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On the natural history of an introduced population of guppies (*Poecilia reticulata* Peters, 1859) in Germany

Jonas Jourdan[1,2]*, Friedrich Wilhelm Miesen[3], Claudia Zimmer[2], Kristina Gasch[4], Fabian Herder[3], Elke Schleucher[4], Martin Plath[1,2,5] and David Bierbach[6]

[1]*Biodiversity and Climate Research Centre (BiK^F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany*
[2]*Goethe University of Frankfurt, Department of Ecology and Evolution, University of Frankfurt, Max-von-Laue-Straße 13, D-60438 Frankfurt am Main, Germany*
[3]*Zoologisches Forschungsmuseum Alexander Koenig, Sektion Ichthyologie, Adenauerallee 160, D-53113 Bonn, Germany*
[4]*J.W. Goethe-University of Frankfurt, Department of Integrative Parasitology and Animal Physiology, Max-von-Laue-Straße 13, D-60438 Frankfurt am Main, Germany*
[5]*College of Animal Science and Technology, Northwest A&F University, Yangling, Shaanxi 712100, P.R. China*
[6]*Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Department of Biology and Ecology of Fishes, Müggelseedamm 310, D-12587 Berlin, Germany*

**Corresponding author*
E-mail: JonasJourdan@googlemail.com

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Abstract

Artificially heated water bodies represent unusual habitats in temperate regions and form a refuge for exceptional fish communities. The Gillbach, a tributary of the river Erft in Germany, receives thermally polluted cooling water from a power plant. Here, we present data on the composition of the fish community in the Gillbach and found a high abundance of invasive species from all over the world, mostly introduced by releases from home aquaria. We found a species composition that is dominated by invasive species containing the same species as 15 years ago. We focused on guppies (*Poecilia reticulata*) and determined population size using the mark-recapture method. Furthermore, we investigated the lower thermal tolerance limit (C_{Tmin}) to determine if Gillbach guppies have already adapted to colder conditions compared to ornamental and Venezuelan wild type fish. We caught guppies of all sizes, and densities of 3.6 adult guppies per square meter were comparable to densities found in their natural distribution area, pointing toward a self-sustaining population in the Gillbach. The C_{Tmin} varied between populations and was significantly lower in ornamental and Gillbach guppies compared to guppies from Venezuela. Despite differences in C_{Tmin} and their well-known potential to adapt to new environments, guppies originally stem from the tropics, and a further spread will likely be restricted by low winter temperatures. Thus, *P. reticulata* in the Gillbach might not represent a threat for local fauna in Central Europe, but provide a unique semi-natural experiment for various questions related to local adaptation of invasive species, as well as ecological interactions with indigenous species.

Key words: *Amatitlania nigrofasciata*, Europe, exotic species, invasive, Rhine drainage, thermal pollution, thermal tolerances

Introduction

Alien species are among the major drivers of species extinctions and, thus, loss of biodiversity (Millennium Ecosystem Assessment 2005), especially in freshwater ecosystems (Mack et al. 2000). In the European Union alone, 12,122 non-native species have been reported so far (DAISIE European Invasive Alien Species Gateway 2013). However, not all of these are predicted to reproduce and expand their current distribution ranges ('invasive alien species', IAS; Williamson and Fitter 1996; Sakai et al. 2001). Nevertheless, even species that are not currently assumed to successfully reproduce in their new environments, or have a very localized occurrence, may occasionally overcome reproductive constraints – and thus reach IAS status – due to global warming, niche shifts, or local adaptation to altered environmental conditions (Whitney and Gabler 2008).

While most species introductions are accidental (Mack et al. 2000), several active introductions have also been documented. An example is the introduction of Nile perch (*Lates niloticus* Linnaeus, 1758) into Lake Victoria, with its disastrous consequences for the endemic fish fauna (Ogutu-Ohwayo 1990; Seehausen et al. 1997; Goldschmidt 1998). Live-bearing fishes of the family Poeciliidae have been widely introduced to tropical and subtropical countries for malaria prophylaxis, i.e., to help control vector (mosquito) populations (Stockwell and Henkanaththegedara 2011). In addition, some poeciliids like guppies (*Poecilia* (*Acanthophacelus*) *reticulata* Peters, 1859), swordtails and platyfish (*Xiphophorus* spp.), and mollies (*Poecilia* (*Mollienesia*) spp.) are among the most popular ornamental fishes, and many introductions may have been the result of occasional releases from home aquaria (Padilla and Williams 2004; Gozlan et al. 2010a; Stockwell and Henkanaththegedara 2011; Strecker et al. 2011). The ability to store sperm from multiple mates for several months secures several consecutive broods and allows a single gravid poeciliid female to found an entire new population (Zane et al. 1999; Evans and Magurran 2000).

