference for the previously unpreferred male.

Preference tests of phase one and three were initiated by introducing a test female into a clear cylinder (> 12 cm diameter) in the centre of the neutral zone of the experimental tank. Two males, differing in size, were then introduced into the stimulus compartments. We randomly started with either the larger or smaller fish at the left or the right side of the tank.

After an acclimatisation period we gently removed the cylinder and immediately started recording the time the female spent in each of the three sections (Tab. 5.2). Then the positions of the stimulus males (live or video-playback) were swapped and the experimental unit was repeated to detect a potential side bias. Thus each preference test consisted of two units. We decided *a priori* that a side bias occurred when a female spent more than 80 % of her time on the same side of the tank after swapping stimuli in the preference tests. In such cases females did not perform consistent preferences for stimuli. Those trials were excluded from further analysis (Tab. 5.1).

As another measure of female responsiveness to the stimuli, we calculated a response index as the percentage of the total observation period females spent outside the neutral zone (Schlüter et al. 1998). Response indices compare the extent of reactions to stimuli in different studies (Tab. 5.1). We assumed these side-biased or non-reacting females to be unmotivated. Those individuals have not been used in this study.

We also decided *a priori* to exclude trials from further analysis in which females did not show an initial preference for the larger male in the first preference test (phase one). Thereby, we checked whether the actual female association preferences are in accordance with the average overall population preference for larger males. By excluding those females that did not show an initial preference for the larger male, we paid attention to the fact that females do not have random mating preferences. It is known from several studies that the population level preference of females is for larger males (Marler & Ryan 1997; Ptacek & Travis 1997; Gabor 1999). Consequently, if a female initially chooses a small male and then modifies her preferences towards the larger male, it is difficult to determine exactly *why* this change has occurred. Any change towards the generally more likely preference for the larger male in the second test might not be due to copying and would result in a false positive data point. It is therefore conservative to exclude such trials.

After the initial preference test, we maintained the focal female in a clear Plexiglas cylinder in the neutral zone. In phase two, we then gave the female the opportunity to observe the smaller, initially less preferred male consorting with a model female. In experiments with live stimuli we covered half of the tank dividers with an opaque screen and additionally divided the stimulus tanks parallel to the long axis of the tank into two separate chambers by

clear Plexiglas panes (Schlupp et al. 1994). We added a model female to the newly created compartments of the stimulus tank. Thus males and the added model female could interact visually. The model female added to the larger, initially preferred male was not visible to the test female in the central cylinder. On the side with the smaller, initially less preferred stimulus male we removed the opaque divider. During the presentation phase the test female could observe the initially less preferred male interacting with a model female and the initially preferred larger male without visible female company.

After the presentation period we removed the model females and additional dividers and repeated the first preference test in phase three. Methodological details and minor differences among protocols of the different studies are summarised in Tab. 5.1.

Tab. 5.1: Methodological details of different mate-copying studies

experiment	conspecific / heterospecific	setup	tested population	SL female [mm] (mean \pm SD)	sym- / allopatry	male population	male size diff. [mm] (mean \pm SD)	model population	SL model [mm] (mean \pm SD)	tank size [l]	mean RI [%]	n side biased	γ initial pref. for smaller male	γ RI < 0.5	single test unit [min]	presentation [min]	control experiments
1a	hetero	video	<i>lat</i> SM	36 \pm 2	sym	<i>lat</i> SM	15	<i>for</i> BT	55	80	75	8	5	2	5	3	1, 2
1b ¹	hetero	live	<i>lat</i> SM	52 \pm 8	sym	<i>lat</i> SM	13 \pm 4	<i>for</i> SM	57 \pm 4	180	92	22	4	3	10	20	1, 2
2	hetero	live	<i>lat</i> AS	31 \pm 2	allo	<i>lat</i> AS	7 \pm 3	<i>for</i> SM	33 \pm 4	80	87	30	9	0	5	5	-
3a	con	video	<i>for</i> BT	44 \pm 4	sym	<i>lat</i> SM	15	<i>for</i> BT	55	80	83	20	4	0	5	3	1, 2
3b	con	live	<i>for</i> SM	47 \pm 5	sym	<i>lat</i> CS	9 \pm 4	<i>for</i> SM	48 \pm 5	180	81	34	21	0	5	5	1, 2
4	hetero	live	<i>mex</i> TAM	35 \pm 5	sym	<i>mex</i> TAM	4 \pm 1	<i>for</i> TAM	32 \pm 2	100	81	11	9	3	5	5	1, 2
5	hetero	live	<i>mex</i> PS0	40 \pm 4	allo	<i>mex</i> PS0	9 \pm 4	<i>for</i> SM	33 \pm 4	180	92	63	3	3	10	20	1
6	con	video ²	<i>mex</i> TAM	39 \pm 5	sym	<i>mex</i> TAM	17	<i>mex</i> TAM	38	200	82	8	5	3	5	5	-

Populations: **lat**: *Poecilia latipinna*, **mex**: *P. mexicana*, **for**: *P. formosa*; **SM**: San Marcos River near Martindale, Texas; USA (Schlupp et al. 1994). **AS**: Aquarena Springs. Spring head San Marcos River, San Marcos, Texas USA; Like other authors, we considered this population allopatric with *P. formosa* (Gabor & Ryan 2001). Recently, very few Amazon mollies have been collected from this site (Schlupp et al. 2002). **CS**: near spring head Comal River, New Braunfels, Texas, USA (Witte & Ryan 2002). **BT**: VI/17, Rio Purificacion, Barretal, Nuevo Leon, Mexico (Körner et al. 1999). **PS0**: Arroyo de Solpho, Tapijulapa, Tabasco, Mexico (Parzefall 2001). **TAM**: III/2, III/13, III/14, IV/5; near Tampico, Tamaulipas, Mexico (Schlüter et al. 1998; Körner et al. 1999). **RI**: response index. **Control 1**: without opportunity for copying in phase two between first and second preference test. **Control 2**: shoaling control using all females controlling for social effects. Monitors used for video playback: Mitsubishi CT-15 MS 1 ETX (experiment 1a & 3a), Saba M5520C Colour TV and BW 15" CCTV CEM 15 A (c). ¹(Schlupp et al. 1994). ²animated slides.

Controls

To ensure our results were due to mate-copying, we controlled for consistency in female mate preferences. We conducted the same experiment without opportunity for copying. Both model females remained visually isolated by opaque dividers from the test female during presentation phase. To control for shoaling effects, we also conducted the same experiment with all-female stimuli. This procedure ensured that sexual and not social motivation of the test female's behaviour led to the results.

Creation of Video-Stimuli

Videotapes of stimuli were produced from recordings of the behaviour of one small and one large *P. latipinna* male and a *P. formosa* model female interacting with the smaller male (Tab. 5.1). Recordings were made using a Panasonic AG 450 S-VHS video camera from 1 m distance in a 50 x 25 x 10 cm Plexiglas tank to facilitate keeping the fish in focus. Sides and background of the tank were covered with light blue cardboard identical to the tank background in the experiments. We used two 500W light bulbs (3200 Kelvin) as a light source coming mainly from above the tank. We chose video sequences of 0.24 – 4.15 min as stimuli for preference tests, opportunity for copying and control experiments. No bottom, water surface or tank sides were visible in the video sequences. The recordings were edited and looped to a final duration sufficient to perform the experiments. After 20 trials, a new set of tape copies was made to maintain a stable good quality of the playbacks. The method of videotaping, editing, and playback was as described in Landmann et al. (1999) and Körner et al. (1999).

Playback with animated slides

Video stimuli for conspecific mate-copying in sympatric *P. mexicana* females (experiment 6) were created by editing a digitised slide of a *P. mexicana* male interacting with a *P. mexicana* female. In Adobe Photoshop 4.0.1 we replaced all background with light blue colour matching the cardboard used as cover for the preference tank and rescaled the sizes of the fish. We had a set of three files showing (1) a male downscaled to small size (25 mm) and the female *P. mexicana*, (2) the downscaled male alone, and (3) an enlarged male alone. The small and the large *P. mexicana* male pictures had a size difference of 40%, which is equivalent to size differences found in nature (Heubel unpublished data). With this technique we created a pair of stimuli that differed only in size. We animated and looped the set of pictures in Adobe Premiere 4.2 and recorded these loops on SVHS tapes showing the fish appearing and moving forward from left to right, disappearing and reappearing and moving from right to left and so forth. The video did not show the fish turning.

Statistical Analysis

We compared copying scores; the relative time spent with the initially less preferred stimulus fish of the preference tests, before and after we gave the opportunity to copy. All statistical tests were non-parametric. Unless noted otherwise, we used Wilcoxon tests for planned comparisons. All p values are two-tailed. Where appropriate, post-hoc pairwise comparisons were corrected using Dunn-Šidák Bonferroni method (Sokal & Rohlf 1995) and thus significance thresholds refer to α' . Data presented in experiment 1b have been published previously (Schlupp et al. 1994). We reanalysed the data and calculated copying scores to confirm compliance with experimental setup, exclusion criteria and statistical analysis used in the other experiments.

Results

Experiment 1: Trials with sympatric P. latipinna as test females and P. formosa as models.

P. latipinna exhibited mate-copying in these experiments. After opportunity to copy, *P. latipinna* spent significantly more time in the preference zone adjacent to the (a) video playback and (b) life stimulus of the initially less preferred and smaller *P. latipinna* male (Tab. 5.2).

Experiment 2: Allopatric P. latipinna as test females and P. formosa as models.

This experiment did not provide evidence that *P. latipinna* females from allopatry show mate-copying when *P. formosa* is the model. We could not reject the null-hypothesis that there is no difference in time allopatric *P. latipinna* females spent in the preference zone in front of the initially less preferred and smaller *P. latipinna* male before and after opportunity for mate-copying of *P. formosa*'s mate-choice (Tab. 5.2).

Experiment 3: Conspecific mate-copying in P. formosa.

P. formosa in these experiments with (a) video stimuli and (b) life stimuli showed mate-copying, as they significantly increased the relative time they spent with the initially less preferred *P. latipinna* male before and after opportunity for copying (Tab. 5.2).

Experiment 4: Sympatric P. mexicana as test females, using P. formosa as models.

P. mexicana exhibited mate-copying with *P. formosa* as the model. Females spent significantly more time with the initially less preferred smaller *P. mexicana* male after observing the smaller male interacting with a heterospecific *P. formosa* model (Tab. 5.2).

Experiment 5: Allopatric P. mexicana as test females, using P. formosa as models.

Allopatric *P. mexicana* females did not exhibit statistically significant mate-copying, although there was a trend in that direction. We were unable to reject the null-hypothesis that there is no difference in time *P. mexicana* females spent in the preference zone in front of the initially less preferred smaller *P. mexicana* male before and after opportunity to copy the mate-choice decision of a *P. formosa* (Tab. 5.2). Nevertheless, unlike the results with allopatric *P. latipinna* (experiment 2) there is still a non-significant trend for allopatric *P. mexicana* females to exhibit heterospecific copying.

Experiment 6: Conspecific mate-copying in P. mexicana.

We also determined if there is conspecific mate-copying behaviour in *P. mexicana* by testing sympatric *P. mexicana* with *P. mexicana* model females with video playback (animated slides). There was a significant difference in time *P. mexicana* females spent in the preference zone near the initially less preferred smaller *P. mexicana* male stimulus before and after opportunity for mate-copying of conspecific mate-choice (Tab. 5.2).

In all control experiments for consistent preferences without opportunity for copying, there was no significant difference in preferences for stimuli between the first and third test phases (Tab. 5.2).

In all experiments controlling for female social shoaling behaviour, there was no significant difference in time spent with female stimuli before and after opportunity for copying.

Tab. 5.2: Results of different mate-copying studies

Experiment	Conspecific / heterospecific	Tested population	Sym- / allopatry	association time [s] small male before median (IQR)	association time [s] small male after median (IQR)	Z	n	^b p (Wilcoxon tests)	copying score [%] median (IQR)	N control 1: n, p	control 1: copying score [%] median (IQR)	N control 2: n, p	control 2: copying score [%] median (IQR)
1a	hetero-	lat SM	sym	132 (98.8)	299 (196.8)	-2.38	8	0.017	19.3 (38.2)	7, NS	0.0 (15.6)	7, NS	0.0 (44.6)
1b ^a	hetero-	lat SM	sym	266.5 (172.5)	387.5 (469.0)	-2.99	20	0.003	17.2 (38.9)	10, NS	-4.2 (9.0)	10, NS	7.6 (29.7)
2	hetero-	lat AS	allo	137 (66.0)	110 (116.0)	-0.24	18	0.811	-2.0 (25.9)	--	--	--	--
3a	con-	for BT	sym	65.5 (124.0)	438 (300.0)	-2.40	10	0.017	77.1 (72.4)	7, NS	0.0 (11.4)	7, NS	9.0 (24.0)
3b	con-	for SM	sym	119 (91.5)	185 (117.3)	-2.57	25	0.01	18.6 (34.1)	12, NS	14.3 (21.7)	15, NS	-8.0 (27.7)
4	hetero-	mex TAM	sym	142 (67.0)	246 (185.5)	-2.56	15	0.011	25.5 (41.0)	10, NS	-1.4 (32.7)	10, NS	0.6 (29.7)
5	hetero-	mex PS0	allo	197 (263.0)	207 (321.0)	-1.71	13	0.087	6.0 (43.6)	5, NS ^c	-2.1 (16.1)	--	--
6	con-	mex TAM	sym	95 (66.3)	236 (188.3)	-2.37	7	0.018	21.5 (40.0)	--	--	--	--

For abbreviations of populations refer to legend of Tab. 5.1.

IQR: interquartile range. Control 1: without opportunity for copying between first and second preference test. Control 2: shoaling control using all females controlling for social effects. ^aData already published in Schlupp et al. (1994). ^bsignificant results are printed in bold. ^csign-test. Copying scores: Percentages shown are relative differences in time spent with initially less preferred male after and before opportunity for copying.

In summary, we found mate-copying in all experiments testing *P. formosa* or sympatric sexual females. We did not detect heterospecific mate-copying in sexual females originating from allopatric populations, although in *P. mexicana* there was a trend towards copying (Tab. 5.3). We also showed that there was conspecific mate-copying behaviour in *P. mexicana* and *P. formosa*. This is the first evidence for mate-copying in these two species.

Comparison of Copying Scores

The relative extent of mate-copying behaviour was independent from the protocol used in the different experiments. We found no relationship between presentation time in which females had the opportunity to observe model females interacting with a male and copying scores (Spearman rank correlation: $r_s = -0.099$, $z = -1.081$, $n = 121$, $p = 0.28$). In addition, graphical analysis of scatter plots did not reveal any impact of presentation duration on copying scores.

We compared copying scores between allopatric and sympatric populations and conspecific versus heterospecific models (see Tab. 5.3). Allopatric and sympatric *P. latipinna* differ in the heterospecific copying score (Mann-Whitney-U-test: $U = 142$, $U' = 362$; $z = -2.48$, $N_1 = 18$, $N_2 = 28$, $\alpha^2 = 0.017$, $p = 0.013$), while *P. mexicana* do not show such a difference (Mann-Whitney-U-test: $U = 80$, $U' = 115$, $z = -0.81$, $N_1 = 13$, $N_2 = 15$, $\alpha^2 = 0.017$, $p = 0.420$; Fig. 5.2).

There is no significant difference in the copying scores between studies in which a conspecific *P. mexicana* or heterospecific *P. formosa* were used as model females (Mann-Whitney-U test: $U = 50$, $U' = 55$, $z = -0.176$, $N_1 = 7$, $N_2 = 15$, $\alpha^2 = 0.017$, $p = 0.860$; Fig. 5.2).

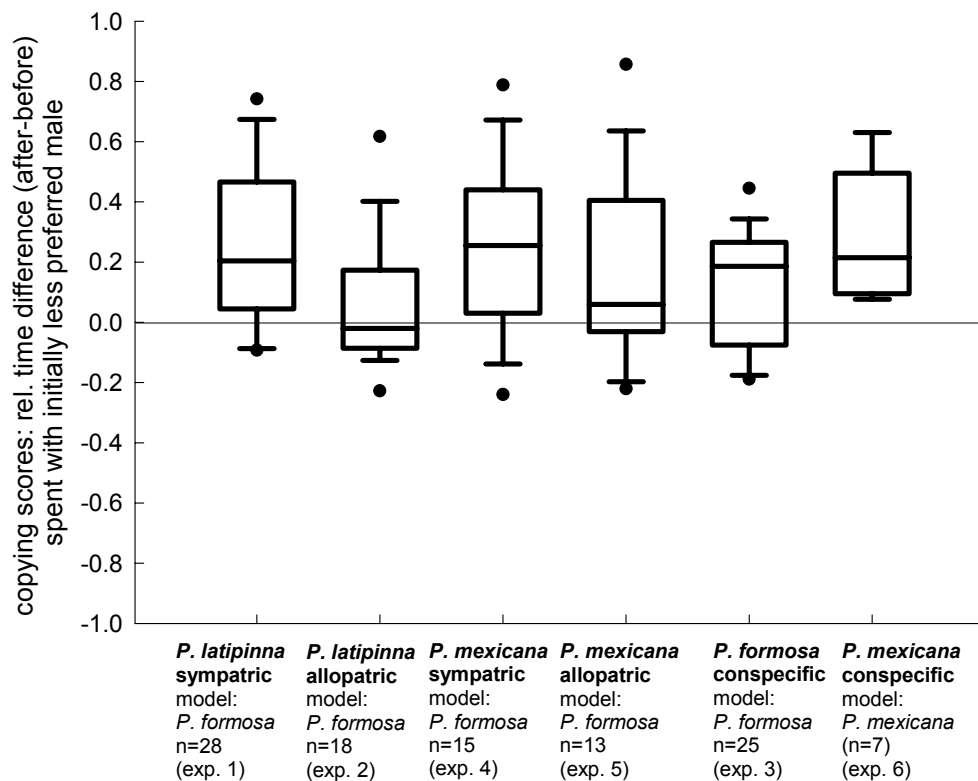


Fig. 5.2: Mate-copying in the mating complex of *P. formosa*. Box plots of copying scores, the relative time differences (before-after opportunity for copying) in allopatric and sympatric populations of *P. latipinna* and *P. mexicana*. First two boxes: *P. latipinna* females from sympatric and allopatric populations with heterospecific model females. Two inner boxes: *P. mexicana* females from sympatric and allopatric populations with heterospecific models. Last two boxes: conspecific models. The lower boundary of the box indicates the 25th percentile and the upper boundary the 75th percentile, the solid line in the centre represents the median. Whiskers indicate the 90th and 10th percentiles. Points show 5th and 95th percentiles. As a reference, a horizontal line at zero is included. Positive data above the line indicate presence of mate-copying, copying scores around zero represent consistency of the initial preference for a male.

Tab. 5.3: Copying scores, the extent of heterospecific mate-copying in studied populations allopatric or sympatric with *P. formosa*

<i>P. formosa</i> model test female	<i>P. formosa</i> sympatric	<i>P. formosa</i> allopatric
<i>P. latipinna</i>	** 20.4% <i>n</i> = 28	ns -2.0% <i>n</i> = 18
<i>P. mexicana</i>	* 25.5% <i>n</i> = 15	ns 6.0% <i>n</i> = 13
<i>P. formosa</i>	** 18.6% <i>n</i> = 25	

* indicates $p < 0.05$, ** indicates $p < 0.01$, ns indicates no significant differences before and after opportunity for mate-copying. Percentages shown are relative differences in time spent with initially less preferred male after and before opportunity for copying. High copying scores indicate a strong mate-copying behaviour.

Discussion

PATTERNS OF MATE-COPYING

We show that the extent of heterospecific mate-copying is highly variable among populations. Mate-copying occurs in sympatric populations of both sexual host species of *P. formosa*. Thus *P. latipinna* and *P. mexicana* males that had interacted visually with *P. formosa* model females increased their attractiveness to conspecific females. Several studies reported conspecific mate-copying for *P. latipinna* (Witte & Ryan 1998; Witte & Noltemeier 2002; Witte & Ryan 2002), indicating the importance of mate-copying in this species.

In our first experiment (1a), we repeated an earlier study (Schlupp et al. 1994) but used video playbacks instead of live stimuli with the same result. The use of video stimuli made it less likely that mate-copying could have been due to cryptic changes in male behaviour, motivation or status that occurred during the presentation phase due to interactions with the test female, the model female, or the other male. This potential confounding effect can now be excluded.

In our experiment on conspecific mate-copying in *P. formosa* using video playback (experiment 3a) we were limited to a very small sample size. The control for shoaling was close to being statistically significant. We therefore decided to analyse our data conservatively and excluded these data from further analysis.

In both allopatric heterospecific mate-copying situations (experiments 2 & 5), females did not significantly copy the mating preference of the Amazon molly.

In summary, we found the same pattern of mate-copying behaviour in both host species systems. While sympatric populations showed strong heterospecific mate-copying, allopatric populations did not. Thus our results support the hypothesis that heterospecific mate-copying is beneficial for males in sympatric populations, at least for the specific case of this mating complex. In general, the adaptive value of mate-copying behaviour is not known yet. Our results indicate that mate-copying in *P. latipinna* (Witte & Ryan 1998; Witte & Noltemeier 2002; Witte & Ryan 2002) is not a non-specific result with any female model. The absence of heterospecific mate-copying in females from allopatry suggests that mate-copying is a specific response relative to the model female used. This interpretation is consistent with previous studies showing that *P. latipinna* females can discriminate between *P. formosa* and *P. latipinna* females (Schlupp & Ryan 1996).

Our use of a population from very recent sympatry allows a glimpse at the evolution of mate-copying. We know that sympatry in the San Marcos river drainage has existed for only about 50 years (Brown 1953), approximately 100-150 generations (Hubbs 1964). Therefore, the evolution of heterospecific mate-copying must have been rapid on an evolutionary time scale (Berthold 1992). While sympatric *P. latipinna* originating from the San Marcos river (SM) showed a copying score of 20.4%, those from allopatric *P. latipinna* originating from the same river (AS) and only 10 km upstream had a negative copying score (Tab. 5.1). The rapid acquisition (whether evolved or learned) of this behaviour suggests heterospecific mate-copying is an adaptation.

