Natural History Note

Parallelism Isn't Perfect: Could Disease and Flooding Drive a Life-History Anomaly in Trinidadian Guppies?

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abstract: Nonparallel evolution, where independent populations occupy similar environments but show phenotypic differences, can uncover previously ignored selective factors. We investigated a non-parallelism in the life-history strategy of a Trinidadian guppy population, a system famous for parallel adaptation to differences in predation risk. We tested the hypothesis that high mortality drives an observed fast life-history pattern (i.e., earlier maturation and more frequent reproductive events) that is atypical for a low-predation environment. Using mark-recapture techniques, we compared neighboring low-predation populations, finding significantly higher mortality rates in the population with atypical life-history traits. Mortality was elevated during the wet season, when flooding was common. Moreover, individuals from the anomalous population were more likely to transition from healthy to infected disease states. Our results stand out against previous patterns observed in this system, indicating that higher mortality caused by disease and flooding may have selected for a faster life history. Thus, we highlight that even in systems famous for parallel adaptation, variation in selective pressures can result in nonparallel phenotypic evolution.

Keywords: parallel evolution, multistate mark-recapture, life-history evolution, Poecilia reticulata.

Introduction

Parallel evolution of similar phenotypes in similar environments has long provided evidence for the deterministic role of natural selection (Endler 1986; Jones et al. 1992; Reznick et al. 1996b; Huey et al. 2000; Schluter et al. 2004; Losos 2009). Typically, parallel evolution is framed in the context of adaptation to analogous environments where environments are classified into discrete types (e.g., benthic vs. limnetic, high predation vs. low predation, ser-

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pentine vs. nonserpentine soil), often ignoring variation in fine-scale selective factors that differ among replicate environmental types (Kaeuffer et al. 2011). In reality, "the environment" is a complex combination of all extrinsic selective forces encountered by a population. However, when parallel evolution is invoked, it is tempting to overlook subtle differences in the environment in place of the primary selective agent (Losos 2011). Thus, examining the mechanisms underlying differing phenotypes among populations in similar environments provides a window into other ecological features that contribute to the local selective regime (Maccoll 2011).

Populations of Trinidadian guppies (Poecilia reticulata) are a textbook example of parallel evolution in response to replicated changes in the environment (Reznick et al. 1996b; Magurran 2005; Gee et al. 2009). The paradigm put forth by decades of extensive research in this system capitalizes on the differences in predation regime experienced by guppies throughout Trinidad. Whereas "high-predation" guppies are found in large, low-elevation streams where they coexist with diverse communities of piscivores, "low-predation" guppies inhabit high-elevation headwater streams and usually coexist only with the gape-limited killifish (Rivulus hartii; Mattingly and Butler 1994). Accordingly, guppy populations in low- and high-predation environments experience differences in extrinsic mortality rates as consistently shown in all previous mark-recapture studies that contrast these environments (Reznick et al. 1996a; Bryant and Reznick 2004; Gordon et al. 2009; Weese et al. 2010). Divergent selection pressure associated with predation has resulted in genetically based adaptive differences in guppy morphology (Alexander et al. 2006), color (Endler 1983), behavior (Seghers 1974; Houde and Endler 1990), and life history (Reznick 1982; Reznick and Endler 1982). In fact, parallel evolution associated with predation regime has been described in 13

independent drainages throughout Trinidad (Reznick et al. 1996*b*). In all, this body of literature provides some of the most robust evidence for parallel evolution in the wild.

Life-history theory predicts that high mortality environments favor a fast life-history strategy in which maturation occurs at an earlier age and reproductive effort is increased and sped up through shortened gestation periods (Gadgil and Bossert 1970; Charlesworth 1994; Abrams and Rowe 1996). Field and common garden studies show that guppies in high-predation environments exhibit a fast life history with early maturation and a shortened gestation period (interbrood interval) compared to upstream low-predation populations in the same drainage (Reznick 1982, 1997; Reznick and Endler 1982; Reznick and Bryga 1996). However, a recent common garden study reports an unusual exception to this pattern: a low-predation environment (Taylor River) in which female guppies exhibit life-history traits intermediate or more similar to their adjacent downstream high-predation counterpart (Guanapo HP) compared to neighboring low-predation populations (Caigual River and Guanapo LP; Torres Dowdall et al. 2012).