Guppies are native to northern South America between Venezuela and northern Brazil, and to several nearby islands like Trinidad and Tobago (Rosen and Bailey 1963; Magurran 2005). Studies on natural populations of Trinidadian guppies reported on geographical variation in morphological, behavioral and life history characteristics, primarily explained by variation in predator regimes (Magurran et al. 1995; Magurran 2005). Within few generations after the exposure to an experimentally altered predator regime, guppy populations responded with an earlier onset of sexual maturity coupled with smaller offspring size at birth (high predation), or delayed onset of sexual maturity and increased offspring size at birth (low predation; Reznick et al. 2008). This ability to rapidly respond to altered selective regimes highlights the invasive potential of guppies (Magurran 2005; Deacon et al. 2011). Guppies have broad environmental tolerances and can withstand – at least for short periods of time – marine salinity (Chervinski 1984), as well as temperatures dropping to 12°C (Fujio et al. 1990) or rising to over 40°C (Chung 2001). This renders a wide range of habitats suitable for guppies and non-native guppy populations are currently reported from at least 69 countries in North and South America, Europe, Asia, Australasia, and Africa (Deacon et al. 2011). However, in contrast to Eastern mosquitofish (*Gambusia holbrooki* Girard, 1859) that were actively released in southern Europe during the 20th century for mosquito prophylaxis, and are nowadays present in virtually any southern European freshwater system (Vidal et al. 2010; pers. obs. for Italian, Spanish and southern French streams), guppies are not widely established in Europe. Exceptions are some isolated populations in a few southern European rivers probably established in recent years (Elvira and Almodovar 2001). Due to their native distribution in the tropics, low winter temperatures prevent self-sustaining populations in large parts of Europe. Nonetheless, there are occasional reports of small populations in Canada, Russia and parts of northern Europe, but these inhabit either geothermal springs or water bodies with artificially increased water temperatures due to thermal pollution arising through influx of cooling water from power plants or surface mining (Arnold 1990; Deacon et al. 2011). Such permanently warm refuges, however, might serve as source populations from where individuals might start spreading into hitherto uninhabited areas following adaptation to cooler conditions (Klotz et al. 2013) or elevated temperatures as a result of climate change (Rahel and Olden 2008; Walther et al. 2009; Wiesner et al. 2010; Bellard et al. 2013).

The present study reports on an artificially heated ecosystem, the upper Gillbach, that is verifiably inhabited by a guppy population since the mid-1970s (Kempkes 2010) and receives cooling water from a power plant. Although other non-native fish are regularly found in the Gillbach (Höfer and Staas 1998), we focused on the guppy due their status as a model species in evolutionary ecology (Magurran 2005; Evans et al. 2011), their well-known success as an invasive species in other parts of the world (Deacon et al. 2011) and the present lack of information regarding their invasiveness for central Europe (Nehring et al. 2010). Our major aims were (1) to provide an overview of the fish community found in the Gillbach 15 years after the last survey (Höfer and Staas 1998), (2) to estimate the population size of guppies using mark-recapture analysis, and (3) to evaluate whether guppies from the Gillbach have already been adapted to colder conditions and tolerate a lower critical minimum temperature (C_{Tmin}) compared to guppies from Venezuela and domesticated ornamental guppies. Our study – even though largely descriptive – is intended as a primer to future projects assessing the status (and invasion potential) of guppies in Central Europe.

Materials and methods

The Gillbach is a stream located west of Cologne in North Rhine-Westphalia (Germany), and meanders for approximately 28 km before it drains into the river Erft, a Rhine tributary (Figure 1). It receives thermally polluted water from the coal-fired power plant “Niederaußem” (50°59'46.82", 6°39'50.56", RWE Power Inc.). The Gillbach is approximately three meters wide and 30–80 cm deep. We measured abiotic water parameters (pH, conductivity, dissolved oxygen and temperature) with a Multi-Parameter Meter (HQ40d Portable Meter, HACH, Loveland, USA) approximately 100 m downstream of the influx pipe at least once a month between August 2011 and April 2012.