Alternatively, mate-copying might be due to individual learning and sexual females might learn that Amazon mollies are adequate models. At least for large male body size (Marler & Ryan 1997), Amazon mollies have sexual preferences identical to those of the sexual females, rendering them adequate models. These interpretations need to be considered cautiously. We only studied one population of *P. latipinna* in allopatry and one in sympatry. Gabor & Ryan (2001) showed there was substantial variation in male mate preferences of *P. latipinna* within the range of both sympatry and allopatry, suggesting caution in any strong conclusion from restricted sampling. Furthermore, in *P. mexicana*, there was no significant difference in the copying scores between the sympatric and the allopatric population; although the pattern was similar to *P. latipinna* (Tab. 5.2). To argue that mate-copying behaviour has been influenced by the presence/absence of *P. formosa* requires study of additional populations.

BENEFIT TO MALES

In a purely sexual population, mate-copying situations provide males with immediate and delayed benefits. The immediate benefit is due to access to the (model) female. Interacting (and mating) with a conspecific female provides a fitness benefit since it directly increases a male's fitness. The delayed benefit derives from mate-copying. It increases future probabilities of gaining mates. In populations with Amazon mollies, males mating with Amazons gain a delayed benefit due to increased attractiveness to sexual conspecifics. In sympatry, sexual interactions of males will be observed by both conspecific and heterospecific females. Thus matings might result in males being more attractive to additional heterospecifics. Therefore, the males benefit derived from conspecific mate-copying, might simultaneously incur a cost via increased attractiveness to Amazon females. In mixed mating situations with sexual and asexual females, *P. formosa* actively block sexual females from mating with males (Foran & Ryan 1994). Hence, it is crucial to differentiate between female choice and male choice. Female mate-copying

affects male mate-choice decisions only by altering males' encounter rates with potential mates. But increased encounter rates with Amazon mollies need not lead to more mating since males can always forsake matings with Amazons. In various studies, it has been shown that males of the sexual host species *P. latipinna* and *P. mexicana* can discriminate between conspecific females and heterospecific Amazons (Schlupp et al. 1991; Ryan et al. 1996; Schlupp & Ryan 1997; Gabor & Ryan 2001). This way they might selectively exploit their increased attractiveness with conspecifics and consequently reduce the "cost" of increased attraction for *P. formosa*.

To what degree the male's benefit from increased attractiveness to conspecific females could be offset by a cost due to his increased attractiveness to heterospecific females depends on several variables. If being more attractive to Amazons means that males actually mate more frequently with Amazons and if mating is costly, males might not gain a net-benefit through mate copying. If such were the case, the net-benefit to males of heterospecific mate-copying will depend partly on the relative strength- the copying scores - of heterospecific and conspecific mate-copying.

In our experiments the copying score in Amazons copying conspecifics (experiment 3b) is slightly lower than copying scores in sympatric studies with sexual and asexual females involved (Tab. 5.2). In addition, the cost of increased attractiveness to Amazons depends on the ratio of sexual and asexual females in a population. It is not yet clear, however, how strong this effect will be, for example, if Amazons outnumber the sexuals. The proportion of *P. formosa* may range from 0 – 100% in the field (Hubbs 1964; Balsano et al. 1989; Heubel & Schlupp pers. obs.). In a population with far more unisexual Amazons than sexual conspecific females, it is more likely that a male increases its attractiveness to other close-by observing Amazon mollies than to sexual females.

COPULATIONS AS CUE

From the male's point of view, another benefit of heterospecific matings that has been overlooked so far is the exploitation of the signal function of this behaviour. Like an ornament, attempted and actual copulations can be considered as behaviour with signal value (Bradbury & Vehrencamp 1998; Negro & Grande 2001). It may indicate the presence and quality of a male. This approach places mate-copying in the context of a social network (McGregor & Peake 2000; Matos & Schlupp [in press] 2004). Assuming a copulation per se is a cue, even copulations with females of a different species, such as the Amazon molly or with other males, may be a sexual signal and in itself beneficial to perform. This aspect of heterospecific or homosexual mating attempts raises the question why those copulations seem so rare in nature. They may have been undetected in the field and underestimated in the laboratory in many species. Especially in populations with high frequencies of Amazon mollies, heterospecific copulations might be a method to attract the few remaining sexual females.

Although it seems counterintuitive, we argue that males strongly benefit from matings with heterospecific females, both via the quantitative increase of attractiveness to conspecific females, and the qualitative signalling function of this behaviour. By courting and copulating with a model female, a male is signalling its property of being a male.

Chapter 6: When does it pay off for males to discriminate?

A game theoretical approach to study the stability of the unisexual / bisexual mating complex of *Poecilia formosa*

The mating complex of *Poecilia formosa* is an extraordinary exception among vertebrates (Vrijenhoek et al. 1989). This gynogenetic all-female species is ovo-viviparous and has internal fertilisation. Females depend upon sperm to trigger embryogenesis to produce asexually all-female offspring (Hubbs & Hubbs 1932). Thus, *P. formosa* “seduces” and obtains sperm from closely related males of host species that exist in mixed shoals with *P. formosa*. Therefore, *P. formosa* can be considered a sexual-parasite. This asexual / sexual mating complex is a model system to study evolution and function of sexual preferences and mate choice.

The main focus of the research project presented in this thesis is the question, how coexistence of Amazons and its host species can be maintained. The previous chapters present data on field ecology and behavioural experiments on mate choice to approach that question.

The aim of this theoretical approach is to explore under which circumstances – theoretically – evolutionary stable strategies (ESS) (Maynard Smith 1972; Maynard Smith 1983; Parker 1984; Grafen & Johnstone 1993) might be present and contribute to the coexistence of asexually and sexually reproducing females.

As suggested in chapter 3, the question, when it pays off for males to enforce preferences for conspecific females, should be dealt with using an asymmetric game theoretical approach (Maynard Smith 1979; Maynard Smith 1982; Parker 1990; Pruett-Jones 1992; Grafen & Johnstone 1993; Beaugrand 1997). The presented game will explore under which circumstances sexual host males of *P. latipinna* should (or should not) enforce preferences for conspecific sexual females in mixed shoals with unisexual *P. formosa*.

In asymmetric games, the two players fill different roles (e.g., a male is interacting with a female, etc.). The roles are known to both players (for example, they both know which of the two is a female). The roles may affect the pay-offs or even the available strategies (males and females have different options), but such differences may also be absent (e.g. males may be of different size, attractiveness, choosiness, courting or coercing differently; females may be sexual or asexual).

In an asymmetric game, we need to write down the payoffs for both roles, i.e., we have two payoff matrices (“bimatrix game”). These are often written in one table as shown in Tab. 6.1: The figures in the lower right corners of the cells are the payoffs to the individual in role A (assume a male), whereas the figures in the upper right corners are the payoffs to role B (assume a female). In each case, the focal individual plays the first strategy in the parenthesis against an opponent with the second strategy. For example, $E_A(R_2, R_1)$ denotes the expected payoff to someone in role A if he plays R_2 (strategy 2, lets say not discriminating between sexual and asexual females) against an opponent who is in role B (a female) and plays R_1 (strategy 1, lets say being sexually reproducing).

Tab. 6.1: General bimatrix of asymmetric games. $E_a(R_1, R_2)$ is the expected payoff, if player in role A plays strategy R_1 against a player in role b playing strategy R_1 (after E. Kisdi, University of Turku).

		role B	
		R_1	R_2
role A	R_1	$E_B(R_1, R_1)$ $E_A(R_1, R_1)$	$E_B(R_2, R_1)$ $E_A(R_1, R_2)$
	R_2	$E_B(R_1, R_2)$ $E_A(R_2, R_1)$	$E_B(R_2, R_2)$ $E_A(R_2, R_2)$

CONDITIONAL STRATEGIES

In asymmetric games, strategies are conditional: “If in role A then play I, and if in role B then play J”. A typical example is the Assessor strategy: “If you are the stronger, play Hawk, if you are the weaker, play Dove”(Parker 1984).

The shorthand notation (I,J) means “play I when in role A and play J when in role B”.

ESS IN AN ASYMMETRIC GAME

Asymmetric games are evolutionary stable strategies (ESS), if no mutant can invade a population where almost everyone plays (I,J). Assume that the mutant plays I' when in role A. It will encounter opponents in role B who play J, and its payoff is then $E_A(I', J)$.

The mutant is doing less well than the resident if $E_A(I', J) < E_A(I, J)$. Similarly, a mutant J' cannot invade if $E_B(J', I) < E_B(J, I)$. If these two conditions hold for every I' and J' different from I and J respectively, then (I,J) is an ESS.

ASYMMETRIC GAMES HAVE NO MIXED ESS

However, asymmetric games will never have mixed ESSs. Suppose there would be an ESS that plays a mixed strategy I when in role A. Let R_1 and R_2 be two pure strategies used by I. By the Bishop-Cannings theorem, we must have $E_A(R_1, J) = E_A(R_2, J) = E_A(I, J)$ (Parker 1984). This means that R_1 and R_2 are strategies that violate the ESS condition (e.g. with $I' = R_1$, it is not true that $E_A(I', J) < E_A(I, J)$).

A first matrix

This asymmetric game theoretical matrix on strategies in the asexual / sexual mating complex of *P. formosa* has players of two roles. Players are either male or female. Both roles have two strategies: males can be either choosy and mate only with conspecific females, rejecting Amazons, or they may be indiscriminate and try to mate indiscriminately with every female they encounter – asexual and sexual females. Players in the role of a female may use the strategy of being sexual or asexual. The pay-off matrix is presented in Tab. 6.2. Benefits occur when fitness increases, costs may be search costs and handling costs. Costs and benefits are presented in Tab. 6.3 for males, and in Tab. 6.4 for females. One should keep in mind that this is no more than a first, but important step to a more detailed work on theoretical modeling in the mating complex of *Poecilia formosa*.

Tab. 6.2: When does it pay off to be choosy?

Asymmetric game theoretical matrix. Males may be choosy or mate indiscriminately with females, females may be sexual or asexual and mate with either choosy (= attractive, courting) or indiscriminate (= unattractive, coercing) males.

In each cell the upper term represents the pay-off from the male's point of view, the lower term shows the pay-off from female's perspective. b = Fitness benefit from mating f = frequency of the asexual females, c = cost due to courtship and mating (time, feeding, missed matings), risk of predation, energy loss, sperm, etc.; h = cost of searching a mate and delaying mating, K_s = fitness reduction due to mating with lower quality male for sexual females, K_a = fitness reduction due to mating with lower quality male for asexual females, $K_s \approx 1$ if we assume that for Amazons any amount and quality of sperm is sufficient to trigger embryogenesis.

		Female	
		sexual p	asexual $1-p$
Male	choosy q	$b - c - h f$ $b - c - h$	$- h f$ $- h$
	indiscriminate $1-q$	$f b - c$ $K_s b - c$	$- c$ $K_a b - c$

Tab. 6.3: From the male's point of view: Expected pay-offs and explanations how they have to be calculated for the male players. Males may play two strategies in a population: either being choosy and rejecting asexual females or indiscriminately mating with any female they encounter.

Male	Female	Payoff	Comment
choosy	sexual	$b - c - hf$	Males benefit from matings with sexual females (b) and have costs of courtship behaviour towards sexual females (c). Males are choosy and reject Amazons, thus, additional costs arise (depending on frequency of Amazons (f)) for actively searching appropriate females, rejecting asexuals and postponing matings (h).
	asexual	$- hf$	Choosy males reject mating with asexual females, thus frequency dependent (f) search costs arise (h), but no offspring, therefore no benefit (b).
indiscriminate	sexual	$fb - c$	Depending on frequency of Amazons, males benefit from matings with sexual females (b) and have costs of courtship behaviour towards sexual females (c). Since males are not choosy, no search costs arise (h).
	asexual	$- c$	Indiscriminate males have no search costs (h), but cost of courtship and mating (c). However, no offspring, therefore no benefit from mating (b).

Tab. 6.4: From the female's point of view: Expected pay-offs and explanations how they have to be calculated for the female players. Females may play two strategies in a population: either being asexual or sexual. I assume that choosy males are more attractive mates.

Female	Male	Payoff	Comment
sexual	choosy (high-quality)	$b - c - h$	Females benefit from matings (b) but have costs of involvement in courtship and mating (c), and search costs (h).
	indiscriminate (low-quality)	$K_s b - c$	Sexual females benefit from mating with males (b). Assuming that indiscriminate males are of lower quality, b depends on quality of males. Hence, benefit from mating is reduced accordingly (K). Females have also costs of courtship interaction and mating (c). No search costs arise for females (h).
asexual	choosy (high-quality)	$- h$	Amazons are rejected by choosy males (no b), but still search costs arise since they also have preferences for choosy males, which they actively approach (h).
	indiscriminate (low-quality)	$K_a b - c$	Asexual females benefit from mating with males (b). Assuming that indiscriminate males are of lower quality, b depends on quality of males. Hence, benefit from mating is reduced accordingly (K). Females also have costs of courtship interaction and mating (c). No search costs arise for females (h).

Perspectives

Ideally, in such a model different pay-offs depending on actual costs and benefits should be considered more detailed. Hereby, frequency dependent and environmentally or genetically constrained costs and benefits of both strategies can be incorporated into a model, including probability and extent of mate-copying behaviour of Amazons and sexual females, and density or frequency of sexual and asexual females.

This model could eventually integrate data on density and relative proportion of Amazons within the complex, sex ratio, body size, receptivity, seasonal and spatial heterogeneity of the environment (e.g. turbidity), from field work (chapter 2) the magnitude and range of these parameters are now at hand. The same applies to behavioural data on the strength of male mating preferences (chapter 3 and 4) and on frequency (or experience) -dependent extent of conspecific and heterospecific female mate-copying behaviour (chapter 5). The probability of increasing a male's attractiveness by mating with females (via mate-copying) (Schlupp et al. 1994; Witte & Noltemeier 2002; Witte & Ryan 2002; Witte & Massmann 2003; Heubel et al. submitted) should be incorporated. Yet, sexual harassment as a decrease of a male's attractiveness could also be incorporated (Magurran & Seghers 1994a; Magurran & Seghers 1994b; Griffiths 1996; Schlupp et al. 2001; Evans et al. 2003; Pilastro et al. 2003; Plath et al. 2003). Results obtained from theoretical models will allow for predictions on the stability of the mating complex of *P. formosa* that can be tested experimentally.

Chapter 7: General Discussion and Conclusion

How can coexistence be maintained in the sexual-asexual mating complex of *Poecilia formosa*? Coexistence of closely related species that depend upon the same resources is a general paradox and addressed by many ecologists (e.g. Hutchinson 1961; MacArthur 1965; Roughgarden 1972). In general, it is expected that ecological niches segregate to avoid competition for the same resource (e.g. MacArthur 1965; MacArthur & Lewins 1967). In the special case of the species complex of unisexual / bisexual fishes, this is complicated by the fact that niches can not be too strongly separated because *P. formosa* depends on sperm supply of its competitor, the closely related syntopically occurring host species. However, data presented in chapter 2 do not indicate niche segregation. Amazon mollies *P. formosa* and sexual females may not only compete for resources but also for access to males (Foran & Ryan 1994). Female - female competition could become even more relevant when sex ratios are highly biased towards females. This aspect needs further investigation.

Studying the population ecology in six different sympatric populations of *P. formosa* and *P. latipinna*, revealed a few fundamental differences between the two species. In the spring habitat (COM) in Central Texas, Amazons had extremely low abundances whereas the environment was extraordinary stable in comparison to all other habitats studied. A similar pattern has also been observed by Balsano et al. (1981) in the *P. formosa* / *P. mexicana* complex where *P. formosa* was less abundant in the headwater sections and more abundant further downstream in a river-system in Mexico. But it is not clear whether this also applies to the *P. formosa* / *P. latipinna* complex since both species have been introduced in Central Texas (Brown 1953; Drewry et al. 1958; Hubbs 1964) and until very recently, *P. formosa* was absent in the spring habitat (Schlupp et al. 2002). It could also be the beginning of an invasion.

Other general differences between the two species that may explain the abundance of *P. formosa* were the fact that higher densities of Amazons correlated with lower overall densities of fishes in samples. Furthermore, relatively more Amazons were sampled in communities with relatively more predators. This suggests that *P. formosa* has a slightly better ability to cope with harsh conditions than the sexual species.

Variables that explained the abundance of Amazons within the asexual / sexual complex, were mainly the same physicochemical parameters that were responsible for the general underlying temporal and spatial variation. After correcting for the general variation, the relative proportion of Amazons was best explained by the heterogeneity of the habitat, community density, predation risk, and life-history parameters of the sexual host species. Nevertheless, I could not observe any clear niche differentiation and thus expect resource competition to exist.

How can this asexual / sexual mating complex remain stable under these conditions? None of the sampled populations reflect a stable equilibrium (perhaps besides the spring population COM). I suggest that environmental disturbances (Hutchinson 1961, Pickett & White 1985; Yodzis 1986) as heavy rainfalls and flash floods in the spring and autumn, rapid and large drops in temperature in the winter, and droughts in the summer prohibit an equilibrium to arise. In the typical open patchy mosaic habitats (Southwood 1977) of mollies, they must regularly invade and re-establish the population, and thus instability of the environment may be an explanation for the persistence of *P. formosa*.

Observing no apparent niche segregation between these two coexisting species, how can we explain that they do not outcompete each other in sympatric populations? Theoretically, asexual organisms have a two-fold advantage (Williams 1975; Maynard Smith 1978) of asexual reproduction since they do not incur the cost of sex. Thus, asexual populations grow at twice the rate as sexual females. However, this assumes Amazons and sexual females have the same fecundity and a primary sex ratio of 1:1. Some studies show that the advantage of asexual reproduction in unisexual / bisexual species complexes is smaller than expected by theory (Hubbs 1964; Case & Taper 1986).

The evolutionary age of Amazons is known to be comparatively old for asexual organisms (Lynch & Gabriel 1990; Avise et al. 1991; Scharl et al. 1995; Möller 2001). This raises the question of whether there might exist an equilibrium of advantages and disadvantage of asexuality in this mating complex that leads to persistence of Amazons. The two-fold cost of sex accounts for short-term advantages of asexual reproduction (Williams 1975), but the long-term disadvantages due to slower genetic adaptation and accumulation of deleterious mutations (Muller 1964; Kondrashov 1988; Lynch & Gabriel 1990) might have an increasingly negative effect on fitness of asexual females, as time goes by. This decreasing 'genetic' fitness of asexuals might counterbalance the two-fold advantage of asexual females and lead to an equilibrium and thus maintenance of coexistence.

Nevertheless, *P. formosa* seems successful. I found a seasonal increase in the relative abundance of Amazons, and in general, *P. formosa* was more abundant than the sexual females. I propose that eventually occurring environmental disturbances balance the faster population growth of asexual females. However, the advantage of asexual reproduction also provides a headstart when re-establishing a population after environmental disturbances. This aspect should be tested experimentally under different environmental conditions

Possibly, this general underlying fitness-advantage of *P. formosa* balances genetic, ecological, or behavioural disadvantages due to male mate discrimination they have to cope with. In mixed populations of *P. latipinna* and *P. formosa*, males encounter two types of potential mates: conspecific sexual females and gynogenetic sexual-parasitic Amazon mollies. Males should discriminate between sexual females and reject mating with *P. formosa* because they do not get any benefits from matings with the asexuals. This behavioural aspect could also influence the persistence of *P. formosa*. In several studies that routinely ignore the natural context (e.g. experience and familiarity with both types of females, seasonality, turbidity), males had a preference to mate with conspecific females (Hubbs 1964; Woodhead & Armstrong 1985; Schlupp et al. 1991; Ryan et al. 1996; Schlupp & Ryan 1997; Gabor & Ryan 2001; Niemeitz et al. 2002). But males do not always prefer conspecific females: Preferences can be seasonally influenced suggesting that males show only preferences for conspecific females at times when most females are receptive in nature and thus distinguishing between the two types of females is most beneficial (chapter 3). I also show that the threshold for male mating preferences for both types of females is higher in turbid water (chapter 4). Under natural conditions in a turbid environment, females may be more difficult to detect and communication may be impaired. Thus, distinguishing between sexual and asexual females may be difficult and time-consuming and males may be more likely to err.

In summary, there is a tendency that males do not strongly prefer conspecific females and thus do not discriminate perfectly between the two types of females. I therefore argue that costs for being indiscriminate cannot be too high. Males do not invest in offspring other than by

providing sperm and it seems unlikely that males are generally sperm limited. In addition, mating seems not time consuming. It is not known yet, how costly mating actually is for males; this aspect needs further investigation.

At the same time, costs for distinguishing between sexual and asexual females may be comparably high. Turbid water complicates mate detection and discrimination. Consequently, the risk of rejecting a conspecific receptive female by mistake might be too high, especially when asexual females mimic their sexual congeners, as shown in the asexual/sexual *Poeciliopsis* complex (Lima et al. 1996). Due to their sexual cycle, only few females are receptive at any given time. Therefore, even among sexual females, males should prefer to mate with receptive females, although females are able to store sperm for several months. As Schlupp et al. (1991) suggested, for males it may pay off rather discriminating between receptive and non-receptive females than between the two types of females. Costs of mate discrimination are investment in time and the effort of assessing females not only for receptive status but also for the type of female. Thereby, males may miss other opportunities to mate with appropriate females, expose themselves to a higher predation risk, or one can speculate that males may even be perceived by the females as sexually harassing and thus females may reject mating with males if assessment of females is too time consuming.

I suggest that Amazons benefit from situations where costs of male mate discrimination are comparably high. Indiscriminate male mate choice can be explained by mate-copying behaviour. Males may benefit from mating with Amazons because it increases their attractiveness to other females and thus the probability to obtain further matings. In sympatric populations, females show a high extent of mate-copying behaviour (chapter 5, Heubel et al. submitted). Thereby, it might become less costly for males to search for females that accept matings. In this context, copulation behaviour itself may be a cue for females to detect males. This could be another explanation for males copulating with asexual females. It might attract conspecific females and increases the likelihood to obtain matings. The costs of male mate discrimination and benefits via mate-copying also depend on the frequency and density of Amazons in a population. Costs should become higher when it is more likely for males to encounter the wrong type of females. This aspect highlights the importance of the natural context on male mating decisions.