Specifically, compared to fish from the nearby Caigual River, female guppies from the Taylor River exhibited earlier age at maturation and a shorter interbrood interval (fig. 1; Torres Dowdall et al. 2012). Traits more closely associated with food availability (e.g., reproductive allocation) did not deviate from the expected pattern. However, low-predation guppies generally show a very stereotypical slow life history in all traits compared to downstream high-predation pop-

ulations (Reznick et al. 1996*b*). Thus, decoupling between traits such as age at maturity and reproductive allocation suggests these traits could be responding to selection from different ecological factors, such as food availability, predation, or other causes of mortality. The population from the Taylor River appears to be an example of nonparallelism, as the population exhibits a life history that is for some traits more similar to a high-predation environment, despite a lack of predators.

Theory emphasizes that what drives life-history evolution is a change in age-specific mortality rates, regardless of the ecological process underlying it (Stearns 1992). For example, divergence in life-history traits are shown among populations that experience different rates of predation (Reznick and Endler 1982), disturbance (Lytle 2002), disease (Fredensborg and Poulin 2006), or anthropogenic sources of mortality such as pollution (Gross 1991), insecticide (Carriere et al. 1994), or fishing (Olsen et al. 2004). We consider the life-history anomaly observed in the Taylor River an opportunity to test for high mortality rates, as theory would support. We also explore ecological factors, aside from the dominant role of predation, which may play a role in causing mortality and a fast life history. Specifically, we investigate mortality due to disease and permanent emigration due to flooding because these are the most apparent sources of extrinsic mortality in low-predation environments (S. W. Fitzpatrick, personal observation).

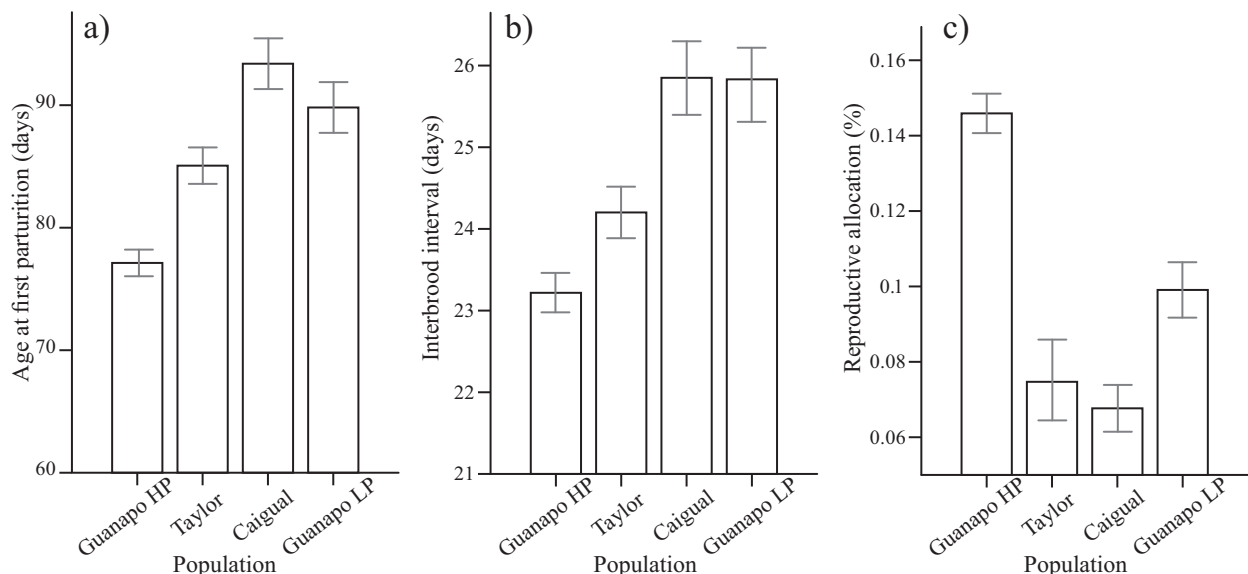We test our main hypothesis that mortality differs be-