To characterize the fish community in the upper Gillbach, we performed electrofishing during 4 days in June 2013 along the first 400 meters downstream of the influx pipe (section I; Figure 1), the next 400 m downstream (section II), and for several hundred meters further downstream using a portable electro fishing device (Hans Grassl IG200-1).

First reports of introduced guppies date back to the 1970s, when first individuals were initially released to the Gillbach by hobbyist fish breeders (Kempkes 2010). Although we assume this feral population has been derived from a mixture of various domesticated ornamental strains, guppies nowadays caught in the Gillbach show an amazing male color polymorphism typically found in natural guppy populations (Figure 2; Haskins and Haskins 1951; Endler 1983; Houde 1997; Brooks 2002). Electrofishing is not an ideal method for catching guppies, mainly due to their small size. To estimate the population size of guppies, we, thus, used a standard mark-recapture approach (Reznick et al. 2001). Guppies were collected in June using a seine (2 mm mesh width) and dip nets along sections I and II. Only adult fish were considered in this approach. Females were included if their body size exceeded 10 mm standard length (SL), they appear to be gravid and they had a clearly visible dark gravid spot above the anal fin, while maturity in males was evaluated by inspecting their gonopodium (the transformed anal fin that develops into a copulatory organ at maturation) and checking for color ornaments on the body. Fish were transferred into well-aerated coolers and subsequently anesthetized with clove oil. Anesthetized fish were marked individually with color polymer tags and transferred to a tank with aerated water for recovery for at least half an hour. No mortality was detected. Recapture took place one week later at the same sites and with comparable sampling effort. At both capture events, body size of adult fish was measured to the nearest millimetre using plastic rulers.

We initially captured 93 adult males and 145 adult females, all of which were marked and released on the same day. During the second capture event, a total of 131 males and 235 females were captured, of which 7 males and 13 females were recaptured individuals. For the estimation of population size (with 95% CI), we used the R package Rcapture (Baillargeon and Rivest 2007; R_Core_Team 2013) assuming a closed population (Mt model). For the Gillbach, this assumption seems reasonable, at least over short periods of time, as the sampling area starts at the influx pipe of the power plant and is confined downstream by a railroad tunnel (Figure 1).

For the measurement of lower thermal tolerance limits (C_{Tmin}), guppies were collected from the Gillbach, and carefully transported to the laboratory of the University of Frankfurt/Main. Fish were acclimated to the laboratory conditions for three months before the measurements started. We further included a color polymorphic stock of guppies derived from various ornamental strains and a stock of guppies descended from animals imported from Venezuela by *Aquarium Dietzenbach*. All fish were maintained in mixed-sex stock tanks (80 to 180-l) at a constant temperature of 28°C under a 12:12 h illumination cycle. Tanks were equipped with natural gravel, internal filters, as well as stones and artificial plants for shelter. Fish were fed twice daily with commercial flake food. For the investigation of C_{Tmin}, we concentrated on females and followed the protocol provided by Bierbach et al. (2010). Test fish were acclimated to 25°C prior to the experiments in 60-l tanks for at least two weeks. The test apparatus consisted of a 10-l test tank connected to a circulating pump with an internal cooling aggregate. An air-pump ensured saturated oxygen concentrations throughout the tests. We gently introduced a test fish and started to decrease water temperature at a constant rate of 0.780±0.007°C min^{-1} once the fish was swimming calmly. Down-regulation of the water temperature was aided by the addition of ice cubes every two minutes. We noted at which temperature the test fish lost motion control as a proxy for the test subjects' absolute physiological tolerance. Directly after the trials, fish were transferred into an aerated 10-l tank in which temperatures were gradually increased again to 25°C. All test fish