In conclusion, there are two aspects that contribute to the coexistence of bisexual and unisexual species in the mating complex of *P. formosa*. The first aspect is that coexistence can be explained by environmental stochastic disturbances that avoid sexual and asexual members of the complex to outcompete each other and thus explain the ecological persistence of *P. formosa*. The second aspect is that the payoff for perfect discrimination is plastic and depends on the social context, the receptive status of females, the environmental conditions, and the probability to encounter the two types of females in nature.

Summary: Population ecology and sexual preferences in the mating complex of the unisexual Amazon molly *Poecilia formosa*

The Amazon molly *Poecilia formosa* is a gynogenetic all-female ovo-viviparous fish. Gynogenesis is a special form of parthenogenesis; sperm is needed to trigger embryogenesis. Males do not contribute to the genome of ameiotically produced all-female offspring. In this unique mating system, asexually reproducing females have to rely on heterospecific matings with males of two closely related sexual host species, *Poecilia latipinna* and *Poecilia mexicana*. This asexual / sexual species complex is a unique model system to study the stability of coexistence of closely related bisexual and unisexual species.

In mixed shoals of a sexual host species and the sexual-parasite *P. formosa*, sperm donating males mate with conspecific sexual females and heterospecific asexual females. Obviously, males benefit from mating with conspecific females, whereas mating with the unisexual *P. formosa* does not increase a male's fitness. Therefore, males should discriminate between the two types of females.

Under perfect mate discrimination, *P. formosa* would disappear. On the other hand, asexually reproducing females theoretically have a faster population growth than sexually reproducing females because they do not have to incur the cost of producing males. This advantage of asexual reproduction would lead to increasingly high proportions of asexual *P. formosa* in mixed populations. By outcompeting its sexual host species, the sexual-parasite *P. formosa* would also disappear. The major question addressed in this thesis was to study the coexistence and stability of the asexual / sexual mating complex of *P. formosa* and which ecological and behavioural factors might contribute to the persistence of the *P. formosa*.

In **chapter 2**, an ecological field study is presented and discussed. The aim of this study was to investigate possible niche differentiation and population dynamics in this species-complex. Therefore, the ecology of the coexistence of the Amazon molly and the closely related sperm donating bisexual species *P. latipinna* has been studied in six sympatric populations in South (old sympatry) and Central (young sympatry) Texas visited nine times between February and September 2001. Environmental heterogeneity, the spatial and temporal variation and stability of habitat properties, the community structure, species diversity, predation risk and life-history parameters (e.g. sex-ratios, juveniles, body size) within the asexual / sexual mating complex, and relationships of frequency of *P. formosa* with other observed variables were of particular interest. Studying the population ecology revealed a strong spatial and temporal heterogeneity among samples. In most samples, *P. formosa* was more abundant than the sexual females. The relative abundances of *P. formosa* varied highly among populations, but there also was a tendency that the proportion of *P. formosa* increased seasonally. Higher densities of Amazons correlated with overall lower densities of fishes in the samples and relatively more Amazons were sampled in communities with relatively more predators. At the end of the season, *P. formosa* was larger and more abundant than the sexual females, and the sex-ratio became even more biased towards females. Variables that explained the abundance of Amazons within the asexual / sexual complex, were mainly the same physicochemical parameters (water temperature, turbidity, chlorophyll concentration) that were also responsible for the general

underlying temporal and spatial variation. In a multiple regression on factors of a principal component analysis of the general underlying variation of the sampled field sites, the relative proportion of Amazons was best explained by the heterogeneity of the habitat, community density, predation risk, and life-history parameters of the sexual host species. I conclude that the typical properties of the habitat as a whole are the best predictors of the relative abundance of *P. formosa* within the asexual / sexual mating complex and suggest that environmental stochastic disturbances (e.g. flooding events, droughts, drops in temperature) are a possible explanation to maintain the coexistence of the Amazon molly *P. formosa* and its host.

While chapter two concentrates on ecological factors that might explain the stability of this asexual / sexual mating complex, **chapter 3, 4, and 5** focus on behavioural aspects that might contribute to the persistence of Amazon mollies. In mixed populations of *P. latipinna* and *P. formosa*, males encounter two types of potential mates: conspecific sexual females and gynogenetic sexual-parasitic Amazon mollies. Because *P. latipinna* males do not benefit from matings with *P. formosa* they should avoid mating with them. Male mate choice might become crucial in this context.

The major question I addressed in **chapter 3**, was to test frequency dependent or seasonally influenced behavioural plasticity in male mating preferences in natural mixed *P. formosa* / *P. latipinna* populations that may contribute to the maintenance of stability in this asexual / sexual mating complex. I studied male mate preferences in *P. latipinna* originating from several populations in South and Central Texas. Association time of males with syntopic adult females of *P. latipinna* or *P. formosa* was measured in a standard visual simultaneous dual choice set-up. There was no general preference for conspecific sexual females in any population. Within populations, there was a high seasonal variation in male association patterns. There was no difference among mixed populations with different relative densities of Amazons. Male mating preferences were seasonally influenced. Males spend less time with asexual *P. formosa* during spring. Male body size and relative proportion of Amazons in the habitats males originated from did not influence male preferences. I discuss how plasticity in male mate choice preferences might contribute to the maintenance of the stability in this sexual / asexual mating complex. I also discuss potential causes of the lack of a sexual preference for conspecific females and whether non-discriminating male mating behaviour can be adaptive in this complex.

Chapter 4 studies the impact of turbidity as an environmental factor that is highly variable among different sympatric populations on male mating preferences of the bisexual-unisexual *P. latipinna* / *P. formosa* species complex. Turbid water interferes with visual communication in Poeciliids. Male mate preferences were studied in the asexual / sexual mating complex of the gynogenetic Amazon molly *Poecilia formosa* in clear and turbid environments. Association time of *P. latipinna* males with conspecific sexual and heterospecific asexual females was sequentially measured in clear and turbid water. It turned out that turbidity has an influence on male mate choice behaviour. Males spent less time with any kind of female stimulus in turbid water. Interestingly, there was no preference for conspecific sexual females – neither in turbid water nor under clear conditions. Also, origin of males and acclimatisation to turbid water had no effect. It is discussed how turbidity as a source of visual noise might affect communication among individuals and how this environmental factor might contribute to the stability of this sexual-aseexual mating complex in nature.

Chapter 5: Courtship and mating of a male and a female in a shoal are not isolated dyadic interactions but rather elements of a social network. Conspecific and heterospecific females can observe these interactions as an audience. Males might benefit from mating with *P. formosa* because heterospecific imitation behaviour of sexual females that copy mate choice decisions of the unisexual *P. formosa* increases the males' attractiveness and thus enhances probability to obtain future matings with conspecific females. This is the only known case of mate-copying between species, and thus a system in which the potential for mate copying could be influenced by the presence or absence of *P. formosa*. Here I show that mate-copying is exhibited by the sexual host species *P. mexicana* (Atlantic molly) and *P. latipinna* (Sailfin molly), and the asexual *P. formosa*. In both systems, sexual and asexual females copy each other's mate choice decisions in sympatry, but heterospecific mate-copying seems to be absent in allopatry. Males benefit from heterospecific matings with Amazon mollies because these increase their attractiveness to the conspecific sexual females. In mixed shoals, mate-copying potentially imposes a cost as it also increases a male's attractiveness to heterospecific females. I argue that the net-effect of mate-copying is beneficial to males because the relative strength of mate-copying is lower in Amazon mollies. Furthermore males can choose to reject matings with Amazon mollies. I hypothesize that an added benefit to males lies in the signal value of copulations.

The different behavioural aspects of the previous chapters lead to the fundamental question: When does it pay off for males to discriminate between sexual and asexual females as potential mates in the mating complex of *P. formosa*? In **chapter 6**, I suggest an asymmetric game theoretical model to address this question of male mate discrimination by integrating male and female behaviour. As a starting point, the prospective pay-off matrix for future theoretical modelling work on the stability of this mating complex is presented. Eventually, such a model could also integrate the extent of female mate-copying behaviour, female receptivity, sexual harassment, and environmental conditions such as turbidity that might affect the ability of the sexes to communicate effectively. Results obtained from theoretical models will allow for predictions on the stability of the mating complex of *P. formosa* that can be tested experimentally.

In **conclusion**, there are two aspects that contribute to the coexistence of bisexual and unisexual species in the mating complex of *P. formosa*. The first aspect is that coexistence can be explained by environmental stochastic disturbances that avoid sexual and asexual members of the complex to outcompete each other and thus explain the ecological persistence of *P. formosa*. The second aspect is that the payoff for perfect discrimination is plastic and depends on the social context, the receptive status of females, the environmental conditions, and the probability to encounter the two types of females in nature.

Population ecology and sexual preferences in the mating complex of the unisexual Amazon molly *Poecilia formosa* (GIRARD, 1859)

Populationsökologie und sexuelle Präferenzen im Paarungskomplex der reinen Weibchenart *Poecilia formosa*

Das Fortpflanzungssystem des lebendgebärenden Zahnkarpfens *Poecilia formosa* (GIRARD, 1859) (Poeciliidae, Teleostei) stellt eine Ausnahme im Tierreich dar. *P. formosa* ist eine reine Weibchenart, die sich gynogenetisch fortpflanzt. Bei der Gynogenese handelt es sich um eine spermienabhängige Parthenogenese. Um die Embryogenese auszulösen, benötigt *P. formosa* Spermien als Stimulus. Daher kopulieren die Amazonenkärpflinge mit Männchen nah verwandter Arten, mit denen sie in gemischten Schwärmen vorkommen. Folglich kann man *P. formosa* als einen Sexualparasiten bezeichnen. Als sexuelle Wirtsarten dienen in Texas der Breitflossenkärpfling *Poecilia latipinna* und in Mexiko vorwiegend der Atlantikkärpfling *Poecilia mexicana*. Von extrem seltenen Ausnahmen abgesehen, leisten die Männchen keinerlei genetischen Beitrag zu den Nachkommen von *P. formosa*. Darum sollte man erwarten, dass die Männchen der sexuellen Wirtsarten zwischen den arteigenen und artfremden Weibchentypen unterscheiden und Verpaarungen mit den arteigenen Weibchen vorziehen. Wenn die Männchen zwischen den Weibchen differenzierten, würde dies dazu führen, dass *P. formosa* aus den gemischten Populationen verschwände. Andererseits besitzen die unisexuellen Amazonenkärpflinge der Theorie zufolge ein höheres Vermehrungspotential als die sich sexuell fortpflanzenden Weibchen, da sie keine Söhne produzieren. Verfolgt man die Theorie weiter, würde der Vorteil der asexuellen Reproduktion zu einem zunehmend hohen Anteil an *P. formosa* in den gemischten Populationen führen. Das sich daraus ergebende Verschwinden der zweigeschlechtlichen Wirtsart würde unmittelbar auch das Aussterben der von ihr abhängigen Amazonenkärpflinge nach sich ziehen. Beide Ansätze erlauben keine stabile Koexistenz im Fortpflanzungskomplex von *P. formosa*. Zwei verschiedene Hypothesen erklären mit unterschiedlichen Ansätzen die Koexistenz in Paarungskomplexen von unisexuellen Fischen und ihren nah verwandten Wirtsarten. Zum Einen kann ökologische Nischendifferenzierung zur Koexistenz führen, zum Anderen eine Regulation durch das Verhalten der Männchen.

In meiner Dissertation beschäftige ich mich mit der Koexistenz von *P. formosa* und ihrer texanischen Wirtsart *P. latipinna*. Dabei konzentriere ich mich auf die beiden o.g. Hypothesen und untersuche, welche Rolle ökologische und verhaltensbiologische Aspekte bei der Stabilisierung und dem Fortbestehen des *P. formosa*-Komplexes spielen.

Anhand verschiedener Populationen wurde die zeitliche und räumliche Dynamik des Fortpflanzungskomplexes und seiner Umwelt untersucht. Dazu wird im **2. Kapitel** eine freiland-ökologische Studie vorgestellt und diskutiert. Ziel dieser Studie war es, zu untersuchen, ob möglicherweise eine Nischendifferenzierung zwischen *P. latipinna* und *P. formosa* vorliegt.

Vor dem Hintergrund dieser Fragestellung wurde die Ökologie der Koexistenz und Populationsdynamik des Amazonenkärpflings und ihrer Wirtsart in sechs unterschiedlichen Habitaten in Süd- und Zentral-Texas untersucht. Die ausgewählten Populationen wurden zwischen Februar und September 2001 in regelmäßigen Abständen jeweils neunmal untersucht. Im Vordergrund stand dabei, zu erforschen, welche Faktoren die relative Häufigkeit von *P. formosa* erklären.

In den meisten Stichproben war *P. formosa* deutlich häufiger vertreten als die Weibchen der Wirtsart. Die relative Häufigkeit der Amazonenkärpflinge variierte sehr stark zwischen den Populationen. Insgesamt stieg der Anteil von *P. formosa* innerhalb des Fortpflanzungskomplexes im Laufe des Untersuchungszeitraums an. Eine höhere relative Abundanz von *P. formosa* korrelierte mit einer abnehmenden Individuendichte in der Lebensgemeinschaft insgesamt. Interessanterweise wurden relativ mehr *P. formosa* in Habitaten gefangen, in denen auch der Anteil an räuberischen Fischen höher war. Gegen Ende der Fangsaison war *P. formosa* durchschnittlich größer und häufiger als *P. latipinna* Weibchen. Gleichzeitig nahm der Anteil der Männchen ab. In einer Hauptkomponentenanalyse und multiplen Regressionsanalyse der Faktoren wurde der Anteil von *P. formosa* im Paarungskomplex durch die Heterogenität des Lebensraumes, die Individuendichte, das Prädationsrisiko, sowie durch populationsökologische Parameter der Wirtsart *P. latipinna* am Besten erklärt. Daraus schließe ich, dass die Häufigkeit des Amazonenkärpflings innerhalb des Fortpflanzungskomplexes von der Gesamtheit der typischen Eigenschaften des Lebensraumes beeinflusst wird und darüber hinaus stark von der Wirtsart abhängt. Als Erklärung für die Beibehaltung der ökologischen Koexistenz des Amazonenkärpflings *P. formosa* und ihres Wirts vermute ich, dass starke Umweltschwankungen, d.h. Störungen wie Überflutung, Austrocknung und starke Temperaturstürze, die Ausbildung eines Gleichgewichts verhindern.

Kapitel 3 beschäftigt sich mit dem Aspekt der frequenzabhängigen und saisonal beeinflussten Plastizität der männlichen Paarungspräferenzen in natürlichen gemischten Populationen von *P. latipinna* und *P. formosa*. Um diesem Phänomen auf den Grund zu gehen, wurden in visuellen Wahlversuchen die Aufenthaltsdauern der *P. latipinna* Männchen mit syntop vorkommenden adulten Weibchen von *P. latipinna* und *P. formosa* ermittelt. Dabei ergab sich in keiner Population eine generelle Präferenz für arteigene Weibchen. Allerdings waren die Wahlentscheidungen der Männchen saisonal unterschiedlich. Männchen verbrachten im Frühling signifikant weniger Zeit mit den Amazonenkärpflingen als zu den übrigen Probenahmeterminen. Sowohl die Körpergröße der Männchen als auch die relative Häufigkeit der Amazonen zur entsprechenden Jahreszeit in der jeweiligen Population, hatte keinen Einfluss auf das Verhalten der Männchen. Zur Hauptfortpflanzungsphase waren Männchen also wählerischer. Dieses Verhalten ist adaptiv und kann zur Stabilität und Koexistenz in diesem Fortpflanzungskomplex beitragen.

Die Trübung des Wassers ist ein im natürlichen Lebensraum hochvariabler Umweltfaktor, der die visuelle Kommunikation bei Poeciliiden beeinträchtigt. In **Kapitel 4** befasse ich mich mit dem Einfluss der Wassertrübung auf die Partnerwahl der Männchen von *P. latipinna* im Fortpflanzungskomplex von *P. formosa*. Die Aufenthaltszeiten als Maß der sexuellen Präferenz der Männchen wurden in sequentiellen visuellen Präferenzexperimenten mit arteigenen Weibchen und Amazonenkärpflingen in klarem und trübem Wasser gemessen. Dabei stellte sich heraus, dass die Trübung des Wassers einen starken Einfluss auf die männliche Partnerwahl hat. Männchen verbrachten im trübem Wasser signifikant weniger Zeit bei den Stimulusweibchen. Interessanterweise wurde keine Präferenz für arteigene Weibchen festgestellt, weder im klaren, noch im trübem Wasser. Sowohl die Herkunftspopulation der Männchen als auch eine vorherige Gewöhnung an trübes Wasser hatte keinen Einfluss auf das Ergebnis.

Kapitel 5: Das Balz- und Paarungsverhalten darf in Schwärmen nicht als dyadische Interaktion zwischen zwei Individuen isoliert betrachtet werden, sondern vielmehr als Bestandteil eines komplexen sozialen Netzwerks. Diese Interaktionen können von einem Publikum aus arteigenen

und artfremden Weibchen beobachtet werden. Bisherige Studien zeigen, dass *P. latipinna* Männchen von Kopulationen mit *P. formosa* profitieren, da die eigenen Weibchen diese Interaktion beobachten und die Partnerwahlentscheidung von *P. formosa* imitieren. Dieser Kopiereffekt der Partnerwahl erhöht die Attraktivität des betreffenden Männchens bei den eigenen Weibchen und damit die Wahrscheinlichkeit, in Zukunft auch zu Verpaarungen mit den art eigenen Weibchen zu gelangen. Der Fortpflanzungskomplex von *P. formosa* ist das einzige bekannte System, in dem ein Kopieren der Partnerwahl auch über Artgrenzen hinweg bekannt ist.

In diesem Kapitel zeige ich, dass die Verhaltensweise des Kopierens der Partnerwahl auch bei den Weibchen im Fortpflanzungskomplex mit der südlichen Wirtsart *P. mexicana* und bei *P. formosa* selbst ausgeprägt ist. Erstmals wird in diesem Kapitel gezeigt, dass in sympatrischen Populationen beider Wirtsartensysteme die sexuellen Weibchen die Partnerwahlentscheidungen der unisexuellen Amazonenkärpflinge imitieren. Dahingegen ist heterospezifisches Kopieren der Partnerwahl bei den Weibchen aus allopatrischen Populationen beider Wirtsartensysteme nicht gefunden worden.

Die verschiedenen verhaltensbiologischen Aspekte, die in dieser Dissertation behandelt werden, führen zu der fundamentalen Frage, wann es sich für die Männchen lohnt, zwischen den art eigenen Weibchen und den Amazonenkärpflingen als potentielle Paarungspartner zu unterscheiden. Dazu habe ich im **6. Kapitel** ein asymmetrisches spieltheoretisches Modell entwickelt. Dieses Modell berücksichtigt sowohl die Strategien der Männchen als auch die der Weibchen. Deshalb wird hier eine Kosten-Nutzen-Matrix als ein Grundstein für zukünftige Arbeit mit theoretischen Modellen zur Stabilität des Paarungskomplexes von *P. formosa* vorgestellt.

Zusammenfassend lassen sich zwei Hauptfaktoren ausmachen, die zur Beibehaltung der Koexistenz von Wirt und Parasit im Fortpflanzungskomplex von *P. formosa* beitragen.

- 1.) Stark schwankende Umweltbedingungen erklären die ökologische Koexistenz. Durch Störungen im Habitat wird verhindert, dass sich die sexuelle Wirtsart und *P. formosa* innerhalb des Komplexes gegenseitig auskonkurrieren.
- 2.) Die plastischen und vom populationsökologischen Kontext abhängigen sexuellen Präferenzen der Männchen regulieren die Koexistenz auf verhaltensbiologischer Ebene.

Literature:

- Abrahams, M. V. 1993. The trade-off between foraging and courting in male guppies. *Animal Behaviour*, 45,673-681.
- Abrahams, M. V. & Kattenfeld, M. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology*, 40,169-174.
- Andersson, M. 1994. *Sexual selection*. Princeton, N. J.: Princeton University Press.
- Angus, R. J. 1983. Meristic variation in homozygous and heterozygous fish. *Copeia*, 287-299.
- Arthur, W. 1982. The evolutionary consequences of interspecific competition. *Advances in Ecological Research*, 12, 127-187.
- Avise, J. C., Trexler, J., Travis, J. & Nelson, W. S. 1991. *Poecilia mexicana* is the recent female parent of the unisexual fish *Poecilia formosa*. *Evolution*, 45, 1530-1533.
- Bagenal, T. 1978. *Methods for assessment of fish production in fresh waters*. Oxford: Blackwell Scientific.
- Baird, R. C. 1968. Aggressive behavior and social organization in *Mollienesia latipinna* Le Sueur. *Texas Journal of Science*, 20/2, 157-176.
- Balsano, J. S., Kucharski, K., Randle, E. J., Rasch, E. M. & Monaco, P. J. 1981. Reduction of competition between bisexual and unisexual females of *Poecilia* in northeastern Mexico. *Environmental Biology of Fishes*, 6, 39-48.
- Balsano, J. S., Randle, E. J., Rasch, E. M. & Monaco, P. J. 1985. Reproductive behavior and the maintenance of all-female *Poecilia*. *Environmental Biology of Fishes*, 12, 251-263.
- Balsano, J. S., Rasch, E. M. & Monaco, P. J. 1989. The evolutionary ecology of *Poecilia formosa* and its triploid associate. In: *Ecology and evolution of livebearing fishes (Poeciliidae)* (Ed. by Meffe, G. K. & Snelson, F. F.), pP. 277-298. New Jersey: Prentice Hall.
- Barus, Libosvaski & Cruz, d. I. 1980. Observations on *Limia vittata* from Kuba. *Folio Zoologica*, 19, 267-287.
- Bayley, P. B. & Herenden, R. A. 2000. The efficiency of a seine net. *Transactions of the American Fisheries Society*, 129, 901-923.
- Beauchamp, D. A., Baldwin, C. M., Vogel, J. L. & Gubala, C. P. 1999. Estimating diel, depth-specific foraging opportunities with a visual encounter rate model for pelagic piscivores. *Canadian Journal of Fisheries and Aquatic Sciences*, 56,128-139.
- Beaugrand, J. P. 1997. Resolution of agonistic conflicts in dyads of acquainted green swordtails (*Xiphophorus helleri*): A game with perfect information. *Behavioural Processes*, 41, 79-96.
- Bell, G. 1982. *The masterpiece of nature*. Berkeley: University of California Press.
- Berglund, A. & Rosenqvist, G. 2001. Male pipefish prefer ornamented females. *Animal Behaviour*, 61, 345-350.