Figure 1: Mean (±SE) age at first parturition (*a*), interbrood interval (*b*), and reproductive allocation (*c*) of second-generation laboratory-reared females for four localities within the Guanapo drainage. Guanapo HP is the only high-predation locality, whereas Taylor, Caigual, and Guanapo LP are all low-predation environments. This figure is adapted from data from Torres-Dowdall et al. (2012).

tween two neighboring low-predation streams using a multistate capture-mark-recapture (MSMR) modeling approach (Williams et al. 2002). To explore the roles of disease and flooding, we estimate temporal and stream differences in survival, capture probabilities, and transition rates between discrete health states (e.g., infected or uninfected with fin-rot, a proxy for overall health status of individual fish). If flooding causes high apparent mortality in the Taylor River compared to the Caigual River, we would expect lower survival in the Taylor River during months associated with higher flooding probability (i.e., wet season: July–December).

Methods

Focal Sites

Our focal sites are two tropical headwater streams (Taylor River and Caigual River) from the Guanapo watershed in the Northern Range Mountains of Trinidad. These sites coincide with the sample sites for the life-history assays in Torres-Dowdall et al. (2012). Stream reaches sampled in the Taylor River (240 m long) and the Caigual River (80 m long) were chosen based on the upstream limit of guppies and were bound on either end by waterfalls, preventing upstream movement. Both streams are natural low-predation guppy habitats compared to low-elevation sites; however, the Caigual River hosts a higher diversity of fish that could potentially prey on guppies (Gilliam et al. 1993). Thus, while both localities rank as "low predation" by our usual criteria because they lack cichlids and characins, there remain differences between them, with the consequence that the Caigual River may have higher overall levels of predation than the Taylor River.

Capture-Mark-Recapture

From June 2009 through June 2010 we uniquely marked and recaptured guppies greater than 14 mm standard length on a monthly basis. Guppies were caught using a combination of butterfly nets, hand nets, and minnow traps. Streams were divided into a series of numbered pools and riffles, allowing fish to be returned to their precise site of capture. Fish were transported to the lab in Nalgene bottles filled with stream water and set up in aerated tanks separated by location and sex. Before processing, fish were anesthetized with a dilute solution of MS-222 to allow individuals to be marked and photographed. Under a dissecting microscope, guppies were marked with elastomer developed for mark-recapture of small fish (Northwest Marine Technologies). Elastomer is injected subcutaneously using twelve colors, eight discrete marking sites, and two marks per fish to provide unique individual marks.

All fish were returned to their capture site 1–2 days after initial capture. Previous capture-mark-recapture studies on guppies demonstrated high recapture probabilities, high mark retention, and low marking mortality using these methods (Reznick et al. 1996a).

Each individual guppy captured was visually scored for the presence or absence of "fin-rot." Fin-rot is easily identifiable as an atrophied caudal fin (see photo in fig. 3). This type of condition is easy to score and often results from fish being in poor health due to other sources of disease, malnutrition, or poor water quality (Latremouille 2003). We consider fin-rot to represent a proxy for overall health status of individual fish in the population but not necessarily a direct cause of mortality (see "Discussion").

Multistate Mark-Recapture Modeling

We used a multistate mark-recapture modeling framework (MSMR; Brownie et al. 1993; Lebreton and Pradel 2002) to estimate apparent survival (Φ), capture probabilities (p), and transition probabilities (Ψ) between healthy and infected states. Apparent survival Φ is the probability that a marked fish alive at sampling occasion t survives and does not permanently emigrate between sampling occasions t and $t + 1$. Encounter histories for each individual were grouped by sex and stream, and on capture, each individual was assigned to one of two states: fin-rot absent or fin-rot present. Individuals have been known to recover from fin-rot, thus an individual may transition between states in either direction between sampling occasions (months), given the individual survives.

Our most general model, Φ(fin-rot × sex × stream × time) Ψ(fin-rot × sex × stream × time) p(fin-rot × stream × time) allowed (i) all parameters to differ between streams; (ii) survival and transition probability to differ based on fin-rot state, sex, and time (month); and (iii) capture probability to differ among fin-rot states and months. We implemented a sequential modeling approach where we first fitted models using the most general structure for apparent survival and transition probability and then modeled variation in capture probability. We expected capture probability to vary by stream due to differences in pool structure and flow, by time due to seasonal differences in flow, and by health due to reduced swimming performance resulting from fin-rot. We included all factors including the three-way interaction, all two-way interactions, and a constant model in the candidate model set for a total of eight capture probability models (table A1).