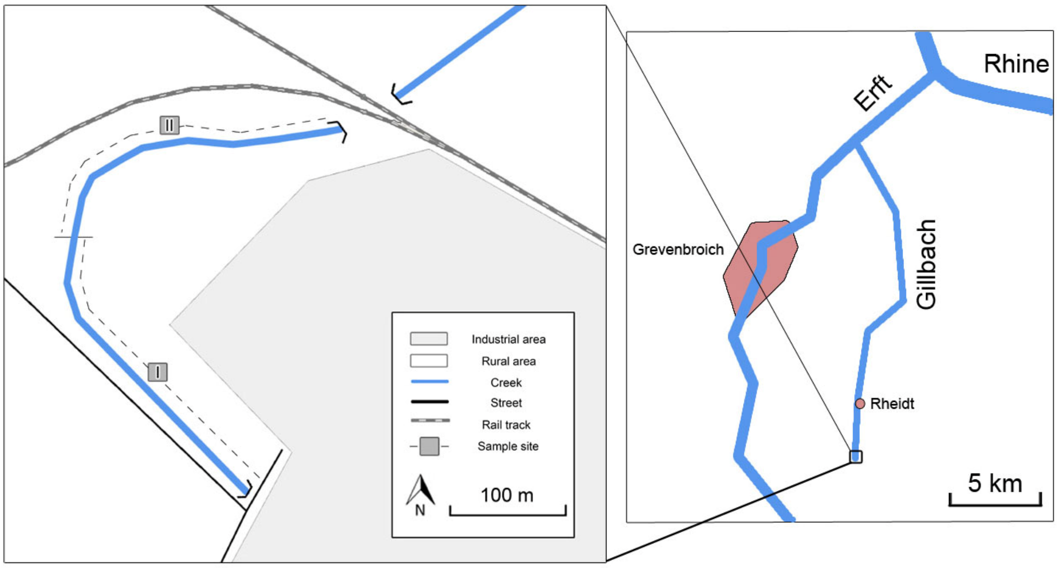

Figure 1. Overview of the study area. Schematic view of the watercourses (blue) and electrofishing sites (I and II) in the Gillbach (North Rhine-Westphalia, Germany).

Figure 2. Variation in body coloration in a sample of males caught from the Gillbach. Photographs by the authors.

regained motion control within few minutes, and no mortality was associated with this experiment. After completion of a trial, test fish were weighed to the nearest 0.1 g using a Sartorius PT 600 scale (accuracy ± 0.1%). In order to compare C_{Tmin} among populations, we used a linear mixed model with population as a fixed factor and log-transformed body mass as a covariate. The interaction term 'population by body mass' was not significant ($F_{2,22}$=2.77, P=0.085), but since the Akaike's Information Criterion (AIC) increased by 21.6% in the simplified model, we used the more complex model retaining the interaction term. To identify significant differences between populations, we used LSD tests for pairwise *post hoc* comparisons of the estimated marginal means derived from our model where body mass was adjusted to -0.29 log(g). The analysis was conducted using SPSS 22 (SPSS Inc. 2013).

Results

Fish community

Electrofishing revealed 11 different fish species, seven of which were non-native (Table 1). The most abundant native species were chub (*Squalius cephalus* Linnaeus, 1758) and barbel (*Barbus barbus* Linnaeus, 1758). Guppies were the most abundant non-native species, but – given the high capture success during the mark recapture approach (see below) – were clearly under-represented during electrofishing. Beside guppies, six other non-native species were recorded (Table 1), of which the Central American convict cichlid (*Amatitlania nigrofasciata* Günther, 1867) was the most abundant.

Sex ratio, population size and body size distribution of guppies

The sex ratio, combined from both capturing events, was female-biased (#males/#females = 0.58). We estimated a total population size of 4,305 (95% CI: 2,963–6,726) adult guppies, translating into an approximated average density of 3.6 adults per square meter. Males showed a very narrow body size range with a mean SL of 16.2 mm (95% CI: 16.0–16.4 mm) while female body size was much more variable, with a mean SL of 19.7 mm (95% CI: 19.2–20.1 mm; Figure 3).

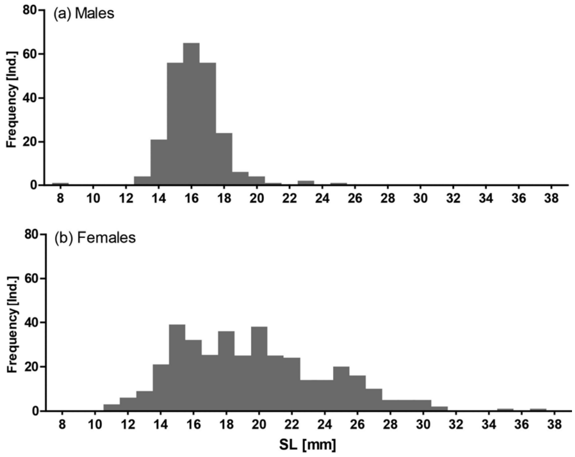

Figure 3. Body size distribution of (a) male and (b) female guppies collected in the Gillbach.