- Berthold, P. 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature*, 360, 668-669.
- Bisazza A. 1989. Male mate preferences in the Mosquitofish *Gambusia holbrooki*. *Ethology*, 83, 335-343.
- Borowsky, R. 1973. Melanomas in *Xiphophorus variatus* (Pisces, Poeciliidae) in the absence of hybridization. *Experientia*, 29, 1431-3.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, MA: Sinauer Associates.
- Breden, F. 1987. Male predation risk determines female preference in the Trinidad guppy. *Nature*, 329, 831-833.
- Briggs, S. E., Godin, J. G. J. & Dugatkin, L. A. 1996. Mate-choice copying under predation risk in the Trinidadian guppy (*Poecilia reticulata*). *Behavioral Ecology*, 7, 151-157.
- Brooks, R. 1998. The importance of mate copying and cultural inheritance of mating preferences. *Trends in Ecology & Evolution*, 13, 45-46.
- Brown, W. H. 1953. Introduced fish species of the Guadeloupe River Basin. *Texas Journal of Science*, 5, 245-251.
- Brown, W. L., Jr. & Wilson, E. O. 1956. Character Displacement. *Systematic Zoology*, 5, 49-64.
- Brumm, H. & Todt, D. 2002. Noise-dependent song amplitude regulation in a territorial songbird. *Animal Behaviour*, 63, 891-897.
- Bush, P. W., Ardis, A. F., Fahlquist, L., Ging, P. B., Hornig, C. E. & Lanning-Rush, J. 2000. *Water Quality in South-Central Texas, Texas, 1996-98*. U.S. Geological Survey Circular, 1212, 32 p.
- Case, T. J. & Taper, M. L. 1986. On the coexistence and coevolution of asexual and sexual competitors. *Evolution*, 40, 366-387.
- Case, T. J., Bolger, D. T. & Petren, K. 1994. Invasions and competitive displacement among house geckos in the tropical Pacific. *Ecology*, 75, 464-477.
- Chapman, L. J., Kramer, D. L. & Chapman, C. A. 1991. Population dynamics of the fish *Poecilia gillii* (Poeciliidae) in pools of an intermittent tropical stream. *Journal of Animal Ecology*, 60, 441-453.
- Cherill. 1988. The shell size-prey size relationship in mudsnails. *Oikos*, 51, 110-112.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199, 1302-1310.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35, 131-138.
- Crow, J. F. & Kimura, M. 1965. Evolution in sexual and asexual populations. *American Naturalist*, 99, 439-450.
- Cummings, M. E., Rosenthal, G. G. & Ryan, M. J., 2003. A private ultraviolet channel in visual communication. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 270, 897-904.

- Darnell, R. M. & Abramoff, P. 1968. Distribution of the gynogenetic fish, *Poecilia formosa*, with remarks on the evolution of the species. *Copeia*, 354-361.
- Dawkins, R. & Krebs, J. R. 1979. Arms races between and within species. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 205, 489-511.
- Dill, L. M., Hedrick, A. V. & Fraser, A. 1999. Male mating strategies under predation risk: Do females call the shots? *Behavioral Ecology*, 10, 452-461.
- Drewry, G. E., Delco, E. A. & Hubbs, C. 1958. Occurrence of the Amazon molly *Mollienesia formosa* at San Marcos, Texas. *Texas Journal of Science*, 10, 489-490.
- Dries, L. A. 2003. Peering through the looking glass at a sexual parasite: Are Amazon mollies red queens? *Evolution*, 57, 1387-1396.
- Duchrow, R. M., Everhart W. H., 1971. Turbidity measurement. *Transactions of the American Fisheries Society*, 1971, 682-690.
- Dugatkin, L. A. 1992. Sexual selection and imitation: Females copy the mate choice of others. *American Naturalist*, 139, 1384-1389.
- Dugatkin, L. A. & Godin, J. G. 1992. Reversal of female mate choice by copying in the guppy *Poecilia reticulata*. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 249, 179-84.
- Dugatkin, L. A. & Godin, J. G. J. 1993. Female mate copying in the guppy (*Poecilia reticulata*): Age-dependent effects. *Behavioral Ecology*, 4, 289-292.
- Dugatkin, L. A. 1996. Copying and mate choice. In: *Social learning in animals: The roots of culture* (Ed. by Galef, B. G., Jr. & M.), pP. 85-105. London: Academic Press, Inc.
- Dunbrack, R. L., Coffin, C. & Howe, R. 1995. The cost of males and the paradox of sex: An experimental investigation of the short-term competitive advantages of evolution in sexual populations. *Proceedings: Biological Sciences*, 262, 45-49.
- Dybdahl, M. F. & Lively, C. M. 1995. Diverse, endemic and polyphyletic clones in mixed populations of a freshwater snail (*Potamopyrgus antipodarum*). *Journal of Evolutionary Biology*, 8, 385-398.
- Dybdahl, M. F. & Lively, C. M. 1998. Host-parasite coevolution: evidence for rare advantage and time-lagged selection in a natural population. *Evolution*, 52, 1057-1066.
- Echelle, A. A. & Echelle, A. F. 1997. Patterns of abundance and distribution among members of a unisexual-bisexual complex of fishes (Atherinidae: *Menidia*). *Copeia*, 1997, 249-259.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*, 197, 215-223.
- Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution*, 34, 76-91.
- Endler, J. A. 1987. Predation, light intensity and courtship behavior in *Poecilia reticulata* (Pisces, Poeciliidae). *Animal Behaviour*, 35, 1376-1385.
- Endler, J. A. 1990. On the Measurement and Classification of Color in Studies of Animal Color Patterns. *Biological Journal of the Linnean Society*, 41, 315-352.

- Endler, J. A. 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Research*, 31, 587-608.
- Endler, J. A. 1992. Signals, signal conditions and the direction of evolution. *American Naturalist*, 139, S125-S153.
- Endler J. A. 1993. Some general-comments on the evolution and design of animal communication-systems. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences*, 340, 215-225.
- Endler, J. A. & Houde, A. E. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution*, 49, 456-468.
- Evans, J. P. & Magurran, A. E. 1999. Geographic variation in sperm production by Trinidadian guppies. *Proceedings of the Royal Society London - Series B: Biological Sciences*, 266, 2083-2087.
- Evans, J. P., Pilastro, A. & Ramnarine, I. W. 2003. Sperm transfer through forced matings and its evolutionary implications in natural guppy (*Poecilia reticulata*) populations. *Biological Journal of the Linnean Society*, 78, 605-612.
- Farr, J. A. 1989. Sexual selection and secondary sexual differentiation in poeciliids: determinants of male success and the evolution of female choice. In: *Ecology and evolution of livebearing fishes (Poeciliidae)* (Ed. by Meffe, G. K. & Snelson, F. F.), pp. 91-123. New Jersey: Prentice Hall.
- Farr, J. A. & Travis, J. 1989. The effect of ontogenetic experience on variation in growth, maturation, and sexual-behavior in the Sailfin molly, *Poecilia latipinna* (Pisces, Poeciliidae). *Environmental Biology of Fishes*, 26, 39-48.
- Fenchel, T. 1975. Character displacement. *Oecologia*, 20, 19-32.
- Fenchel, T. & Kofoed, L. 1976. Evidence for exploitative interspecific competition in mud snails (Hydrobiidae). *Oikos*, 27, 367-376.
- Fisher, R. A. 1930. *The genetical theory of Natural Selection*. Oxford: Clarendon Press.
- Fleishman, L. J. 1992. The influence of the sensory system and the environment on motion patterns in the visual displays of anoline lizards and other vertebrates. *American Naturalist*, 139, S36-S61.
- Foran, C. M. & Ryan, M. J. 1994. Female-female competition in a unisexual / bisexual complex of mollies. *Copeia*, 1994, 504-508.
- Franck, D., Dikomey, M., Schartl, M., 2001. Selection and the maintenance of a colour pattern polymorphism in the green swordtail (*Xiphophorus helleri*). *Behaviour*, 138, 467-486.
- Fuller, R.C. 2002. Lighting environment predicts the relative abundance of male colour morphs in Bluefin killifish (*Lucania goodei*) populations. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 269, 1457-1465.
- Gabor, C. 1999. Association patterns of Sailfin mollies (*Poecilia latipinna*): Alternative hypotheses. *Behavioral Ecology and Sociobiology*, 46, 333-340.

- Gabor, C. R. & Ryan, M. J. 2001. Geographical variation in reproductive character displacement in mate choice by male Sailfin mollies. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 268, 1063-1070.
- Galef, B. G., Jr. & White, D. J. 2000. Evidence of social effects on mate choice in vertebrates. *Behavioural Processes*, 51, 167-175.
- Garcia, C. M., Saborio, E. & Berea, C. 1998. Does male-biased predation lead to male scarcity in viviparous fish? *Journal of Fish Biology*, 53, 104-117.
- Garza, A. A. 1999. Hidalgo County. *The Handbook of Texas Online*, <http://www.tsha.utexas.edu/handbook/online/articles>.
- Garza, A. A. & Long, C., 1999. Cameron County. *The Handbook of Texas Online*, <http://www.tsha.utexas.edu/handbook/online/articles>.
- Geiser, S. W. 1924. Sex-ratios and spermatogenesis in the top-minnow *Gambusia holbrooki*. *Grd. Biol. Bull.*, 47, 175-207.
- Ghiselin, M. T. 1974. *The economy of nature and the evolution of sex*. Berkeley: University of California Press.
- Gibson, R. M. & Höglund, J. 1992. Copying and sexual selection. *Trends of Ecology and Evolution*, 7, 229-232.
- Godin, J. G. J. 1995. Predation risk and alternative mating tactics in male Trinidadian guppies (*Poecilia reticulata*). *Oecologia*, 103, 224-229.
- Godin, J. G. J. & Briggs, S. E. 1996. Female mate choice under predation risk in the guppy. *Animal Behaviour*, 51, 117-130.
- Godin, J. G. J. & McDonough, H. E. 2003. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behavioral Ecology*, 14, 194-200.
- Gonçalves, D. M., Oliveira, R. F., Koerner, K., Poschadel, J. R. & Schlupp, I. 2000. Using video playbacks to study visual communication in a marine fish, *Salaria pavo*. *Animal Behaviour*, 60, 351-357.
- Gonçalves, D., Oliveira, R. F., Körner, K. & Schlupp, I. 2003. Intersexual copying by sneaker males of the Peacock blenny. *Animal Behaviour*, 65, 355-361.
- Gong, A. & Gibson, R. M. 1996. Reversal of a female preference after visual exposure to a predator in the guppy, *Poecilia reticulata*. *Animal Behaviour*, 52, 1007-1015.
- Gong, A. 1997. The effects of predator exposure on the female choice of guppies (*Poecilia reticulata*) from a high-predation population. *Behaviour*, 134, 373-389.
- Grafen, A. & Johnstone, R. A. 1993. Why we need ESS signalling theory. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences*, 340, 245-250.
- Grant, P. R. 1994. Ecological Character Displacement. *Science*, 266, 746-747.
- Gray, M. M. & Weeks, S. C. 2001. Niche breadth in clonal and sexual fish (*Poeciliopsis*): A test of the frozen niche variation model. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1313-1318.

- Gregory, R. S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences, 50, 241-246.
- Gregory, R. S., & Northcote, T. G. 1993. Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Canadian Journal of Fisheries and Aquatic Sciences, 50, 233-240.
- Gregory, R. S. & Levings, C. D. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society, 127, 275-285.
- Griffiths, S. W. 1996. Sex differences in the trade-off between feeding and mating in the guppy. Journal of Fish Biology, 48, 891-898.
- Hakoyama, H., Nishimura, T., Matsubara, N. & Iguchi, K. 2001. Difference in parasite load and nonspecific immune reaction between sexual and gynogenetic forms of *Carassius auratus*. Biological Journal of the Linnean Society, 72, 401-407.
- Halliday, T.R. & Slater, P. J. B. 1983. Communication. New York: W. H. Freeman.
- Hamilton, W. D., Axelrod, R. & Tanese, R. 1990. Sexual reproduction as an adaptation to resist parasites (A Review). Proceedings of the National Academy of Sciences of the United States of America, 87, 3566-3573.
- Hankison, S. J. & Morris, M. R. 2003. Avoiding a compromise between sexual selection and species recognition: female swordtail fish assess multiple species-specific cues. Behavioral Ecology, 14, 282-287.
- Harshman, L. G. & Futuyma, D. J. 1985. The origin and distribution of clonal diversity in *Alsophila pometaria* (Lepidoptera: Geometridae). Evolution, 39, 315-324.
- Hartman, E. J. & Abrahams, M. V. 2000. Sensory compensation and the detection of predators: The interaction between chemical and visual information. Proceedings of the Royal Society London - Series B: Biological Sciences, 267, 571-575.
- Haskins, Haskins, McLaughlin & Hewitt. 1961. Polymorphism and population structure in *Lebistes reticulatus*, an ecological study. In: Vertebrate speciation (Ed. by Blair, W. F.), pP. 320-395. Austin: University of Texas Press.
- Heavens O, Ditchburn R, 1991. Insight into Optics. Chichester: John Wiley & Sons Ltd.
- Hestmark, G. 1992. Sex, size, competition and escape: Strategies of reproduction and dispersal in *Lasallia pustulata* (Umbilicariaceae, Ascomycetes). Oecologia, 92, 305-312.
- Heubel, K. U. & Schlupp, I. Turbidity affects association behavior in male Sailfin mollies (*Poecilia latipinna*). submitted.
- Heubel, K., Hornhardt, K., Ollmann, T., Parzefall, J., Ryan, M. J. & Schlupp, I. Geographic variation in female mate-copying in the species complex of a unisexual fish, *Poecilia formosa*. Animal Behaviour, submitted.
- Höglund, J. & Alatalo, R. V. 1995. Leks. Princeton, New Jersey: Princeton University Press.
- Holt, R. D. 1977. Predation, apparent competition and its structure of prey communities. Theoretical Population Biology, 11, 197-229.

- Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences on an optimal habitat distribution. *Theoretical Population Biology*, 28, 181-208.
- Hubbs, C. 1953. The fishes of the upper Guadalupe River, Texas. *Texas Journal of Science*, 2, 216-244.
- Hubbs, C. 1964. Interactions between bisexual fish species and its gynogenetic sexual parasite. *Bulletin Texas Memorial Museum*, 8, 1-72.
- Hubbs, C., Edwards, R. J. & Garrett, G. P. 1991. An annotated checklist of the freshwater Fishes of Texas, with Keys to identification of species. *Texas Journal of Science*, 43, 1-56.
- Hubbs, C. L. & Hubbs, L. C. 1932. Apparent parthenogenesis in nature in a form of fish of hybrid origin. *Science*, 76, 628-630.
- Hutchinson, J. M. C. 1961. The paradox of plankton. *American Naturalist*, 95, 137-145.
- Jepsen, N., Beck, S., Skov, C. & Koed, A. 2001. Behavior of Pike (*Esox lucius* L.) >50 cm in a turbid reservoir and in a clearwater lake. *Ecology of Freshwater Fish*, 10, 26-34.
- Johnson, J. E. & Hines, R.T. 1999. Effect of suspended sediment on vulnerability of young Razor-back suckers to predation. *Transactions of the American Fisheries Society* 128, 648-655.
- Jokela, J., Lively, C. M., Dybdahl, M. F. & Fox, J. A. 1997. Evidence for a cost of sex in the freshwater snail *Potamopyrgus antipodarum*. *Ecology*, 78, 452-460.
- Jokela, J., Lively, C. M., Fox, J. A. & Dybdahl, M. F. 1997b. Flat reaction norms and "frozen" phenotypic variation in clonal snails (*Potamopyrgus antipodarum*). *Evolution*, 51, 1120-1129.
- Kawecki, T. J. 1988. Unisexual / bisexual breeding complexes in Poeciliidae: Why do males copulate with unisexual females? *Evolution*, 42, 1018-1023.
- Kelly, D. A. 2001. Rapid gonopodium movement in the Sailfin molly (*Poecilia latipinna*). *American Zoologist*, 41, 1491.
- Kondrashov, A. S. 1988. Deleterious mutations and the evolution of sexual reproduction. *Nature*, 336, 435-440.
- Körner, K. E., Lütjens, O., Parzefall, J. & Schlupp, I. 1999. The role of experience in mating preferences of the unisexual Amazon molly. *Behaviour*, 136, 257-268.
- Kraak, S. B. M. & Bakker, T. C. M. 1998. Mutual mate choice in sticklebacks: Attractive males choose big females, which lay big eggs. *Animal Behaviour*, 56, 859-866.
- Kramer, D. L. & Mehegan, J. P. 1981. Aquatic surface respiration, an adaptive response to hypoxia in the guppy, *Poecilia reticulata* (Pisces, Poeciliidae). *Environmental Biology of Fishes*, 6, 299-313.
- Krebs, C. J. 1994. *Ecology: the experimental analysis of distribution and abundance*. Harper Collins.
- Krebs, C. J. 1999. *Ecological Methodology*. Addison Wesley Longman.

- Krumholz, L. A. 1963. Relationships between fertility, sex ratio, and exposure to predation in populations of the Mosquitofish *Gambusia manni* Hubbs at Bimini, Bahamas. *Int. Rev. ges. Hydrobiol.*, 48, 201-256.
- Ladle, R. J., Johnstone, R. A. & Judson, O. P. 1993. Coevolutionary dynamics of sex in a metapopulation: Catching the Red Queen. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 253, 155-160.
- Lamatsch, D. K., Nanda, I., Epplen, J. T., Schmid, M. & Schartl, M. 2000. Unusual triploid males in a microchromosome-carrying clone of the Amazon molly, *Poecilia formosa*. *Cytogenetics and Cell Genetics*, 91, 148-156.
- Lamatsch, D. K., Schmid, M. & Schartl, M. 2002. A somatic mosaic of the gynogenetic Amazon molly. *Journal of Fish Biology*, 60, 1417-1422.
- Lampert, W. & Sommer, U. 1993. *Limnoökologie*. Stuttgart: Georg Thieme Verlag.
- Landmann, K., Parzefall, J. & Schlupp, I. 1999. A sexual preference in the Amazon molly, *Poecilia formosa*. *Environmental Biology of Fishes*, 56, 325-331.
- Leberg, P. L. & Vrijenhoek, R. C. 1994. Variation among desert topminnows in their susceptibility to attack by exotic parasites. *Conservation Biology*, 8, 419-424.
- Lengagne, T., Aubin, T., Lauga, J. & Jouventin, P. 1999. How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 266, 1623-1628.
- Lengagne, T. & Slater, P. J. B. 2002. The effects of rain on acoustic communication: Tawny owls have good reason for calling less in wet weather. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 269, 2121-2125.
- Lewis, S. R., Rasch, E. M., Hossler, F. E., Kalbfleisch, J. H. & Monaco, P. J. 1999. Comparative study of dentition among species of *Poecilia* (Pisces). *Journal of Morphology*, 239, 271-282.
- Lima, N. R. W., Kobak, C. J. & Vrijenhoek, R. C. 1996. Evolution of sexual mimicry in sperm-dependent all-female forms of *Poeciliopsis* (Pisces: Poeciliidae). *Journal of Evolutionary Biology*, 9, 185-203.
- Lively, C. M. 1990. The Red Queen hypothesis supported by parasitisms in sexual and clonal fish. *Nature*, 344, 864-866.
- Long, K. D. & Houde, A. E. 1989. Orange spots as a visual cue for female mate choice in the guppy (*Poecilia reticulata*). *Ethology*, 82, 316-324.
- Long, K. D. & Rosenqvist, G. 1998. Changes in male guppy courting distance in response to a fluctuating light environment. *Behavioral Ecology and Sociobiology*, 44, 77-83.
- Losey, G. S., Stanton, F. G., Telecky, T. M. & Tyler, W. A. 1986. Copying others an evolutionarily stable strategy for mate choice a model. *American Naturalist*, 128, 653-664.
- Losey, G. S., Cronin, T. W., Goldsmith, T. H., Hyde, D., Marshall, N. J. & McFarland W.N. 1999. The UV visual world of fishes: a review. *Journal of Fish Biology*, 54, 921-943.

- Lynch, M. 1984. Destabilizing hybridization, general purpose genotypes and geographic parthenogenesis. *Quarterly Review of Biology*, 59, 257-290.
- Lynch, M. & Gabriel, W. 1990. Mutation load and the survival of small populations. *Evolution*, 44, 1725-1737.
- Lynch, M. & Deng, H.-W. 1994. Genetic slippage in response to sex. *American Naturalist*, 144, 242-261.
- MacArthur, R. H. 1965. Patterns of species diversity. *Biological Reviews*, 40, 510-533.
- MacArthur, R. H. & Lewins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. *American Naturalist*, 101, 377-385.
- Magurran, A. E. & Seghers, B. H. 1994a. A cost of sexual harassment in the guppy, *Poecilia reticulata*. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 258, 89-92.
- Magurran, A. E. & Seghers, B. H. 1994b. Sexual conflict as a consequence of ecology: Evidence from guppy, *Poecilia reticulata*, populations in Trinidad. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 255, 31-36.
- Marler, C. A. & Ryan, M. J. 1997. Origin and maintenance of a female mating preference. *Evolution*, 51, 1244-1248.
- Marler, C. A., Foran, C. & Ryan, M. J. 1997. The influence of experience on mating preferences of the gynogenetic Amazon molly. *Animal Behaviour*, 53, 1035-1041.
- Matos, R. J. & Schlupp, I. [in press] 2004. Performing in front of an audience - Signalers and the social environment. In: *Animal communication networks* (Ed. by McGregor, P. K.). Cambridge: Cambridge University Press.
- Mayama H, 1998. Effects of turbidity on the feeding behavior of juvenile Masu salmon (*Oncorhynchus masou*). *Bulletin of the National Salmon Resources Center* 0:1-11.
- Maynard Smith, J. 1972. *On Evolution*. Edinburgh: Edinburgh University Press.
- Maynard Smith, J. 1978. *The evolution of sex*. Cambridge: Cambridge University Press.
- Maynard Smith, J. 1979. Game theory and the evolution of behaviour. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 205, 475-488.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge: Cambridge University Press.
- Maynard Smith, J. 1983. Models of evolution. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 219, 315-326.
- McGregor, P. K. 1993. Signaling in territorial systems - a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences*, 340, 237-244.
- McGregor, P. K. & Peake, T. M. 2000. Communication networks: social environments for receiving and signaling behaviour. *Acta Ethologica*, 2, 71-81.
- McKay, F. E. 1971. Behavioral aspects of population dynamics in unisexual-bisexual *Poeciliopsis* (Pisces: Poeciliidae). *Ecology*, 52, 778-790.

- McKinsey, D. M. & Chapman, L. J. 1998. Dissolved oxygen and fish distribution in a Florida spring. *Environmental Biology of Fishes*, 53, 211-223.
- McNeely, D. L. & Wade, C. E. 2003. Relative abundance of the gynogen *Poecilia formosa* and its sexual host *Poecilia latipinna* (Teleostei: Poeciliidae) in some southern Texas habitats. *The Southwestern Naturalist*, 48, 451-453.
- Meador, M. R., Cuffney, T. F. & Gurtz, M. E. 1993. Methods for sampling fish communities as a part of the national Water quality assessment program. USGS open file report 93-104.
- Meffe, G. K. & Snelson, F. F. 1989. An ecological overview of poeciliid fishes. In: *Ecology and evolution of livebearing fishes (Poeciliidae)* (Ed. by Meffe, G. K. & Snelson, F. F.), pp. 13-31. New Jersey: Prentice Hall.
- Miller, R. R. 1983. Checklist and key to the mollies of Mexico (Pisces: Poeciliidae: *Poecilia*, subgenus *Mollienesia*). *Copeia*, 1983 (3), 817-822.
- Möller, D. 2001. Aspekte zur Populationsgenetik des eingeschlechtlichen Amazonenkärpflings *Poecilia formosa* (Girard 1859) unter Berücksichtigung der genetischen parentalen Arten, dem Breitflossenkärpfling *Poecilia latipinna* (LeSueur 1821) und dem Atlantikkärpfling *Poecilia mexicana*, Steindachner 1863. Dissertation. Universität Hamburg.
- Monaco, P. J., Rasch, E. M. & Balsano, J. S. 1978. Cytological evidence for temporal differences during asynchronous ovarian maturation of bisexual and unisexual fishes of genus *Poecilia*. *Journal of Fish Biology*, 13, 33-44.
- Monaco, P. J., Rasch, E. M. & Balsano, J. S. 1981. Sperm availability in naturally occurring bisexual-unisexual breeding complexes involving *Poecilia mexicana* and the gynogenetic teleost, *Poecilia formosa*. *Environmental Biology of Fishes*, 6, 159-166.
- Moore, W. S. & McKay, F.E. 1971. Coexistence in unisexual-bisexual breeding complexes of *Poeciliopsis* (Pisces: Poeciliidae). *Ecology*, 52, 791-799.
- Moore, W. S. 1975. Stability of small unisexual-bisexual populations of *Poeciliopsis* (Pisces - Poeciliidae). *Ecology*, 56, 791-808.
- Moore, W. S. 1976. Components of fitness in the unisexual fish *Poeciliopsis monacha occidentalis*. *Evolution*, 30, 564-578.
- Moore, W. S., Miller, R. R. & Schultz, R. J. 1970. Distribution, adaptation and probable origin of an all-female form of *Poeciliopsis* (Pisces: Poeciliidae) in Northwestern Mexico. *Evolution*, 24, 789-795.
- Morris, M. R. 1990. Age at sexual maturity of male *Xiphophorus nigrensis* in Nature. *Copeia*, 747-751.
- Moulton, S. R., Kennen, J. G., Goldstein, R. M. & Hambrook, J. A. 2002. Revised protocols for sampling algal, invertebrate, and fish communities as part of the National Water-Quality Assessment Program. USGS Open-File Report 02-150.
- Muller, H. J. 1964. The relation of recombination to mutational advance. *Mutation Research*, 1, 2-9.
- Negro, J. J. & Grande, J. M. 2001. Territorial signalling: a new hypothesis to explain frequent copulation in raptorial birds. *Animal Behaviour*, 62, 803-809.

- Nielsen, L. A. & Johnson, D. L. 1983. Fisheries techniques. Bethesda, Md.
- Niemeitz, A., Kreutzfeldt, R., Schartl, M., Parzefall, J. & Schlupp, I. 2002. Male mating behaviour of a molly, *Poecilia latipunctata*: a third host for the sperm-dependent Amazon molly, *Poecilia formosa*. *Acta Ethologica*, 5, 45-49.
- Oliveira, R. F., Rosenthal, G. G., Schlupp, I., McGregor, P. K., Cuthill, I., Endler, J. A., Fleishman, L., Zeil, J., Barata, E., Burford, F., Gonçalves, D., Haley, M., Jakobsson, S., Jennions, M., Körner, K. E., Lindström, L., Peake, T., Pilastro, A., Pope, D., Roberts, S., Rowe, C., Smith, J. & Waas, J. 2000. Considerations on the use of video-playback as visual stimuli: the Lisbon workshop consensus. *Acta Ethologica*, 3, 61-65.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist*, 103, 91-93.
- Parker, E. D., Jr., Selander, R. K., Hudson, R. O. & Lester, L. J. 1977. Genetic Diversity in colonizing parthenogenetic cockroaches. *Evolution*, 31, 836-842.
- Parker, E. D., Jr. 1979. Phenotypic consequences of parthenogenesis in *Cnemidophorus* Lizards. I. Variability in parthenogenetic and sexual populations. *Evolution*, 33, 1150-1166.
- Parker, G. A. 1984. Evolutionary stable strategies. In: *Behavioural ecology: an evolutionary approach* (Ed. by Krebs, J. R. & Davies, N. B.). Oxford: Blackwell Scientific Publications.
- Parker, G. A. 1990. Sperm competition games: Raffles and roles. *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 242, 120-126.
- Parzefall, J. 1969. Zur vergleichenden Ethologie verschiedener *Mollienesia*-Arten einschliesslich einer Höhlenform von *M. sphenops*. *Behaviour*, 33, 1-37.
- Parzefall, J. 1973. Attraction and sexual cycle of poeciliids. In: *Genetics and mutagenesis of fish* (Ed. by Schröder, J. H.), pP. 177-183. Berlin: Springer.
- Parzefall, J. 2001. A review of morphological and behavioural changes in the cave molly, *Poecilia mexicana*, from Tabasco, Mexico. *Environmental Biology of Fishes*, 62, 263-275.
- Pickett, S. & White, P. S. 1985. *The Ecology of Natural disturbance on patch dynamics*. New York: Academic Press.
- Pilastro, A. & Bisazza, A. 1999. Insemination efficiency of two alternative male mating tactics in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London - Series B: Biological Sciences*, 266, 1887-1891.
- Pilastro, A., Benetton, S. & Bisazza, A. 2003. Female aggregation and male competition reduce costs of sexual harassment in the mosquitofish *Gambusia holbrooki*. *Animal Behaviour*, 65, 1161-1167.
- Plath, M., Parzefall, J. & Schlupp, I. 2003. The role of sexual harassment in cave and surface dwelling populations of the Atlantic molly, *Poecilia mexicana* (Poeciliidae, Teleostei). *Behavioral Ecology and Sociobiology*, 54, 303-309.
- Pruett-Jones, S. 1992. Independent versus nonindependent mate choice: Do females copy each other? *American Naturalist*, 140, 1000-1009.

- Ptacek, M. B. & Travis, J. 1997. Mate choice in the Sailfin molly *Poecilia latipinna*. *Evolution*, 51, 1217-1231.
- Quinn, G. P. & Keough, M. J. 2002. Experimental design and data analysis for biologists. Cambridge: Cambridge University Press.
- Rasch, E. M. & Balsano, J. S. 1989. Trihybrids related to the unisexual molly fish, *Poecilia formosa*. In: *Evolution and Ecology of unisexual vertebrates* (Ed. by Dawley, R. M. & Bogart, J. P.), pP. 252-267. Albany: New York State Museum.
- Reid SM, Fox MG, Whillans TH, 1999. Influence of turbidity on piscivory in Largemouth bass (*Micropterus salmoides*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:1362-1369.
- Reznick, D. N. & Miles, D. B. 1989a. Poeciliid life history patterns. In: *Ecology and evolution of livebearing fishes (Poeciliidae)* (Ed. by Meffe, G. K. & Snelson, F. F.). New Jersey: Prentice Hall.
- Reznick, D. N. & Miles, D. B. 1989b. A review of life history patterns in poeciliid fishes. In: *Ecology and evolution of livebearing fishes (Poeciliidae)* (Ed. by Meffe, G. K. & Snelson, F. F.). New Jersey: Prentice Hall.
- Reznick, D. N., Butler, M. J. V., Rodd, F. H. & Ross, P. 1996. Life-history evolution in guppies (*Poecilia reticulata*): 6. Differential mortality as a mechanism for natural selection. *Evolution*, 50, 1651-1660.
- Ridley, M. 1993. *Evolution*. Boston: Blackwell Scientific Publications.
- Ridley, M. 1994. *The Red Queen: Sex and the evolution of human nature*. London: Penguin Books.
- Robinson, B. T. & Wilson, D. S. 1994. Character release and displacement in fishes: a neglected literature. *American Naturalist*, 144, 506-627.
- Rosen, D. E. & Bailey, R. M. 1963. The poeciliid fishes (Cyprinodontiformes) : their structure, zoogeography, and systematics. *Bulletin of the American Museum of Natural History*, 126, 1-176.
- Roughgarden, J. 1972. Evolution of Niche Width. *American Naturalist*, 106, 683-718.
- Rowe, D.K & Dean, T.L. 1998. Effects of turbidity on the feeding ability of the juvenile migrant stage of six New Zealand freshwater fish species. *New Zealand Journal of Marine & Freshwater Research*, 32, 21-29.
- Ryan, M. J., Dries, L. A., Batra, P. & Hillis, D. M. 1996. Male mate preferences in a gynogenetic species complex of Amazon mollies. *Animal Behaviour*, 52, 1225-1236.
- Ryan, M. J., Rosenthal, G.G., 2001. Variation and selection in swordtails. In: *Model systems in behavioral ecology*. (Dugatkin, L.A., ed). Princeton: Princeton University Press; 133-148.
- Schartl, M., Wilde, B., Schlupp, I. & Parzefall, J. 1995. Evolutionary origin of a parthenoform, the Amazon molly *Poecilia formosa*, on the basis of a molecular genealogy. *Evolution*, 49, 827-835.

- Schartl, A., Hornung, U., Nanda, I., Wacker, R., Muller-Hermelink, H. K., Schlupp, I., Parzefall, J., Schmid, M. & Schartl, M. 1997. Susceptibility to the development of pigment cell tumors in a clone of the Amazon molly, *Poecilia formosa*, introduced through a microchromosome. *Cancer Research*, 57, 2993-3000.
- Schenck, R. A. & Vrijenhoek, R. C. 1986. Spatial and temporal factors affecting coexistence among sexual and clonal forms of *Poeciliopsis*. *Evolution*, 40, 1060-1070.
- Schlosser, I. J., Doeringsfeld, M. R., Elder, J. F. & Arzayus, L. F. 1998. Niche relationships of clonal and sexual fish in a heterogeneous landscape. *Ecology*, 79, 953-968.
- Schlupp, I., Parzefall, J. & Schartl, M. 1991. Male mate choice in mixed bisexual/unisexual breeding complexes of *Poecilia* (Teleostei: Poeciliidae). *Ethology*, 88, 215-222.
- Schlupp, I., Marler, C. & Ryan, M. J. 1994. Benefit to male Sailfin mollies of mating with heterospecific females. *Science*, 263, 373-374.
- Schlupp, I. & Ryan, M. J. 1996. Mixed-species shoals and the maintenance of a sexual-asexual mating system in mollies. *Animal Behaviour*, 52, 885-890.
- Schlupp, I. & Ryan, M. J. 1997. Male Sailfin mollies (*Poecilia latipinna*) copy the mate choice of other males. *Behavioral Ecology*, 8, 104-107.
- Schlupp, I., Nanda, I., Döbler, M., Lamatsch, D. K., Epplen, J. T., Parzefall, J., Schmid, M. & Schartl, M. 1998. Dispensable and indispensable genes in an ameiotic fish, the Amazon molly *Poecilia formosa*. *Cytogenetics and Cell Genetics*, 80, 193-198.
- Schlupp, I., Waschulewski, M. & Ryan, M. J. 1999. Female preferences for naturally-occurring novel male traits. *Behaviour*, 136, 519-527.
- Schlupp, I., Mc Knab, R. & Ryan, M. J. 2001. Sexual harassment as a cost for molly females: Bigger males cost less. *Behaviour*, 138, 277-286.
- Schlupp, I., Parzefall, J. & Schartl, M. 2002. Biogeography of the unisexual Amazon molly, *Poecilia formosa*. *Journal of Biogeography*, 29, 1-6.
- Schlupp, I., Rioux, A., Heubel, K. & Ryan, M. J. Presence of another male modifies a sexual preference in male Sailfin mollies. submitted.
- Schlüter, A., Parzefall, J. & Schlupp, I. 1998. Female preference for symmetrical vertical bars in male Sailfin mollies. *Animal Behaviour*, 56, 147-153.
- Schluter, D. 1994. Experimental evidence that competition provokes divergence in adaptive radiation. *Science*, 266, 798-801.
- Schultz, R. J. 1971. Special adaptive problems associated with unisexual fishes. *American Zoologist*, 11, 351-360.
- Schultz, R. J. 1989. Origins and relationships of unisexual poeciliids. In: *Ecology and evolution of livebearing fishes (Poeciliidae)* (Ed. by Meffe, G. K. & Snelson, F. F.). New Jersey: Prentice Hall.
- Schultz, R. J. & Fielding, E. 1989. Fixed genotypes in variable environments. In: *Evolution and ecology of unisexual vertebrates* (Ed. by Dawly, R. & Bogar, J.), pP. 32-38. Albany: New York State Museum.

- Seehausen, O., van Alphen, J. J. M. & Witte, F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*, 277, 1808-1811.
- Semlitsch, R. D., Hotz, H. & Guex, G.-D. 1997. Competition among tadpoles of coexisting hemiclones of hybridogenetic *Rana esculenta*: Support for the frozen niche variation model. *Evolution*, 51, 1249-1261.
- Slabbekoorn, H. & Peet, M. 2003. Birds sing at a higher pitch in urban noise - Great tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature*, 424, 267-267.
- Smith, E. J., Partridge, J. C., Parsons, K. N., White, E. M., Cuthill, I. C., Bennett, A.T.D. & Church, S.C. 2002. Ultraviolet vision and mate choice in the guppy (*Poecilia reticulata*). *Behavioral Ecology*, 13, 11-19.
- Snelson, F. F., & Wetherington, J. D. 1980. Sex-ratio in the Sailfin molly, *Poecilia latipinna*. *Evolution*, 34, 308-319.
- Snelson, F. F. 1986. The relationship between interbrood interval and yolk loading in a generalized poeciliid fish, *Poecilia latipinna*. *Copeia*, 295- 304.
- Snelson, F. F. 1989. Social and environmental control of life history traits in poeciliid fishes. In: *Ecology and evolution of livebearing fishes (Poeciliidae)* (Ed. by Meffe, G. K. & Snelson, F. F.). New Jersey: Prentice Hall.
- Snelson, F. F. & Meffe, G. K. 1989. Poeciliid biology: Where we are and where we should be going. In: *Ecology and evolution of livebearing fishes (Poeciliidae)* (Ed. by Meffe, G. K. & Snelson, F. F.). New Jersey: Prentice Hall.
- Sohn, J. J. 1977. Socially induced inhibition of genetically determined maturation in the platyfish, *Xiphophorus maculatus*. *Science*, 195, 199-201.
- Sokal, R., R. & Rohlf, F. J. 1995. *Biometry*. New York: W.H. Freeman and Company.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, 46, 337-365.
- Spearing, D. 1991. *Roadside Geology of Texas*. Missoula, MT.: Mountain Press Publishing Company.
- Stenseth, N. C., Kirkendall, L. R. & Moran, C. 1985. On the evolution of pseudogamy. *Evolution*, 39, 294-307.
- Sweka, J. A. & Hartman, K. J. 2001a. Effects of turbidity on prey consumption and growth in Brook trout and implications for bioenergetics modeling. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 386-393.
- Sweka, J. A & Hartman, K. J. 2001b. Influence of turbidity on Brook trout reactive distance and foraging success. *Transactions of the American Fisheries Society*, 130, 138-146.
- Tabachnick, B. G. & Fidell, L. S. 2001. *Using multivariate statistics*, 4th ed. Boston: Allyn and Bacon.
- TDH. 1997. Fishing advisories and bans. Seafood Safety Division. pP. 21P. Austin, Texas: Texas Department of Health.

- TNRCC. 1994. Regional assessment of water quality in the Rio Grande basin including the Pecos river, the Devils river, the Arroyo Colorado and the Lower Laguna Madre. AS-34, Watershed Management Division, TNRCC, Austin, Texas. Texas Natural Resource Conservation Commission.
- TNRCC. 2001. TMDL document four: total maximum daily loads for legacy pollutants in the Arroyo Colorado above tidal and the donna reservoir and canal system. Texas Natural Resource Conservation Commission.
- Tokeshi, M. 1999. Species coexistence. Ecological and Evolutionary Perspectives. Oxford: Blackwell Science.
- Travis, J. & Woodward, B. D. 1989. Social context and courtship flexibility in male sailfin mollies, *Poecilia latipinna* (Pisces: Poeciliidae). *Animal Behaviour*, 38, 1001-1011.
- Trexler, J. 1989a. Traits known to be plastic in poeciliids. In: Ecology and evolution of livebearing fishes (Poeciliidae) (Ed. by Meffe, G. K. & Snelson, F. F.). New Jersey: Prentice Hall.
- Trexler, J. C. 1989b. Phenotypic plasticity in poeciliid life histories. In: Ecology and evolution of livebearing fishes (Poeciliidae) (Ed. by Meffe, G. K. & Snelson, F. F.). New Jersey: Prentice Hall.
- Trexler, J. C., Travis, J. & McManus, M. 1992. Effects of habitat and body size on mortality rates of *Poecilia latipinna*. *Ecology*, 73, 2224-2236.
- Trexler, J. C., Tempe, R. C. & Travis, J. 1994. Size-selective predation of sailfin mollies by two species of heron. *Oikos*, 69, 250-258.
- Trexler, J. C. 1997. Resource availability and plasticity in offspring provisioning: Embryo nourishment in sailfin mollies. *Ecology*, 78, 1370-1381.
- Trexler, J. C., Travis, J. & Dinep, A. 1997. Variation among populations of the sailfin molly in the rate of concurrent multiple paternity and its implications for mating-system evolution. *Behavioral Ecology and Sociobiology*, 40, 297-305.
- Turner, B. J. 1982. The evolutionary genetics of a unisexual fish, *Poecilia formosa*. In: Mechanisms of speciation (Ed. by Barigozzi, C.), pP. 265-305. New York: Alan R. Liss.
- Turner, B. J., Balsano, J. S., Monaco, P. J. & Rasch, E. M. 1983. Clonal diversity and evolutionary dynamics in a diploid-triploid breeding complex of unisexual fishes (*Poecilia*). *Evolution*, 37, 798-809.
- TWC (Texas Water Commission) 1990. Waste load evaluation for the Arroyo Colorado in the Nueces-Rio Grande Coastal basin. Segment 2201 - Arroyo Colorado Tidal, Segment 2202 - Arroyo Colorado Above Tidal. WLE 90-04,. Austin, Texas: Texas Water Commission.
- Ulery, R. L. & Brown, M. F. 1995. Water-quality assessment of the Trinity River basin, Texas - Review and analysis of available pesticide information, 1968-91.: U.S. Geological Survey Water-Resources Investigations Report 94-4218. pP. 88
- Utne, A. C. W. 1997. The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. *Journal of Fish Biology*, 50, 926-938.

- Utne-Palm, A. C. 1999. The effect of prey mobility, prey contrast, turbidity and spectral composition on the reaction distance of *Gobiusculus flavescens* to its planktonic prey. *Journal of Fish Biology*, 54, 1244-1258.
- van Eerden, M. R. & Voslamber, B. 1995. Mass fishing by Cormorants *Phalacrocorax carbo sinensis* at lake IJsselmeer, The Netherlands: A recent and successful adaptation to a turbid environment. *Ardea*, 83, 199-212.
- van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory*, 1, 1-31.
- Vogel, J.L. & Beauchamp, D.A. 1999. Effects of light, prey size, and turbidity on reaction distances of Lake trout (*Salvelinus namaycush*) to salmonid prey. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1293-1297.
- Vrijenhoek, R. C. & Pfeiler, E. 1997. Differential survival of sexual and asexual *Poeciliopsis* during environmental stress. *Evolution*, 51, 1593-1600.
- Vrijenhoek, R. C. 1978. Coexistence of clones in a heterogeneous environment. *Science*, 199, 549-552.
- Vrijenhoek, R. C. 1979. Genetics of a sexually reproducing fish in a highly fluctuating environment. *American Naturalist*, 113, 17-29.
- Vrijenhoek, R. C. 1984. Ecological differentiation among clones: the frozen niche variation model. In: *Population biology and evolution* (Ed. by Woehrmann, K. & Loeschke, V.), pP. 217-231. Berlin, Germany: Springer Verlag.
- Vrijenhoek, R. C. 1984b. The evolution of clonal diversity in *Poeciliopsis*. In: *Evolutionary Genetics of Fishes* (Ed. by Turner, B. J.). New York: Plenum Press.
- Vrijenhoek, R. C. 1989. Genotypic diversity and coexistence among sexual and clonal lineages of *Poeciliopsis*. In: *Speciation and its Consequences* (Ed. By Otte, D. & Endler, J. A.), pP. 386-400. Sunderland, MA: Sinauer.
- Vrijenhoek, R. C., Dawley, R. M., Cole, C. J. & Bogart, J. P. 1989. A list of known unisexual vertebrates. In: *Evolution and Ecology of unisexual vertebrates* (Ed. by Dawley, R. M. & Bogart, J. P.), pP. 19-23. Albany: New York State Museum.
- Vrijenhoek, R. C. 1994. Unisexual fish: model systems for studying ecology and evolution. *Annual Review of Ecology and Systematics*, 25, 71-96.
- Walsh, S. J. & Meador, M. R. 1998. Guidelines for quality assurance and quality control of fish taxonomic data collected as part of the National Water-Quality Assessment Program. pP. 33.: US Geological Survey Water-Resources Investigations report 98-4239.
- Webster, C. F., Buchanan, T. A., Kirkpatrick, J. & Miranda, R. 1998. Polychlorinated biphenyls in Donna reservoir and contiguous waters - Results of intensive sediment, water and fish sampling and human health risk assessment. Special Study Report No. AS-161. Austin: Field Operations Division, Texas Natural Resource Conservation Commission.
- Wermund, E. G. 1999a. Land Resources of Texas. Bureau of Economic Geology SM0007.: The University of Texas at Austin, 1999.
- Wermund, E. G. 1999b. Physiographic Map of Texas. Bureau of Economic Geology SM0005. The University of Texas at Austin.