Abiotic habitat characteristics

As a consequence of a constant warm water discharge from the power plant, abiotic water parameters (temperature, pH, specific conductivity and dissolved oxygen) remained stable during the winter months (Table 2) and water temperatures

Table 1. Fish communities in the Gillbach inferred by electrofishing in June 2013.

Species	Origin	I	II	Further down-stream	Total
Cichlidae					
Amatitlania nigrofasciata (Günther, 1867)	Central America	11	6	3	20
Oreochromis sp.	Africa	6	0	1	7
Loricariidae					
Ancistrus sp.	South America	1	2	10	13
Cyprinidae					
Barbus barbus (Linnaeus, 1758)	native	2	1	37	40
Carassius auratus (Linnaeus, 1758)	Ornamental fish	0	5	0	5
Chondrostoma nasus (Linnaeus, 1758)	native	0	0	1	1
Cyprinus carpio (Linnaeus, 1758)	Asia	0	0	2	2
Gobio gobio (Linnaeus, 1758)	native	0	0	22	22
Pseudorasbora parva (Temminck & Schlegel, 1846)	Asia	1	0	0	1
Squalius cephalus (Linnaeus, 1758)	native	6	12	70	88
Poeciliidae					
Poecilia reticulata (Peters, 1859)	South America	10	20	11	32
Total		37	46	148	224

Table 2. Fluctuation in temperature and water chemistry of the Gillbach in 2011 and 2012.

Date	Daytime	t [°C]	pH	Specific conductivity [µS/cm]	DO [mg/L]	DO saturation [%]
Sept. 2011	11:30	23.2	8.10	1815	8.96	109.06
Oct. 2011	11:30	21.3	8.06	1877	8.46	99.16
Nov. 2011	12:00	19.4	8.34	1741	9.21	104.06
Dec. 2012	11:30	20.8	8.45	1778	9.14	98.13
Jan. 2012	16:00	19.0	8.28	1654	9.46	106.04
Feb. 2012	16:00	22.0	8.43	1915	8.73	103.72
Mar. 2012	14:30	23.1	8.46	1906	8.67	105.14
Apr. 2012	16:00	23.0	8.36	2026	8.30	100.50

never dropped below 19°C at the core area around the water influx. However, additional measurements approximately 2 km downstream in Rheidt (+51°00'50.88", +6°41'03.3") revealed a decline to 13.7°C in February 2012.

Thermal tolerances

Our linear mixed model detected a significant difference in C_{Tmin} between populations ($F_{2,22}$=5.484, P=0.012). Venezuelan guppies had a C_{Tmin} of 14.6 ± 0.6°C (mean ± SE), while it was significantly lower in fish from the Gillbach (12.4 ± 0.4°C; *Post-hoc* LSD test: *P*=0.007) and the ornamental population (12.5 ± 0.2°C; *Post-hoc* LSD test: *P*=0.004; Figure 4). The Gillbach and ornamental populations did not differ significantly in their thermal tolerance (*Post-hoc* LSD test: *P*=0.842).

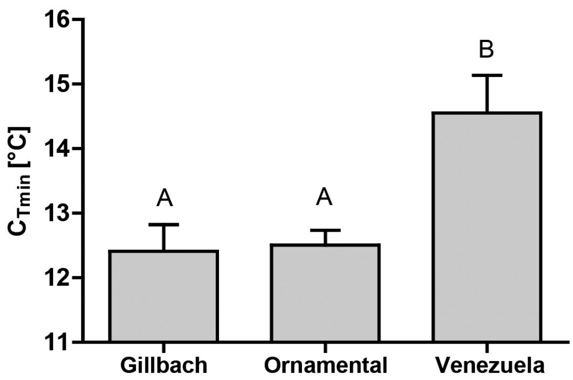

Figure 4. Lower critical minimum temperature (C_{Tmin}) of guppies from the Gillbach, an ornamental strain and descendants of wild-caught fish from Venezuela. Shown are estimated marginal means (EMM) from a linear model with (log-transformed) body mass as covariate. Different letters indicate significant differences in *post-hoc* LSD tests.