- Werner, E. E. & Hall, D. J. 1988. Ontogenetic Habitat Shifts in Bluegill: The Foraging Rate-Predation Risk Trade-off. *Ecology*, 69, 1352-1366.
- Westneat, D. F., Walters, A., McCarthy, T. M., Hatch, M. I. & Hein, W. K. 2000. Alternative mechanisms of non-independent mate choice. *Animal Behaviour*, 59, 467-476.
- Wetherington, J. D., Schenck, R. A. & Vrijenhoek, R. C. 1989a. The origins and ecological success of unisexual *Poeciliopsis*: The frozen niche-variation model. In: *Ecology and evolution of livebearing fishes (Poeciliidae)* (Ed. by Meffe, G. K. & Snelson, F. F.). New Jersey: Prentice Hall.
- Wetherington, J. D., Weeks, S. C., Kitora, K. E. & Vrijenhoek, R. C. 1989. Genotypic and environmental components of variation in growth and reproduction of fish hemiclones (*Poeciliopsis*: Poeciliidae). *Evolution*, 43, 635-645.
- White, D. H., Mitchell, C. A., Kennedy, H. D., Krynitsky, A. J. & Ribick, M. A. 1983. Elevated DDE and toxaphene residues in fishes and birds reflect local contamination in the lower Rio Grande Valley, Texas. *Southwestern Naturalist*, 28, 325-333.
- Whiteside, B. G. & McNatt, R. M. 1972. Fish species diversity in relation to stream order and physicochemical conditions in the Plum Creek drainage basin. *American Midland Naturalist*, 88, 90-101.
- Wiley, R.H. & Richards, D.G. 1982. Adaptations for acoustic communications in birds: sound transmission and signal detection. In: *Acoustic communication in birds* (Miller EK, ed). New York: Academic press. 132-181.
- Williams, G. C. 1975. *Sex and evolution*. Princeton: Princeton University Press.
- Witte, K. & Ryan, M. J. 1998. Male body length influences mate-choice copying in the Sailfin molly *Poecilia latipinna*. *Behavioral Ecology*, 9, 534-539.
- Witte, K. & Noltemeier, B. 2002. The role of information in mate-choice copying in female Sailfin mollies (*Poecilia latipinna*). *Behavioral Ecology and Sociobiology*, 52, 194-202.
- Witte, K. & Ryan, M. J. 2002. Mate choice copying in the Sailfin molly, *Poecilia latipinna*, in the wild. *Animal Behaviour*, 63, 943-949.
- Witte, K. & Massmann, R. 2003. Female sailfin mollies, *Poecilia latipinna*, remember males and copy the choice of others after 1 day. *Animal Behaviour*, 65, 1151-1159.
- Woodhead, A. D. & Armstrong, N. 1985. Aspects of the mating behavior of male mollies (*Poecilia* spp.). *Journal of Fish Biology*, 27, 593-601.
- Wright, J. W. & Lowe, C. H. 1968. Weeds, polyploids, parthenogenesis and the geographical and ecological distribution of all-female species of *Cnemidophorus*. *Copeia*, 1968, 128-138.
- Yodzis, P. 1986. Competition, mortality and community structuring. In: *Community ecology* (Ed. by Diamond, J. & Case, T. J.), pP. 480-491. New York: Harper & Row.

Danksagung / Acknowledgments:

HAMBURG:

An dieser Stelle möchte ich mich ganz herzlich bei allen bedanken, die mich im Laufe meiner Doktorandenzeit begleitet haben.

Zuallererst möchte ich mich bei meinem Projektleiter und Mentor Herrn PD Dr. Ingo Schlupp bedanken für seine Begabung, mich jederzeit motivieren zu können. Die Liste, wofür ich mich noch bei Dir bedanken möchte, ist lang und reicht von der Stellung des Themas, über die Vermittlung von unschätzbaren Kontakten, ständige Diskussionsbereitschaft, die hervorragende Anleitung, aber auch den Freiheiten, die Du mir gelassen hast, die Heranführung an die Freilandarbeit, vielfältige gute Ratschläge, bis zuletzt zur Tatsache, dass Du Dich von mir manchmal bei der Freilandarbeit zum fieldassistant hast degradieren lassen, der bis zur Brust im Schlammwasser stehen musste.

Bei meinem Doktorvater Prof. Dr. Parzefall möchte ich mich für seine unkomplizierte und offene Art bedanken, mit der er mich in Hamburg begleitet hat und die ich sehr zu schätzen weiß. Vielen Dank für die Betreuung meiner Arbeit und die vielen guten, von langjähriger Erfahrung geprägten Fragen und Anregungen.

Bedanken möchte ich mich natürlich bei der gesamten Arbeitsgruppe in der Ethologie für ihre Diskussionsbereitschaft und vielerlei Hilfe. Für die vielen guten Gesprächen danke ich meinen Mitdoktoranden Antje, Inga und Martin.

Insbesondere möchte ich mich auch bei Angelika, Karin, Marilen, Dorle, Tomma, Detlef und Sabine bedanken für Ihre Erfahrung und Ihren Einsatz, aus einer Insektenkundlerin doch noch eine Fischfrau zu machen. Vielen Dank auch für die große Hilfe bei der Fischpflege.

Annika, Christine, Helmuth, Inga, Kerstin und Paul danke ich für Ihr Engagment, mit dem sie ihre Projekte rund um die Amazonen durchgeführt haben.

Bei Tanja Ollmann und Katja Hornhardt möchte ich mich für die Überlassung von Daten zum mate-copying aus Ihren Examensarbeiten bedanken.

Den Studierenden der Medieninformatik an der Fachhochschule Wedel und ihrem Dozenten M. Hinck gilt mein Dank für Ihr Engagement bei den Versuchen, interaktives Video-Playback zu realisieren. An dieser Stelle möchte ich mich auch bei Kai Marholdt bedanken, der viel Zeit in der Weiterentwicklung des Programms gesteckt hat.

Ich möchte mich bei den Veranstaltern der DZG Fortbildungsveranstaltung "Evolutions- und populationsökologische Modellierungsansätze in der Bioinformatik", Dr. Barbara Hellriegel, Dr. Klaus Reinhold und Dr. Thomas S. Hoffmeister, sowie bei Elke Reichwaldt für ihre Diskussionsbereitschaft zum spieltheoretischen Ansatz des Amazonenkomplexes bedanken.

Bei Dr. David Thomson bedanke ich mich für seine unkomplizierte Hilfe beim Begutachten des Englischen.

Mein Dank gilt auch Antje, Axel, Christine, Dirk, Jens, Julia, Kerstin, Mareike, Matthias und Phillip, die in der heißen Endphase zum Gelingen dieser Arbeit beigetragen haben.

Phillip Gienapp verdanke ich unzählige "Guppygespräche", vielen Dank für Deine Kritik und Toleranz.

AUSTIN:

Prof. Dr. Michael J. Ryan, University of Texas, Austin, for being a great host, providing facilities and resources, discussion, and advice. I would also like to thank all members of the “Ryan lab” – I always felt at home in Austin. Thanks, Mike.

PD Dr. Ingo Schlupp for his encouragement, for initiating this study, support, help and advice throughout all stages of my Ph. D. project.

For helping in the field, with fish care and running tests: Allison Abel, Ashley Rioux, Ben Gartner, Caitlin Gabor, Carla Gonzalez, Cristina Papp, Dave McNeely, Diane Mollaghan, Ingo Schlupp, Julia Heubel, Karolina Chmielowietz, Kathy Boul, Marcos Gidi Papp, Martin Plath, Mike Ryan, Molly Cummings, Nadia Parvaze, Phillip Gienapp, Ray Engeszer, Rayne Hurzeler, Salvador Contreras-Balderas, Sarah Keaton, Stephanie Repka, Susanna Scott, Thomas Kellermann. Thanks a lot!

I thank Prof. Dr. David Mc Neely, UT Brownsville for sharing his local knowledge on field sites in Brownsville.

Thanks to Gil G. Rosenthal for introducing me to the secrets of computer-animated video-playback and 3D Studiomax.

Without Dean A Hendrickson, University of Texas, Austin, Curator of Ichthyology, Texas Natural History Collections, and Clark Hubbs, University of Texas, Austin, it would have been impossible to identify fish species.

I thank Texas Parks & Wildlife Department, State Fish Hatchery, Brownsville for access to field site SFH and David R. Blankinship for access to facilities at SFH.

Thanks to Landa Park, New Braunfels, for access to the environmentally protected area of Comal Springs.

I would also like to thank all landowners for access to their properties.

Dr. Robert Cashner, New Orleans provided data on *P. latipinna* sizes from Louisiana.

I also thank Brackenridge Field Laboratory at the University of Texas at Austin for use of their facilities.

I thank the Mexican government for permission 210696-213-03 and permit number 291002-613-1577 to collect fishes.

Thanks Kristina, for always offering a place to stay!

Financial support was provided by: NATO, Deutsche Forschungsgemeinschaft (DFG), Deutscher Akademischer Austauschdienst DAAD (HSP III), Hansische Universitätsstiftung, Deutsche Zoologische Gesellschaft (DZG), and Hamburgische Gesellschaft für Verhaltensbiologie e.V (HGV) .

Appendix:

ABBREVIATIONS:

ANCOVA: Analysis of Covariance
 ANOVA: Analysis of Variance
 ASR: Aquatic Surface Respiration
 Co 101: County Road 101 (SM near Martindale)
 CPUE: Catch Per Unit Effort
 CV: Coefficient of Variation
 DF: Degrees of Freedom
 EARDC: Edwards Aquifer Research Data Center
 FNV: Frozen Niche Variation
 GLM: Generalised Linear Model
 HWY: National Highway
 IQR: Inter Quartile Range
 MS: Mean Squares
 MSE: Mean Squares Error
 NAWQA: National Water-Quality Assessment Program
 NTU: Nephelometric Turbidity Units
 OSR: Operational Sex Ratio
 PAR: Photosynthetic Active Radiation
 PCA: Principal Component Analysis
 SD: Standard Deviation
 SE: Standard Error
 SL: Standard Length
 SM: San Marcos River (Martindale)
 SS: Sums of Squares
 TDH: Texas Department of Health
 TNHC: Texas Natural History Museum Collection
 TNRCC: Texas Natural Resource Conservation Commission
 TWC: Texas Water Commission
 USGS: United States Geological Survey

Tab. 8.1: UTM coordinates of field sites.

Population name	code	UTM east	UTM north
Comal	COM	14 58 3606 E	32 87 1820 N
San Marcos River at Co 101	CO 101	14 60 6577 E	33 03 2600 N
San Marcos River at Martindale	SM	14 60 9783 E	33 32 1900 N
Weslaco North Floodway	WES	14 60 3861 E	28 89 3870 N
Lincoln Park Brownsville	LPK	14 65 2272 E	28 65 2360 N
State Fish Hatchery at Olmito	SFH	14 64 7095 E	28 74 7050 N

LOGGER:

Onset Optic StowAway™ underwater temperature loggers had a range of -4°C to +37°C and an accuracy of $\pm 0.2^\circ\text{C}$.

Tab. 8.2: Specifications of Hydrolab DataSonde 4a Multiprobe.

Parameter	Range	Accuracy	Resolution
Temperature	-5° to 50°C	$\pm 0.10^\circ\text{C}$	0.01°C
Specific Conductance	0 to 100 mS/cm	$\pm 1\%$ of reading ± 0.001 mS/cm	4 digits
pH	0 to 14 units	± 0.2 units	0.01 units
Dissolved Oxygen	0 to 50 mg/L	± 0.2 mg/L	0.01mg/L
Turbidity (Shuttered)	0 to 100 or 100 to 1000 NTU	$\pm 2.6\%$ of range 0.1 or 1 NTU	
Ambient Light	0 to 10,000 $\mu\text{mols}^{-1}\text{m}^{-2}$	$\pm 5\%$ of reading or ± 1 $\mu\text{mols}^{-1}\text{m}^{-2}$	1 $\mu\text{mols}^{-1}\text{m}^{-2}$
Chlorophyll	0.02ug/l to 150 ug/l	0.01 $\mu\text{g/l}$	

Measuring Chlorophyll *a* with the Turner Designs SCUFA Fluorometer and ambient light with a LI-COR radiation sensor LI-193 SA Spherical Quantum sensor. It measures photosynthetic radiation (PAR as photosynthetic photon flux fluence rate (PPFFR) in $\mu\text{mols}^{-1}\text{m}$ per μA from all directions. It can be used in air and water.

Sonde calibrated before every southern and central sampling session interval and serviced when any sensor calibration failed. The DO sensor failed in session 3.

HYDROLAB company P.O. Box 389, Loveland, CO 80539-0389, United States.
<http://www.hydrolab.com>

ADDITIONAL DATA:Tab. 8.3 a: sampling data *Poecilia* Central Texas

population	session	date	time effort [min]	haul effort	<i>n P. formosa</i>	<i>n P. latipinna</i> male	<i>n P. latipinna</i> sexfemale	Relative proportion <i>P. formosa</i>	Relative proportion <i>Poecilia</i> juveniles	Relative proportion males (total)	Relative proportion males (sexuals)	<i>n Poecilia</i>	<i>n pisces</i>	sum Poeciliids	total number fish	% <i>Poecilia</i> sp.	% Poeciliids	% predators
SM	1	2-19-01	30	3	5	1	6	0.417	0.000	0.083	0.143	12	58	44	70	34	63	37
SM	2	3-19-01	31	4	6	0	0	1.000	0.000	0.000		6	51	14	57	21	25	75
SM	3	4-6-01	30	3	7	1	0	0.875	0.000	0.125	1.000	13	60	46	73	36	63	37
SM	4	5-3-01			28	12	17	0.491	0.000	0.211	0.414	57	57	228	443	18	52	48
SM II	4	5-3-01	20	2	2	1	0	0.667	0.000	0.333	1.000	3	49					
SM	4	5-14-01	35	5	5	6	2	0.385	0.000	0.462	0.750	13	264					
SM	5	6-12-01	43	2	49	4	2	0.891	0.018	0.073	0.667	55	147	167	202	55	83	14
SM	6	7-9-01	50	1	307	3	14	0.927	0.033	0.009	0.125	326	362	672	688	95	98	2
SM	7	7-26-01	15	2	128	0	0	1.000	0.023	0.000		128	137	262	265	97	99	0
SM	8	8-23-01	10		1	1	3	0.125	0.500	0.125	0.143	8	18	182	218	37	84	14
SM II	8	8-23-01	30	1	87	0	0	0.978	0.146	0.000	0.000	72	120					
SM	9	9-13-01	10	1	17	0	0	1.000	0.000	0.000		17	49	34	66	52	52	49
SM		9-9-02	20	3	21	0	2	0.840	0.600	0.000	0.000	34	70					
SM		10-4-02	20	5	369	0	5	0.956	0.920	0.000	0.000	406	517					
Co101	2	3-19-01	33	4	7	1	2	0.700	0.000	0.100	0.333	10	48	38	58	35	66	0
Co101	3	4-6-01	30	5	15	4	7	0.577	0.154	0.154	0.364	30	117	100	147	41	68	11
Co101	4	5-3-01	35	4	34	2	3	0.872	0.000	0.051	0.400	39	371	101	410	19	25	13
Co101	5	6-12-01	41	6	7	1	2	0.700	0.000	0.100	0.333	10	431	37	439	5	8	3
Co101	6	7-9-01	35	3	31	2	0	0.939	0.333	0.061	1.000	31	137	82	168	37	49	9
Co101	7	7-26-01	25	2	41	1	1	0.911	0.378	0.022	0.250	45	225	145	270	33	54	2
Co101	8	8-23-01	20	2	108	4	8	0.777	0.705	0.029	0.129	130	191	285	321	81	89	4
Co101	9	9-13-01	35	3	9	0	0	1.000	0.222	0.000		11	110	46	121	18	38	3
COM	1	2-19-01	40	6	1	12	8	0.048	0.000	0.571	0.600	21	2023	2042	2044	2	100	0
COM	2	3-21-01	40	5	3	54	41	0.031	0.000	0.551	0.568	98	1100	1196	1198	16	100	0
COM	3	4-6-01	40	4	0	6	12	0.000	0.000	0.333	0.333	18	1023	1036	1041	4	100	0
COM	4	5-3-01	35	4	0	12	10	0.000	0.000	0.545	0.545	23	4031	4046	4054	1	100	0
COM	5	6-12-01	36	1	2	101	70	0.009	0.249	0.441	0.445	201	813	1002	1014	40	99	1
COM	6	7-9-01	70	2	2	29	54	0.019	0.202	0.279	0.284	102	1608	1704	1710	12	100	0
COM	7	7-26-01	40	2	5	54	83	0.017	0.531	0.178	0.181	321	3329	3642	3650	18	100	0
COM	8	8-23-01	32	1	4	51	129	0.020	0.118	0.250	0.255	204	514	708	718	57	99	1
COM	9	9-13-01	60	1	6	111	281	0.014	0.087	0.255	0.258	436	3447	3872	3883	23	100	0
COM		9-9-02	25	2	1	62	126	0.005	0.149	0.279	0.281	256	1429					
COM		10-4-02	30	2	1	29	59	0.009	0.219	0.254	0.257	114	1116					
COM		10-16-02	60		11	40	100	0.068	0.068	0.248	0.267	161	215					
Σ			1106	91	1320	605	1047					3411	24237	21731	23328			

Tab. 8.3 b: sampling data *Poecilia* South Texas

population	session	date	time effort	haul effort	<i>n P. formosa</i>	<i>n P. latipinna</i> male	<i>n P. latipinna</i> sexfemale	Relative proportion <i>P. formosa</i>	Relative proportion <i>Poecilia</i> juveniles	Relative proportion males (total)	Relative proportion males (sexuals)	<i>n Poecilia</i>	<i>n pisces</i>	sum Poeciliids	total number fish	% <i>Poecilia</i> sp.	% Poeciliids	% predators
SFH	1	2-18-01	40	5	0	0	0					0	x	x	x	0	x	x
SFH	2	3-8-01	35	5	0	0	0					0	2	2	2	0	100	0
SFH	3	4-11-01	46	7	0	0	0					0	690	45	690	0	7	6
SFH	4	5-5-01	60	8	0	0	0					0	262	46	270	1	17	24
SFH II	4	5-5-01	30	4	3	0	0	1.000	1.000	0.000		3	6					
SFH	5	5-30-01	36	3	3	1	0	0.750	0.000	0.250	1.000	6	377	266	909	3	29	30
SFH II	5	5-30-01	37	4	9	2	6	0.529	0.059	0.118	0.250	17	510					
SFH	6	6-26-01	64	6	27	1	3	0.500	0.852	0.019	0.037	53	1078	466	1234	4	38	15
SFH	7	7-18-01	33	5	32	0	4	0.780	0.390	0.000	0.000	45	547	570	592	15	96	2
SFH	8	8-15-01	15	3	18	1	0	0.947	0.947	0.053	1.000	19	54	143	328	13	44	13
SFH II	8	8-15-01	40	5	24	0	0	1.000	0.792	0.000		24	231					
SFH	9	9-12-01	30	3	4	0	0	1.000	0.500	0.000		5	18	19	23	44	83	17
WES	1	2-17-01	60	5	47	35	29	0.294	0.356	0.219	0.310	160	161	320	321	100	100	0
WES	2	3-7-01	60	5	89	102	160	0.228	0.103	0.262	0.339	389	1195	1178	1584	49	74	0
WES	3	4-11-01	40	5	73	21	21	0.635	0.000	0.183	0.500	170	523	440	693	49	64	11
WES	4	5-6-01	50	7	101	31	15	0.253	0.792	0.078	0.492	525	1584	1350	2109	50	64	0
WES	5	5-31-01	46	4	59	14	26	0.484	0.434	0.115	0.222	162	554	374	706	46	53	34
WES	6	6-25-01	33	3	139	43	33	0.602	0.442	0.186	0.467	195	313	465	507	77	92	0
WES	7	7-18-01	30	2	133	43	53	0.482	0.319	0.156	0.301	325	473	750	798	82	94	1
WES	8	8-16-01	120	5	148	9	16	0.796	0.462	0.048	0.237	730	1120	1615	1850	79	87	2
WES	9	9-11-01	40	3	73	10	28	0.619	0.102	0.085	0.222	74	430	156	504	29	31	8
WES		9-27-02	30	3	50	8	23	0.463	0.444	0.074	0.138	118	262					
LPK	1	2-17-01	40	5	32	4	1	0.865	0.865	0.108	0.800	37	37	74	74	100	100	0
LPK	2	3-8-01	40	6	7	25	13	0.064	0.591	0.227	0.243	110	283	360	393	56	92	0
LPK	3	4-10-01	35	6	6	16	12	0.167	0.056	0.444	0.533	56	446	382	502	22	76	1
LPK	4	5-6-01	40	4	31	21	13	0.211	0.639	0.143	0.375	145	1562	840	1707	17	49	0
LPK	5	5-31-01	29	4	137	48	6	0.268	0.873	0.094	0.276	511	702	1092	1213	84	90	0
LPK	6	6-26-01	45	5	603	29	6	0.629	0.960	0.030	0.082	935	1655	2280	2590	72	88	3
LPK	7	7-17-01	35	3	122	92	236	0.210	0.303	0.158	0.200	580	1512	1910	2092	55	91	1
LPK	8	8-16-01	55	5	502	37	154	0.316	0.860	0.023	0.034	1338	2597	3776	3935	68	96	2
LPK	9	9-12-01	40	4	149	10	11	0.482	0.906	0.032	0.063	390	656	860	1046	75	82	2
LPK		9-12-02	20	4	43	2	7	0.269	0.931	0.013	0.017	171	456					
Σ			1354	146	2664	605	876					7293	20296	19779	26672			

Tab. 8.4 a: sampling data water quality **Central Texas**

population	session	date	air temp [°C]	rain code	rel. cloud cover	Width [m]	water color class	water current code	surface cover code	water level code	Mean water temp [°C]	Mean spec. cond. [mS/cm]	Mean turbidity [NTU]	mean pH	Mean water PAR	Mean air PAR	Mean DO [mg/l]	Mean Chlorophyll [µg/l]	Salinity [ppt]	rel. shade
SM	1	2-19-01	24	1		3	clear	3	3	4	17.5	0.62	49	7.9	598	1599	6.7	12.7	0	
SM	2	3-19-01	15	2	0.7	3	grey	3	3	5	16.1	0.62	122	8.1	98	88	6.0	3.9	0	
SM	3	4-6-01	27	2	0.9	3	brown	3	3	4	23.0	0.62	74	7.3	115	1781		1.2	0	0.95
SM	4	5-3-01	30	0	0.75	5	green	0	1	3	25.0	0.52	563	7.5	2107	3909	8.4	2.6	0	0.0
SM II	4	5-3-01	27	0	0.4	3	grey	3	3	3	22.4	0.62	85	7.6	82	196	8.4	1.7	1	
SM	4	5-14-01	29	0	0.5	5	green	0	1	3	24.9	0.51	115	8.0	477	566	10.4	9.6	0	
SM	5	6-12-01	32	2	0.3	3	grey	3	3	4	28.7	0.64	19	7.5	140	1198	7.3	2.3	0	
SM	6	7-9-01	35	0	0	3	brown	3	3	3	29.1	0.62	56	7.5	1810	2018	8.1	1.3	0	
SM	7	7-26-01	33	0	0.3	3	brown	3	2	3	28.2	0.65	129	7.6	14	3393		1.8	0	
SM	8	8-23-01	35	1	0.7	3	grey	3	3	3.5	28.0	0.63	151	7.6	184	1863	6.6	1.0	0	
SM	9	9-13-01	29	0	0.6	3	grey	4	1	3	26.7	0.63	187	7.7	19	962	7.7	2.6	0	0.9
SM		9-9-02	25	2	0.9	3	brown	3	2	5	25.2	0.61	68	7.5	184	346		1.3	0	1.0
SM		10-4-02	30	0	0.15	6	grey	3	1	4	26.2	0.60	42	7.6	78	275	6.6	4.8	0	0.75
Co101	2	3-19-01	16	2	0.8	20	clear	3.5	3	5	16.2	0.50	8	8.4	624	1107	7.3	0.3	0	
Co101	3	4-6-01	26	0	0.9	20	milky	3.5	3	4	22.5	0.51	12	8.4	1224	2151	13.3	1.2	0	0.0
Co101	4	5-3-01	31	0	0.8	20	grey	3	2	3	23.3	0.53	18	7.9	1702	3783	9.4	0.5	0	0.0
Co101	4	5-14-01	32	0	0.3	20	green	3	2	3	24.2	0.51	10	8.0	1037	3390	12.9	0.2	0	
Co101	5	6-12-01	34	2	0.2	20	grey	3	3	3	24.7	0.56	1	7.9	2026	4381	9.8	0.1	0	
Co101	6	7-9-01	36	0	0	20	green	3	0	2	24.8	0.58	17	7.8	2043	3628	9.3	0.0	0	0.0
Co101	7	7-26-01	36	0	0.15	20	milky	4	0	3	24.7	0.58	0	8.0	1485	1486		0.1	0	0.0
Co101	8	8-23-01	35	1	0.25	20	grey	4	2	2	25.1	0.57	25	8.0	1135	1537	9.1	1.2	0	0.0
Co101	9	9-13-01	31	2	0.5	20	milky	4	2	3	24.3	0.54	6	7.9	665	879	8.9	0.3	0	0.0
Co101		9-9-02	26	2	0.95	20	green	4	2	4.5	23.9	0.53	11	7.8	295	593		3.4	0	0.0
COM	1	2-19-01	22	1		5	clear	1.5	1	3	23.5	0.53	3	7.4	277	1362	3.8	1.0	0	
COM	2	3-21-01	20	2	0.01	5	clear	1.5	1	3.5	23.5	0.52	2	7.6	2046	2938	4.0	0.2	0	0.8
COM	3	4-6-01	23	0	0.95	5	clear	1.5	0	4	23.5	0.52	1	7.7	396	1082		1.1	0	0.8
COM	4	5-3-01	30	0	0.9	5	clear	2	3	3	23.5	0.52	5	7.1	1022		7.7	0.6	0	0.8
COM	5	6-12-01	32	2	0.2	5	clear	2	2	4	23.6	0.53	1	7.2	1343	3438	7.8	1.2	0	0.8
COM	6	7-9-01	32	0	0	5	clear	2	1	3	23.6	0.53	0	7.1	1584		8.3	0.5	0	0.8
COM	7	7-26-01	31	0	0.7	5	clear	2	1	3	23.6	0.53	0	7.2	2123	1421		0.1	0	0.2
COM	8	8-23-01	31	1	0.5	5	clear	2	1	3	23.5	0.52	0	7.2	804	1042	7.5	0.3	0	0.8
COM	9	9-13-01	30	2	0.1	5	clear	2	1	3.5	23.5	0.53	1	7.2	1424	3587	7.1	0.4	0	0.4
COM		9-9-02	23	3	1	5	clear	2	1	4	23.3	0.52	15	7.1	68	131		0.4	1	1.0
COM		10-4-02	28	0	0.05	5	clear	2	1	4	23.5	0.53	7	7.2	1337	1983	5.6	0.4	0	0.3

Tab. 8.4 b: sampling data water quality **South Texas**

population	session	date	air temp [°C]	rain code	rel. cloud cover	Width [m]	water color class	water current code	surface cover code	water level code	Mean water temp [°C]	Mean spec. cond. [mS/cm]	Mean turbidity [NTU]	mean pH	Mean water PAR	Mean air PAR	Mean DO [mg/l]	Mean Chlorophyll [µg/l]	Salinity [ppt]	rel. shade
SFH	1	2-18-01	18	1	0.05	4	green	0	1	3	15.7	1.62	106	8.6	607	3053	4.3	22.6	0	
SFH	2	3-8-01	28	2	0.85	4	green	0	1	5	19.7	1.90	58	8.6	898	1662	4.2	14.1	0	
SFH	3	4-11-01	31	0	0.85	4	green	0	1	4	25.6	2.07	165	7.6	221	726	10.3	1		
SFH	4	5-5-01	32	3	0.95	4	green	0	1	3	26.1	2.19	254	7.9	269	1612	6.7	8.4		
SFH II	4	5-5-01	30	2	0.8	10	green	0.5	1	3	27.5	1.99	172	7.7	61	496	6.6	10.0	0	
SFH	5	5-30-01	33	0	0.2	10	green	0	1	3	32.4	2.15	122	7.6	298	438	8.4	8.0	0	
SFH II	5	5-30-01	33	0	0.1	5	brown	0	1	2	30.7	2.66	238	8.1	1677	2837	11.9	3.7	1	
SFH	6	6-26-01	33	2	0.25	5	green	0	1	1	29.8	2.65	194	8.1	1424	683	8.7	4.9	0	
SFH	7	7-18-01	35	0	0.25	3	green	0	1	1	35.2	3.76	440	8.5	2899	3276	10.1	6.2	0 0.1	
SFH	8	8-15-01	37	0	0	1	green	0	0	0	38.5	9.71		7.8		3178	5.7	10.0	7 0.0	
SFH II	8	8-15-01	37	0	0	6	brown	0	2	1	37.1	2.42		8.3	386	2334	6.3	8.1	0	
SFH	9	9-12-01	32	2	0.5	1	clear	0	1	0.5	33.4	4.40	0	7.8	2179		7.3	2.4	1 0.0	
SFH II	9	9-12-01	30	3	0.5	5	brown	0	1	1	29.6	1.67	389	8.8	1882	4588	7.8	9.3	0 0.2	
SFH		9-13-02	32	2	0.2	1.5	clear	0	1	1	29.1	2.46	15	7.4	1231	2584	6.1	2.2	0 0.1	
WES	1	2-17-01	24	1	0	4	grey	1	1	3	20.5	4.25	483	8.1	2331	4228	6.6	18.1	0	
WES	2	3-7-01	25	0	0.9	3	brown	1	1	4	22.5	4.21	203	8.3	595	1858	6.7	14.8	0 0.0	
WES	3	4-11-01	32	0	0.95	4	green	0.5	2	3	27.8	3.11	219	8.1	1262	3252	12.0	0	0.0	
WES	4	5-6-01	32	2	1	5	grey	0	1	3.5	28.2	3.86	383	8.0	1035	2037	9.1	11.2	2 0.0	
WES	5	5-31-01	31	3	0.7	4	green	1	1	3	28.5	4.10	260	7.8	261	1674	12.6	11.1	1 0.0	
WES	6	6-25-01	29	2	0.95	5	green	2	1	2	31.0	4.47	320	8.3	209	1742	13.6	18.8	3 0.0	
WES	7	7-18-01	29	0	0.5	5	green	2	2	3	29.1	4.23	159	8.0	364	1402	8.6	17.9	2 0.05	
WES	8	8-16-01	31	0	0	4	brown	1	1	2	27.8	4.52	237	7.9	508	3683	10.3	10.5	2 0.0	
WES	9	9-11-01	32	3	0.95	5	brown	1	1	5	27.5	0.44	367	7.9	2	2448	4.6	4.3	0	
WES		9-13-02	36	2	0.05	4	brown	2	2	4	32.0	2.78	236	7.5	1957	4600	4.5	1.1	0 0.0	
WES		9-27-02	34	2	0	4	brown	1.5	2	4	31.9	4.49	169	8.0	1645	4294	10.1	6.8	0 0.0	
LPK	1	2-17-01	16	1	0.4	20	brown	0	1	4	17.4	1.72	132	8.0	442	1298	4.7	10.4	0	
LPK	2	3-8-01	23	0	0.5	20	brown	0	1	3	18.6	2.37	232	8.2	123	702	4.8	21.1	0	
LPK	3	4-10-01	31	0	0	30	green	0	3	3	27.4	3.02	154	8.4	527	1760	17.9	0		
LPK	4	5-6-01	28	2	0.99	30	green	0	2	3.5	25.1	1.60	245	7.7	9	312	6.5	15.9	0	
LPK	5	5-31-01	33	2	0.5	20	brown	1	1	2	29.4	1.51	338	8.3	1329	2499	10.6	14.8	0	
LPK	6	6-26-01	31	2	0.25	30	green	0	1	3	27.5	2.06	296	7.6	195	542	6.2	11.2	1 0.5	
LPK	7	7-17-01	34	0	0.15	15	brown	0	2	1	31.3	1.75	317	8.6	150	1859	9.3	16.3	0 0.5	
LPK	8	8-16-01	34	0	0.3	15	brown	1	2	1	29.5	3.54	295	8.1	1787	3139	9.9	10.7	1.5 0.5	
LPK	9	9-12-01	28	2	0	20	brown	1	2	5	27.9	0.83	108	7.5	72	1797	6.3	7.8	0 0.8	
LPK		9-12-02	31	2	0.25	30	green	0	1	3.5	31.3	1.44	88	9.3	572	3323	11.7	15.3	0 0.5	

Tab. 8.5a: Standard length of *P. latipinna* males measured in the course of the study throughout February – September 2001 in six populations and nine three-weekly sampling sessions.

latmale	session	Mean	S.E.	n	Min.	Max.	C.V.	Median	IQR	Mode
total		27.6	0.2	779	16	53	0.2	27.0	6.0	25
SM	1	43.0	.	1	43	43	.	43.0	0.0	43
SM	3	35.0	.	1	35	35	.	35.0	0.0	35
SM	4	28.1	0.8	20	21	35	0.1	27.0	4.5	27
SM	5	32.3	3.9	4	25	40	0.2	32.0	13.5	.
SM	6	27.0	.	1	27	27	.	27.0	0.0	27
SM	8	33.0	.	1	33	33	.	33.0	0.0	33
Co 101	2	24.0	.	1	24	24	.	24.0	0.0	24
Co 101	3	25.5	0.9	4	24	28	0.1	25.0	2.0	25
Co 101	4	32.5	9.5	2	23	42	0.4	32.5	19.0	.
Co 101	5	31.0	.	1	31	31	.	31.0	0.0	31
Co 101	6	30.5	6.5	2	24	37	0.3	30.5	13.0	.
Co 101	7	30.0	.	1	30	30	.	30.0	0.0	30
Co 101	8	26.5	0.5	2	26	27	0.0	26.5	1.0	.
COM	1	27.9	1.1	12	23	36	0.1	27.5	4.5	.
COM	3	28.0	1.4	6	22	32	0.1	28.0	4.0	28
COM	4	29.8	1.1	14	23	35	0.1	30.0	6.0	.
COM	5	28.0	0.5	80	18	44	0.2	27.5	5.0	25
COM	6	27.9	1.0	26	22	43	0.2	27.0	7.0	.
COM	7	26.8	0.6	46	20	43	0.2	26.5	5.0	24
COM	8	30.6	1.0	25	23	48	0.2	29.0	5.0	28
COM	9	33.3	0.8	67	21	53	0.2	33.0	8.8	.
SFH	5	31.3	1.3	3	30	34	0.1	30.0	3.0	30
SFH	6	25.0	.	1	25	25	.	25.0	0.0	25
SFH	8	18.0	.	1	18	18	.	18.0	0.0	18
WES	1	26.1	0.8	30	20	37	0.2	24.0	5.0	24
WES	2	25.5	0.7	52	19	37	0.2	25.0	8.0	20
WES	3	33.5	1.9	11	24	45	0.2	34.0	9.8	38
WES	4	24.8	0.9	27	17	37	0.2	24.0	4.0	.
WES	5	23.3	1.1	14	17	32	0.2	23.0	4.0	22
WES	6	24.7	0.8	43	17	35	0.2	24.0	6.8	23
WES	7	26.5	0.7	40	18	46	0.2	25.0	5.0	25
WES	8	28.2	1.4	9	22	32	0.1	30.0	7.8	32
WES	9	30.0	0.9	10	26	36	0.1	30.0	1.0	30
LPK	2	28.4	1.5	20	19	46	0.2	28.0	8.0	.
LPK	3	29.9	2.0	16	19	46	0.3	27.5	12.0	.
LPK	4	27.6	1.1	21	21	40	0.2	27.0	6.0	30
LPK	5	24.1	0.8	48	16	40	0.2	24.0	6.5	25
LPK	6	24.4	0.7	29	19	35	0.2	24.0	3.5	25
LPK	7	28.7	0.6	40	21	40	0.1	29.0	5.5	30
LPK	8	26.7	0.6	37	21	37	0.1	26.0	3.3	.
LPK	9	25.5	1.6	10	21	35	0.2	23.5	4.0	22

Tab. 8.5 b: Standard length of *P. latipinna* females measured in the course of the study throughout February – September 2001 in six populations and nine three-weekly sampling sessions.

latfemale	session	Mean	S.E.	n	Min.	Max.	C.V.	Median	IQR	Mode
total		37.5	0.2	773	30	61	0	36.0	8.3	30
SM	1	45.5	2.3	6	36	52	0.1	46.5	6.0	49
SM	4	38.2	1.3	18	32	53	0.1	37.5	7.0	.
SM	5	45.5	0.5	2	45	46	0.0	45.5	1.0	.
SM	6	50.1	3.4	8	30	60	0.2	51.5	10.0	.
SM	8	33.0	1.2	3	31	35	0.1	33.0	3.0	.
Co 101	2	34.0	.	1	34	34	.	34.0	0.0	34
Co 101	3	35.9	2.5	7	31	47	0.2	32.0	10.3	31
Co 101	4	42.0	1.7	3	39	45	0.1	42.0	4.5	.
Co 101	5	45.0	1.0	2	44	46	0.0	45.0	2.0	.
Co 101	7	30.0	.	1	30	30	.	30.0	0.0	30
Co 101	8	37.3	2.3	6	30	47	0.1	37.0	3.0	38
COM	1	37.0	2.6	4	32	44	0.1	36.0	8.0	.
COM	3	35.1	0.8	11	30	39	0.1	35.0	4.5	.
COM	4	39.6	1.0	10	35	46	0.1	39.5	5.0	.
COM	5	37.2	0.6	67	30	54	0.1	38.0	7.8	.
COM	6	41.4	0.8	54	30	55	0.1	42.0	8.0	.
COM	7	37.8	0.9	49	30	49	0.2	35.0	12.0	.
COM	8	38.5	0.5	129	30	61	0.2	37.0	9.0	35
COM	9	36.8	0.7	61	30	48	0.1	36.0	9.0	30
SFH	5	47.2	2.9	6	33	52	0.2	50.0	4.0	50
SFH	6	35.0	1.5	3	33	38	0.1	34.0	3.8	.
SFH	7	34.8	2.5	4	31	42	0.1	33.0	6.5	.
WES	2	36.8	0.7	55	30	50	0.1	36.0	7.8	.
WES	3	36.8	1.2	16	31	49	0.1	35.0	6.0	35
WES	4	42.0	1.2	8	36	47	0.1	41.5	4.0	41
WES	5	35.2	1.2	23	30	50	0.2	33.0	5.0	31
WES	6	32.9	0.9	33	30	50	0.2	30.0	4.3	30
WES	7	38.1	0.7	40	30	53	0.1	38.0	4.0	.
WES	8	35.4	1.1	16	30	43	0.1	34.5	7.5	.
WES	9	37.7	1.0	27	32	52	0.1	36.0	6.8	.
LPK	2	33.0	0.8	8	31	36	0.1	32.0	4.5	31
LPK	3	31.0	1.0	2	30	32	0.0	31.0	2.0	.
LPK	4	34.0	1.2	10	30	42	0.1	33.5	5.0	.
LPK	5	32.8	1.5	5	30	37	0.1	31.0	6.3	30
LPK	6	34.7	1.3	6	30	39	0.1	35.0	5.0	35
LPK	7	35.1	0.6	40	30	43	0.1	35.0	5.5	.
LPK	8	36.3	1.0	18	30	43	0.1	36.0	8.0	32
LPK	9	33.9	1.3	11	30	41	0.1	31.0	6.8	30

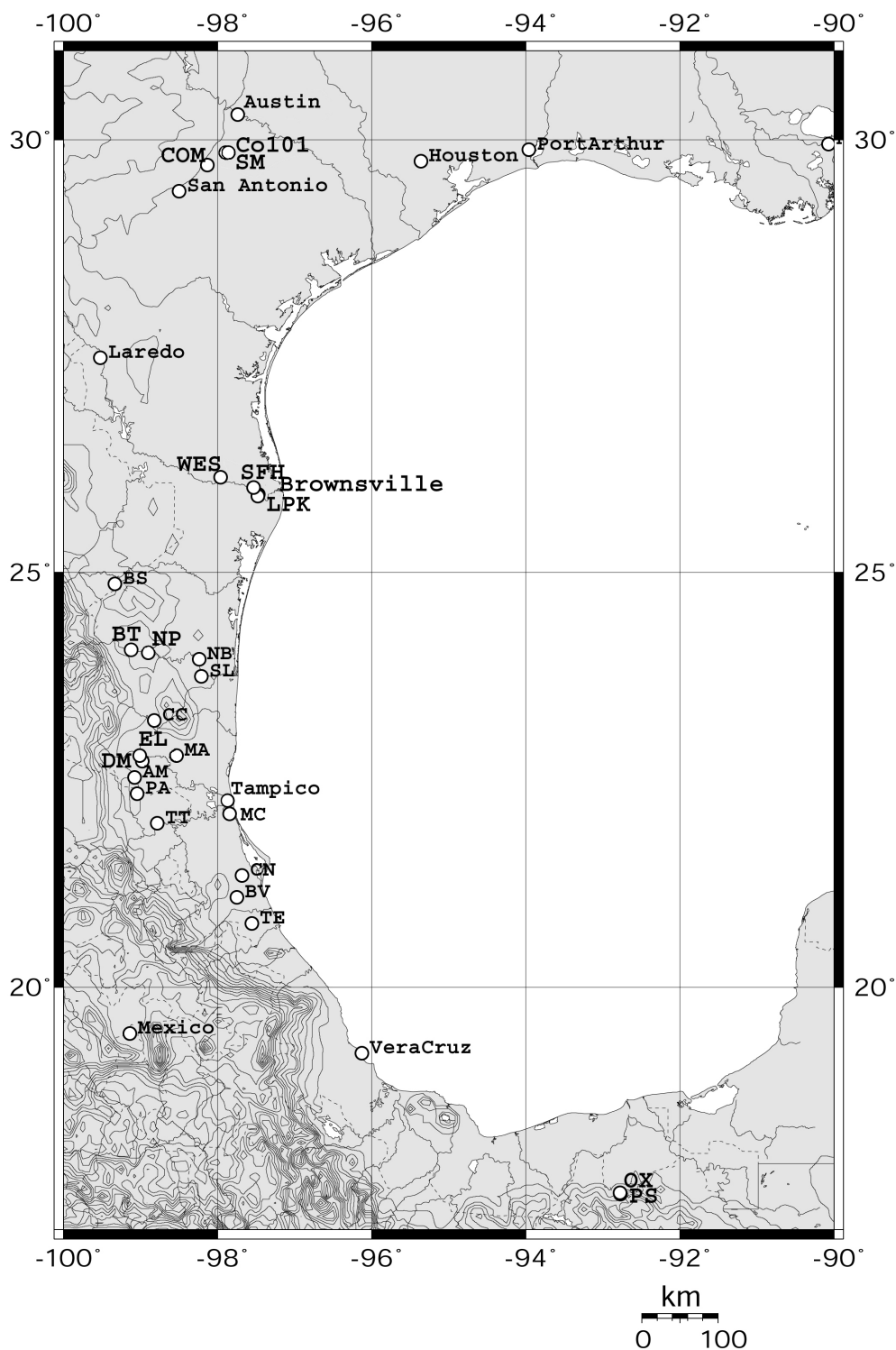
Tab. 8.5 c: Standard length of *P. formosa* measured in the course of the study throughout February – September 2001 in six populations and nine three-weekly sampling sessions.