Discussion

Due to a constant warm water influx from the coal power plant 'Niederaußem', the Gillbach serves as a refuge for many tropical fish species and seven out of eleven species found in our survey are non-natives. Although most introduced species fail to establish self-sustaining populations (Williamson and Fitter 1996), high local densities and the presence of juveniles are indicators of a well-established population of guppies (*P. reticulata*) in the Gillbach. This assumption is further underpinned by consistent reports on guppies that date back to the mid-1970s (Kempkes 2010) and their wild-type-like morphology. Likewise, convict cichlids (*A. nigrofasciata*) were reported already 15 years ago (Höfer and Staas 1998) and different age-classes have been found in the current study. Beside guppies and convict cichlids, the survey from 1998 reported on other tropical species like Lake Malawi cichlids (*Pseudotropheus* sp.), as well as two additional undetermined representatives of the family Poeciliidae inhabiting the Gillbach. Native fishes recorded in 1998 were chub (*Squalius cephalus*), gudgeon (*Gobio gobio* Linnaeus, 1758), barb (*Barbus barbus*) and European eel (*Anguilla anguilla* Linnaeus, 1758). In our present study, we did not detect European eel or Lake Malawi cichlids, and the guppy was the only representative of poeciliid fishes. The undetermined poeciliids found in 1998 were presumably released by private pet fish keepers but, unlike guppies, failed to establish. Nevertheless, in addition to the previous report, we found a single specimen of common nase (*Chondrostoma nasus* Linnaeus, 1758), and two specimens of common carp (*Cyprinus carpio* Linnaeus, 1758). Like in 1998, we also caught one specimen of the Asian cyprinid *Pseudorasbora parva* Temminck & Schlegel, 1846, which has been accidently introduced in the 1960s with translocations of cyprinids for aquaculture, and is nowadays widely established in Europe (Kottelat and Freyhof 2007; Gozlan et al. 2010b). Interestingly, our survey found several adult individuals, breeding females as well as juveniles, of the mouthbrooding African cichlid *Oreochromis* sp., well known as 'tilapia' in aquaculture. This species was deliberately introduced throughout the world to facilitate aquaculture development, and is nowadays invasive in many tropical countries, but has failed to establish in Europe (Canonico et al. 2005; Garcia-Berthou et al. 2005). In the Gillbach, the occurrence of breeding adults and juveniles suggests a stable population; founder individuals most likely stemmed from a recently closed aquaculture facility that used the power plant's cooling water. Beside the variety of invasive fish species, also the invertebrate fauna of the Gillbach is affected by exotic species. Recently, Klotz et al. (2013) reported on two invasive species of freshwater shrimps (*Neocaridina davidi* Bouvier, 1904 and *Macrobrachium dayanum* Henderson, 1893) from Asia in this stream.

Our density estimates of 3.6 adult guppies per m^2 are similar to those reported on Trinidadian populations. Reznick and Endler (1982) found slightly lower densities (approximately 2 guppies per m^2) in high predation sites ("Crenicichla-sites") and higher densities (app. 9 guppies per m^2) in low predation sites ("Rivulus-sites"), while a subsequent study reported densities of approximately 4 individuals per m^2 at both high and low predation sites (Reznick et al. 2001). Similar to the Gillbach population, adult sex ratios in Trinidadian guppy populations are often female-biased, since males likely face higher predation rates (Magurran 2005; Arendt et al. 2014).

Our data on adult body size distributions reflect the findings from previous studies (Endler 1995). Like in many other poeciliids (Hughes 1985; Plath et al. 2003), male Trinidadian guppies are smaller (SL: 13–19 mm) than females (18–24 mm; Magurran 2005) and wild-type guppies are usually smaller than fish from domesticated strains (males: 21.5–27.5 mm, females: 23.8–35.5 mm; Zimmer et al. 2014). Predation has been identified as a major selective force for body size evolution, whereby high predation rates select for smaller body size in Trinidadian guppies. For example, Reznick and Endler (1982) reported on body lengths of 14.88 ± 0.10 mm (SL ± SE) for males caught at 'high predation' sites with abundant cichlid predators and 16.42 ± 0.14 mm for 'low predation' sites without predatory cichlids present (Reznick and Endler 1982).

Exposure to predation has a strong effect on virtually all aspects of a population's biology, as selection from predation is a powerful driver of behavioral, morphological and life-history trait evolution (Endler 1995). Predation also influences male ornamentation (Endler 1980), and guppy males from 'high predation' sites are often less conspicuous and bright (Rodd and Reznick 1997; Magurran 2005). Even though body coloration was not quantified in the present study, we found color polymorphic male phenotypes qualitatively resembling those found in natural guppy populations. Investigations of Gillbach guppies in the 1970s reported males carrying traits typical for ornamental fish, like elongated fins and single-color morphs (Kempkes 2010), and further releases of ornamental breeds over the last years cannot be ruled out. However, these forms seem to have disappeared, leaving polymorphic traits similar to native guppies from Trinidad (Endler 1983) or feral guppies from Japan (Karino and Haijima 2001) with a high variation of dorsal and caudal fin lengths and color spot patterns. As a logical extension of this interpretation, we argue that the Gillbach population likely faces predation pressures comparable to natural Trinidadian and South American 'high predation' populations (Reznick and Endler 1982; Figure 2) – most likely by piscivorous species like the native *S. cephalus* and *B. barbus*, as well as the invasive *A. nigrofasciata*. Furthermore, bird predation (e.g. by *Alcedo atthis* Linnaeus, 1758 or *Ardea cinerea* Linnaeus, 1758) is expected to occur. An alternative explanation is that the ornamental guppy strains are not hardy enough (i.e. insufficient thermal tolerance, handicapped due to elongated fins), so that only wild-type strains survived.

With a minimum water temperature of 19.2°C in January 2012, and a total annual temperature range of only 4.2°C, the Gillbach provides suitable temperature conditions for guppies along its first few kilometers. The constant outflow of cooling water provides even more stable conditions than in some natural Trinidadian habitats, where water temperatures can be highly variable (up to 7°C per day, Reeve et al. 2014). Nevertheless, water temperatures dropped to 13.7°C within the first 2 km in February 2012 and even though Gillbach guppies (and ornamental breeds) tolerated a lower critical minimum temperature (C_{Tmin}) than fish from a wild-type Venezuelan stock, it is unlikely that guppies will survive outside the core area close to the warm water influx during winter.

While increasing air temperatures are expected for the Rhine basin as an effect of climate change (up to 2.3°C in the lowland area during winter, projected to the year 2050; Middelkoop et al. 2001), water temperatures sometimes decrease to less than +1°C in the river Rhine (e.g. February 2012; measuring station Mainz-Wiesbaden, HLUG 2013). Even if climate change alters pathways of invasive species and modify ecological impacts (Rahel and Olden 2008; Walther et al. 2009), the overwinter survival of guppies should not be possible in German river areas without warm water influx. Poeciliids exhibit a great potential to adapt to new environments (Meffe and Snelson 1989; Stockwell and Henkanaththegedara 2011), and the C_{Tmin} of the Gillbach population recorded here is congruent with another study reporting on some domesticated guppy strains that tolerate temperatures of 12°C for at least 24 h (Fujio et al. 1990). However, guppies stem from the tropics and a further spread in Central Europe will probably be restricted by low winter temperatures. Similarly, the survival of the other non-native tropical fishes found in the Gillbach can be assumed to fully rely on the power plant's cooling water discharge.

In summary, the Gillbach is characterized by an unusual species composition, dominated by invasive species that established stable populations in the artificially heated creek. The guppy population consists of more than 4000 individuals in the core area around the water influx. The source of the guppies is suspected to be ornamental animals; nevertheless, we could not find evidence for adaptation to lower temperatures, as no difference in C_{Tmin} between ornamental- and Gillbach guppies was detected. The establishment of introduced species is influenced by many factors. Understanding the complex interactions between the invading species and the recipient environment is a fundamental challenge to ecologists and conservation managers (Mooney and Cleland 2001; Hayes and Barry 2008). Beside the limited invasive potential, the Gillbach population of introduced guppies with its assumed 'spread and diminish' characteristic may provide a fruitful semi-natural experiment for questions related to local adaptation of invasive populations and ecological interactions with indigenous ones. Even though the risk of a further spread of guppies in Central Europe may seem unlikely, we recommend the continuous monitoring of this system with a special focus on changes in the invasive status of the species inhabiting the Gillbach, since the thermal gradient is connected directly to native ecosystems and may serve as a source habitat for species invasions.

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