formosa	session	Mean	S.E.	n	Min.	Max.	C.V.	Median	IQR	Mode
total		41.2	0.3	867	30	67	0	40.0	14.0	30
SM	1	39.2	2.6	5	32	48	0.1	38.0	5.5	38
SM	2	33.0	1.8	4	30	38	0.1	32.0	5.0	.
SM	3	36.8	3.7	5	30	49	0.2	32.0	13.0	.
SM	4	41.5	1.5	31	31	67	0.2	40.0	6.8	.
SM	5	48.3	0.7	48	39	61	0.1	48.0	6.0	.
SM	6	53.2	0.5	46	46	61	0.1	53.0	4.0	53
SM	7	54.2	0.7	50	41	64	0.1	55.0	6.0	.
SM	8	52.5	0.6	42	38	60	0.1	52.0	5.0	52
SM	9	55.5	1.2	17	43	64	0.1	56.0	6.8	.
Co 101	2	36.0	2.6	5	31	45	0.2	34.0	8.0	.
Co 101	3	38.4	1.6	9	30	44	0.1	41.0	7.5	41
Co 101	4	39.9	0.9	31	30	48	0.1	40.0	6.8	37
Co 101	5	43.6	0.7	7	42	47	0.0	43.0	2.3	43
Co 101	6	36.2	2.0	19	30	57	0.2	32.0	2.8	.
Co 101	7	39.9	1.9	26	30	58	0.2	36.0	19.0	30
Co 101	8	34.5	0.9	26	30	45	0.1	32.5	7.0	30
Co 101	9	36.3	3.1	7	30	50	0.2	32.0	12.0	31
COM	5	34.0	.	1	34	34	.	34.0	0.0	34
COM	7	41.2	4.6	5	33	54	0.3	34.0	18.0	34
COM	8	44.3	3.5	4	37	52	0.2	44.0	11.5	.
COM	9	40.5	3.5	6	30	53	0.2	39.5	13.0	.
SFH	5	43.2	3.0	11	30	59	0.2	47.0	15.5	47
SFH	6	44.8	4.9	4	35	55	0.2	44.5	16.5	.
SFH	7	41.1	2.1	21	30	60	0.2	36.0	11.0	.
SFH	8	33.4	0.5	5	32	35	0.0	33.0	1.5	33
SFH	9	35.0	3.0	2	32	38	0.1	35.0	6.0	.
WES	2	37.5	0.7	47	30	52	0.1	37.0	5.8	37
WES	3	39.5	0.5	58	32	48	0.1	39.5	7.0	.
WES	4	42.3	1.4	26	30	59	0.2	43.0	7.0	30
WES	5	41.9	1.5	27	32	57	0.2	44.0	12.5	35
WES	6	34.3	0.6	44	30	50	0.1	33.0	6.0	.
WES	7	36.0	0.7	40	30	50	0.1	35.0	8.0	40
WES	8	36.1	0.7	37	30	45	0.1	36.0	7.3	30
WES	9	36.8	0.7	38	30	46	0.1	35.5	6.0	35
LPK	2	31.3	0.8	4	30	33	0.0	31.0	2.5	30
LPK	3	31.7	1.1	6	30	37	0.1	30.5	2.0	30
LPK	4	35.8	1.0	18	30	44	0.1	36.0	5.0	.
LPK	5	34.2	0.6	10	30	36	0.1	34.5	3.0	36
LPK	6	35.0	2.9	3	30	40	0.1	35.0	7.5	.
LPK	7	37.6	0.5	40	30	42	0.1	38.0	4.0	40
LPK	8	32.6	0.7	24	30	41	0.1	30.5	5.0	30
LPK	9	32.3	1.3	8	30	41	0.1	31.0	2.5	30

Tab. 8.6: overview over fish community sampled.

population	session	n predatory species	n fish species	Poeciliidae Centrarchidae Cichlidae Cyprinidae																	total number fish sampled	% Poecilia sp.	% predators				
				<i>P. formosa</i>	<i>P. latipinna</i>	<i>Gambusia affinis/gambusia</i>	<i>Micropogonias undulatus</i>	<i>Lepomis cyanellus</i>	<i>Lepomis macrochirus</i>	<i>Lepomis humilis</i>	<i>Lepomis gulosus</i>	<i>Cichlasoma cyanoguttatum</i>	<i>Oreochromis aureus</i>	<i>Astyanax mexicanus</i>	<i>Dorosoma cepedianum</i>	<i>Menidia berillina</i>	<i>Gyrinocheilus ariagatus</i>	Catostomidae	<i>Etheostoma</i>	<i>Dionda episcopa</i>				<i>Pomoxinus anostomatus</i>	<i>Cyprinus carpio</i>	<i>Cyprinella venusta</i>	<i>Notropis amabilis</i>
SM	1	4	7	B	B	D	-	x	x	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-	70	34	37
SM	2	4	6	B	-	A ₂	A ₂	E	A ₁	-	-	-	A ₂	-	-	-	-	-	-	-	-	-	-	-	57	21	75
SM	3	3	6	C	A ₁	D	-	D	-	-	-	A ₂	-	C	-	-	-	-	-	-	-	-	-	-	73	36	37
SM	4	7	12	B	B	C	A ₂	C	A ₁	C	-	-	-	B	-	A ₂	-	-	-	-	-	-	-	-	443	18	48
SM	5	4	10	D	A ₃	D	-	C	-	-	-	-	A ₁	A ₁	-	-	-	A ₂	-	-	-	A ₂	-	-	202	55	14
SM	6	4	8	F	B	B	A ₁	A ₃	-	-	-	-	-	A ₁	-	-	-	A ₂	-	-	-	-	-	-	688	95	2
SM	7	1	4	F	-	A ₃	-	-	-	-	-	-	A ₁	-	-	-	-	-	-	-	-	A ₂	-	-	265	97	0
SM	8	2	7	D	A ₃	B	-	B	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-	218	37	14
SM	9	4	5	D	-	-	A ₁	D	A ₁	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-	66	52	49
Co101	2	0	5	B	A ₂	D	-	-	-	-	-	-	-	-	-	C	-	-	C	-	-	-	-	-	58	35	0
Co101	3	2	8	B	B	D	-	-	B	B	-	-	-	-	-	A ₃	-	A ₁	C	-	-	-	-	-	147	41	11
Co101	4	4	14	B	A ₂	B	A ₃	B	-	-	-	B	-	A ₂	-	C	-	A ₂	A ₃	B	-	A ₃	D	A ₁	410	19	13
Co101	5	3	13	A ₃	A ₂	A ₃	A ₂	A ₃	-	-	-	A ₁	-	-	-	-	A ₁	A ₃	-	A ₂	-	A ₃	F	-	439	5	3
Co101	6	3	11	C	B	C	A ₁	A ₂	-	-	-	-	B	-	-	-	-	-	-	-	-	B	-	-	168	37	9
Co101	7	3	8	C	A ₂	C	-	-	-	-	-	A ₂	A ₂	-	-	-	-	-	-	-	-	C	D	-	270	33	2
Co101	8	2	9	E	C	B	-	-	-	-	-	A ₃	A ₃	-	-	-	-	A ₁	-	-	-	B	A ₃	-	321	81	4
Co101	9	3	8	B	-	C	A ₁	A ₁	-	A ₂	-	-	-	-	-	-	-	A ₁	-	-	-	E	B	-	121	18	3
COM	1	0	5	A ₁	A ₃	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A ₁	-	2044	2	0
COM	2	1	4	A ₂	C	F	-	-	-	-	-	-	A ₂	-	-	-	-	A ₁	-	-	-	-	-	-	1198	16	0
COM	3	2	5	-	A ₃	F	-	-	A ₁	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1041	4	0
COM	4	1	6	A ₁	A ₃	F	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	A ₁	-	4054	1	0
COM	5	2	5	A ₁	D	E	-	-	A ₂	-	-	-	-	A ₃	-	-	-	-	-	-	-	-	-	-	1014	40	1
COM	6	2	5	A ₂	B	F	-	-	-	-	-	-	A ₂	A ₂	-	-	-	-	-	-	-	-	-	-	1710	12	0
COM	7	2	6	A ₃	B	F	-	-	-	-	-	-	A ₂	A ₂	-	-	-	-	-	-	-	-	-	-	3650	18	0
COM	8	1	4	A ₂	D	E	-	-	-	-	-	-	-	A ₃	-	-	-	-	-	-	-	-	-	-	718	57	1
COM	9	2	5	A ₃	B	F	-	-	A ₁	-	-	-	-	A ₃	-	-	-	-	-	-	-	-	-	-	3883	23	0
SFH	1	3	4	-	-	A ₃	x	-	x	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x
SFH	2	0	1	-	-	A ₂	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0	0
SFH	3	2	8	-	-	B	-	-	B	-	A ₁	-	-	F	-	A ₂	-	-	-	-	x	-	-	A ₃	690	0	6
SFH	4	4	11	A ₂	-	C	A ₃	x	-	C	A ₂	-	-	D	A ₃	D	-	-	-	-	-	-	A ₁	270	1	24	
SFH	5	2	10	A ₃	A ₃	C	C	-	-	-	-	-	B	-	D	A ₃	-	-	-	-	-	-	A ₂	909	3	30	
SFH	6	3	11	A ₃	A ₃	D	B	A ₂	-	-	-	-	A ₃	-	C	C	B	-	-	-	-	-	A ₃	1234	4	15	
SFH	7	2	8	B	A ₃	F	A ₂	-	-	-	-	-	A ₃	-	A ₃	-	A ₂	A ₁	-	-	-	-	-	-	592	15	2
SFH	8	3	8	B	A ₁	C	A ₂	A ₃	-	-	-	-	B	-	D	B	-	-	-	-	-	-	-	-	328	13	13
SFH	9	2	4	A ₂	-	D	-	-	A ₂	-	-	-	A ₂	-	-	-	-	-	-	-	-	-	-	-	23	44	17
WES	1	1	7	C	D	-	-	-	-	-	-	-	A ₂	-	-	-	C	A ₃	-	-	-	-	-	-	321	100	0
WES	2	2	8	B	D	D	-	-	-	-	-	-	A ₁	A ₂	-	-	D	A ₃	-	-	-	-	-	-	1584	49	0
WES	3	3	11	C	B	C	-	-	-	-	-	-	A ₃	A ₂	B	-	C	B	-	-	-	A ₃	-	-	693	49	11
WES	4	3	10	B	B	C	-	A ₂	-	-	-	-	A ₁	-	A ₂	-	D	A ₃	-	-	-	A ₁	-	-	2109	50	0
WES	5	3	8	C	C	B	A ₂	-	-	-	-	-	-	B	D	-	C	-	-	-	-	-	-	-	706	46	34
WES	6	1	6	D	C	C	-	-	-	-	-	-	A ₁	-	-	-	B	-	-	-	-	-	-	-	507	77	0
WES	7	2	6	D	D	C	-	-	-	-	-	-	A ₂	A ₂	-	-	B	-	-	-	-	-	-	-	798	82	1
WES	8	2	8	D	D	B	-	-	-	-	-	-	A ₃	A ₃	A ₃	C	A ₂	-	-	-	-	-	-	-	1850	79	2
WES	9	2	8	B	B	A ₃	-	-	-	-	-	-	A ₁	B	-	C	D	A ₃	-	-	-	-	-	-	504	29	8
LPK	1	0	5	D	B	D	-	-	-	-	-	-	-	-	-	-	B	A ₃	-	-	-	-	-	-	74	100	0
LPK	2	0	5	A ₃	D	D	-	-	-	-	-	-	-	-	-	-	B	B	-	-	-	-	-	-	393	56	0
LPK	3	1	8	A ₃	B	E	-	-	-	-	-	-	A ₂	-	-	-	B	B	-	-	-	-	-	-	502	22	1
LPK	4	0	6	A ₃	A ₃	D	-	-	-	-	-	-	-	-	-	A ₃	E	A ₃	-	-	-	-	-	-	1707	17	0
LPK	5	1	7	D	D	B	-	-	-	-	-	-	A ₁	-	-	-	A ₃	C	A ₂	-	-	-	-	-	1213	84	0
LPK	6	2	7	C	B	D	-	-	-	-	-	-	-	A ₃	-	-	B	A ₃	-	-	-	-	-	-	2590	72	3
LPK	7	2	8	B	D	E	-	-	-	-	-	-	-	A ₃	-	A ₂	B	A ₃	-	-	-	-	-	-	2092	55	1
LPK	8	1	6	C	D	D	-	-	-	-	-	-	-	A ₃	-	-	A ₃	A ₃	-	-	-	-	-	-	3935	68	2
LPK	9	2	8	D	D	B	-	-	-	-	-	-	A ₂	A ₃	-	-	C	A ₃	-	-	-	-	-	-	1046	75	2

Only species with a total of more than 5 individuals sampled are presented. x: present; -: absent (0%); A1: one (1 individual); A2: rare (2-5 individuals; < 5%) A3: occasional (< 5%); B: frequent (5-15%); C: common (15-25%); D: abundant (25-50%); E: super abundant (50-75%); F: extremely abundant (75-100%).



Map. 8.1: Map of field sites in of the two bisexual-unisexual species complexes *P. latipinna* / *P. formosa* and *P. mexicana* / *P. formosa*. List of field sites see Tab. 8.7.

Source: GMT (Generic Mapping Tools) at http://www.aquarius.geomar.de/omc/omc_intro.html.

Sampling of 25 populations throughout Texas (*P. latipinna*/*P. formosa*) and Mexico (*P. mexicana* / *P. formosa*) in September 2001.

Sampling of populations in Texas (*P. latipinna*/*P. formosa* complex): nine regular visits between February and September 2001.

Additional irregular sampling at SM, SFH, WES, COM, AS: (between Sept. 1999 and Oct. 2002)

Tab. 8.7: List of field sites sampled in September 2001: 6 populations in Texas (*P. latipinna* / *P. formosa*), 22 populations in Mexico (*P. mexicana* / *P. formosa*)

data	allopatric/ sympatric	country	population name	river / water body	river system	site code	date in 2002	latitude (N)	longitude (W)	Altitude (m)	<i>P. formosa</i> n total	<i>P. latipinna</i> n total	<i>P. mexicana</i> n total
+	sym-	texas	San Marcos Co 101	San Marcos River	Guadalupe R.	Co101	sept-09	29°51.43'	097°53.80'		0	0	0
+	sym-	texas	San Marcos Martindale	San Marcos River	Guadalupe R.	SM	sept-09	29°51.48'	097°51.85'	211	21	4	0
+	sym-	texas	Comal Landa Park	Comal river	Guadalupe R.	COM	sept-09	29°42.76'	098°08.16'	211	1	221	0
+	sym-	texas	Weslaco Floodway	North Floodway	Nueces - Rio Grande R.	WES	sept-27	26°07.20'	097°57.67'	28	50	58	0
+	sym-	texas	SFH Olmito	ditch	Nueces - Rio Grande R.	SFH	sept-13	25°59.19'	097°31.88'	13	0	0	0
+	sym-	texas	Lincoln Park Brownsville	resaca Brownsville	Nueces - Rio Grande R.	LPK	sept-12	25°53.98'	097°28.77'	0	43	117	0
+	sym-	mexico	Banos de San Ignacio	Banos de San Ignacio	R. Conchos / R. San Fernando	BS	sept-14	24°51.87'	099°20.07'	286	163	0	0
+	sym-	mexico	Barretal Rio Purificacion	Rio Purificacion	R. Soto La Marina	BT	sept-14	24°04.71'	099°07.39'	213	24	0	16
+	sym-	mexico	Nuevo Padilla Rio Purificacion	Rio Purificacion	R. Soto La Marina	NP	sept-15	24°02.52'	098°54.12'	120	18	0	93
-	allo-	mexico	Nicolas Bravo	Arroyo	R. Soto La Marina	NB	sept-15	23°58.07'	098°14.27'	39	0	0	1
-	allo-	mexico	Soto la Marina	Rio Soto La Marina	R. Soto La Marina	SL	sept-15	23°45.75'	098°12.61'		0	0	1
+	sym-	mexico	Casa de Campesino	Rio Guayalejo	R. Guayalejo - Rio Tamesi	CC	sept-16	23°14.11'	098°49.35'	191	17	0	16
+	sym-	mexico	Magiscatzin	ditch	R. Guayalejo - Rio Tamesi	MA	sept-26	22°48.81'	098°32.15'	84	10	0	6
+	sym-	mexico	El Limon	El Limon ditch	R. Mante - R. Guay. - R. Tam.	EL	sept-26	22°48.74'	099°00.75'	87	48	0	35
+	sym-	mexico	Downtown Mante	Mante canal	R. Mante - R. Guay. - R. Tam.	DM	sept-17	22°44.71'	098°58.78'	84	6	0	23
+	allo-	mexico	Antiguo Morelo	Arroyo	R. Guayalejo - R. Tamesi	AM	sept-18	22°33.10'	099°04.73'	187	0	0	11
+	sym-	mexico	Puente el Aquiche	Aquiche grande	R. Guayalejo - R. Tamesi	PA	sept-18	22°21.24'	099°02.53'	241	1	0	29
+	allo-	mexico	Mata de Chavez	Laguna	R. Panuco	MC	sept-19	22°06.81'	097°50.68'	27	0	0	205
+	allo-	mexico	Tamuin, Puente Rio Florido	Rio Florido	R. Tampuan - R. Panuco	TT	sept-18	21°59.82'	098°46.93'	25	0	0	25
-	allo-	mexico	Naranjos	Arroyo	R. Panuco / R. Tuxpan	NA	sept-19	21°21.83'	097°41.09'	89	0	0	13
+	sym-	mexico	Buena Vista	Rio Buena Vista	R. Tuxpan	BV	sept-25	21°05.93'	097°44.90'	93	25	0	70
-	sym-	mexico	Alamo Rio Tuxpan	Rio Tuxpan	R. Tuxpan	AL	sept-24	21°?	097°?		0	0	0
-	allo-	mexico	Tecomate	Arroyo	R. Tuxpan	TE	sept-24	20°46.76'	097°33.32'	41	0	0	24
-	allo-	mexico	Oxolotan, Tapijulapa	Rio Oxolotan	R. Oxolotan - R. Almandro	Ox	sept-23	17°27.61'	092°46.65'	60	0	0	1
+	allo-	mexico	PS0 Arroyo del Solpho	Arroyo del Solpho	R. Oxolotan - R. Almandro	Ps0	sept-21	17°26.54'	092°46.49'	85	0	0	337
+	allo-	mexico	PS13 Cueva del Azufre	Arroyo del Solpho	R. Oxolotan - R. Almandro	PS 13	sept-22	17°26.54'	092°46.49'	85	0	0	70
+	allo-	mexico	Ps0cc Arroyo del Solpho	Arroyo del Solpho	R. Oxolotan - R. Almandro	PS0cc	sept-21	17°26.54'	092°46.49'	85	0	0	66
-	allo-	mexico	PS10 Cueva del Azufre	Arroyo del Solpho	R. Oxolotan - R. Almandro	PS 10	sept-22	17°26.54'	092°46.49'	85	0	0	0

CURRICULUM VITAE

Name **Katja U. HEUBEL**
 Address home Ostlandstr. 12, D – 21391 Reppenstedt, Germany
 Institute Biozentrum Grindel, Martin-Luther-King-Platz 3, D-20146 Hamburg
 E-mail kheubel@uni-hamburg.de
 Date of birth 24 June 1972

ACADEMIC POSITIONS

1999 - 2003 Research associate at the Zoological Institute, Department of Animal Behaviour, University of Hamburg, Germany. DFG-funded research project on the evolution and function of mate choice and sexual preferences in the mating complex of *Poecilia formosa*.
 1995 - 1998 Research assistant at the Centre of Ecology, University of Kiel, Germany. Project on ecosystem research of the "Bornhöved Lake System".

ACADEMIC EDUCATION

February 2004 Thesis defense, University of Hamburg, Germany.
 Title of the dissertation thesis: "Population ecology and sexual preferences in the mating complex of the unisexual Amazon molly *Poecilia formosa* (GIRARD, 1859)".
 Supervised by Prof. Dr. J. Parzefall and PD Dr. I. Schlupp.
 September 2000 – October 2001 Research fellowship for PhD studies at the University of Texas in Austin, USA. Supervised by Prof. Dr. M. J. Ryan, Section of Integrative Biology. Funded by HSPIII of the DAAD (German Academic Exchange Service).
 July 1999 Diplom (Biology), Christian-Albrechts-University of Kiel, Germany.
 May 1998 – May 1999 Diploma thesis work in the Behavioural & Evolutionary Ecology Lab at the Zoological Institute of the University of Kiel. Diploma thesis title: "The mating system of the fruit fly *Myoleja lucida* (Diptera:Tephritidae)"
 Supervised by PD Dr. Thomas Hoffmeister and Prof. Dr. Thomas Bauer.
 April 1998 Final diploma exams in zoology, botany, soil science.
 November 1994 Vordiplom. Preliminary examinations in zoology, botany, mathematics, and chemistry.
 October 1992 – July 1999 Studies of Biology (Diploma) at the Christian-Albrechts-University of Kiel, Germany.

Hamburg, March 16, 2004

Erklärung

Hiermit versichere ich eidesstattlich, dass ich diese Abhandlung selbst verfasst habe und sie – abgesehen von der Beratung durch meine akademischen Lehrer – nach Inhalt und Form meine eigene Arbeit ist und dass ich keine anderen als die angegebenen Hilfsmittel und Quellen verwendet habe. Die Arbeit hat bisher weder ganz noch zum Teil an anderer Stelle im Rahmen eines Prüfungsverfahrens vorgelegen.

Teile dieser Arbeit wurden als Manuskripte bei Zeitschriften eingereicht. Kapitel 4 wurde eingereicht bei Behavioral Ecology mit Ingo Schlupp als Koautor. Kapitel 5 wurde bei Animal Behaviour eingereicht mit Katja Hornhardt, Tanja Ollmann, Jakob Parzefall, Michael J. Ryan und Ingo Schlupp als Koautoren.

Dr. David L. Thomson, Netherlands Institute of Ecology, Heteren, Niederlande hat die sprachliche Korrektheit der von mir in Englisch verfassten Abhandlung begutachtet und bestätigt.