Next, we modeled variation in apparent survival to test our a priori hypotheses about temporal and health differences in survival between streams. Here, we used the most general model structure for transition probability, the best-supported model for capture probability and modeled ap-

parent survival with the four-way interaction among all factors (fin-rot, sex, stream, and time), all reduced three-way and two-way interactions among factors, all single factors, and a constant model for a total of 16 models.

Finally, we tested the a priori hypothesis that the Taylor and Caigual Rivers differ in their tendency to acquire fin-rot and remain infected. We used the same scheme for our candidate model set as above with the four-way interaction model and all reduced interactions and single factor models for a total of 16 models. For all transition probability model structures we used the best-supported structure for both capture probability p and survival Φ.

We used program MARK v.6.1 to obtain maximum likelihood estimates of parameters and to rank MSMR models (table 1; White and Burnham 1999). Model selection methods based on Akaike's Information Criterion adjusted for sample size (AICc) were used to provide parameter estimates and to assess statistical differences in these parameters among streams, sex, time, and fin-rot state. A universal goodness-of-fit test for MSMR models does not exist in Program MARK, but we used our most general model and the median $\hat{c}$ approach to estimate overdispersion and adjust model selection criteria and variance estimates (White and Burnham 1999).

Results

Capture-Mark-Recapture

Throughout 13 capture events from June 2009 through June 2010, we made a total of 8,731 captures of 1,908 and 2,194 individuals in the focal reaches of the Taylor and Caigual Rivers, respectively. In the Taylor River we cap-

tured 1,040 females and 868 males, and in the Caigual River we captured 1,365 females and 829 males.

Multistate Mark-Recapture Modeling

In our capture probability (p) models, we found strong support for the most general model structure. The top-ranking model, with 100% of the weight of evidence, supported a three-way interaction among stream, time, and fin-rot state (table A1). Capture probabilities were high in both streams (range and median in the Taylor River = 0.23–0.99, 0.58; in the Caigual River = 0.23–0.99, 0.76). Temporal variation in capture probability is consistent with seasonal changes in water level and flow, but our overall high detection rates assure confident estimates for the parameters of biological interest (apparent survival and transition probability). Additionally, we found little evidence of overdispersion in our data based on our median $\hat{c}$ value ($\hat{c} = 1.29$).

The best-supported model for apparent survival, Φ(stream × sex × time) had 100% of the weight of evidence and suggested that apparent survival Φ differs temporally and between sex and stream but not fin-rot state (table 1). This model supports the hypothesis that the guppy population in the Taylor River experiences higher mortality than the population in the Caigual River. Males in both streams show increased temporal variation in survival corresponding to sample occasions during the wet season; however, the seasonal effects were much greater in the Taylor River for both males and females (fig. 2; data available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.88dj4; Fitzpatrick et al. 2014). In

Table 1: Highest-supported model selection results for transition (Ψ) and survival (Φ) probabilities

	AICc	ΔAICc	w	K	Deviance
Ψ model structure:					
Fin-rot × sex × stream × time	15,022	.0	.91	234	3,948
Fin-rot × stream × time	15,027	4.7	.09	188	4,050
Fin-rot × sex × time	15,142	119.4	.00	188	4,165
Fin-rot × stream	15,157	133.9	.00	144	4,271
Fin-rot × time	15,167	144.1	.00	164	4,240
Φ model structure:					
Sex × stream × time	14,979	.0	1.00	188	4,001
Stream × time	14,997	17.6	.00	165	4,068
Fin-rot × stream × time	15,021	41.3	.00	189	4,041
Fin-rot × sex × stream × time	15,023	43.2	.00	234	3,948
Sex × stream	15,164	184.6	.00	147	4,272

Note: Model structures ranked using Akaike Information Criteria corrected for sample size (AIC$_c$). Relative AIC$_c$ (ΔAIC$_c$), Akaike weight (w), model likelihood, number of parameters (K), and deviance are reported for the five best-supported models. Reported model structures for the parameter being tested were run with the best-supported model structures in other parameters: Ψ(fin-rot × sex × stream × time), Φ(sex × stream × time), and p(fin-rot × stream × time).
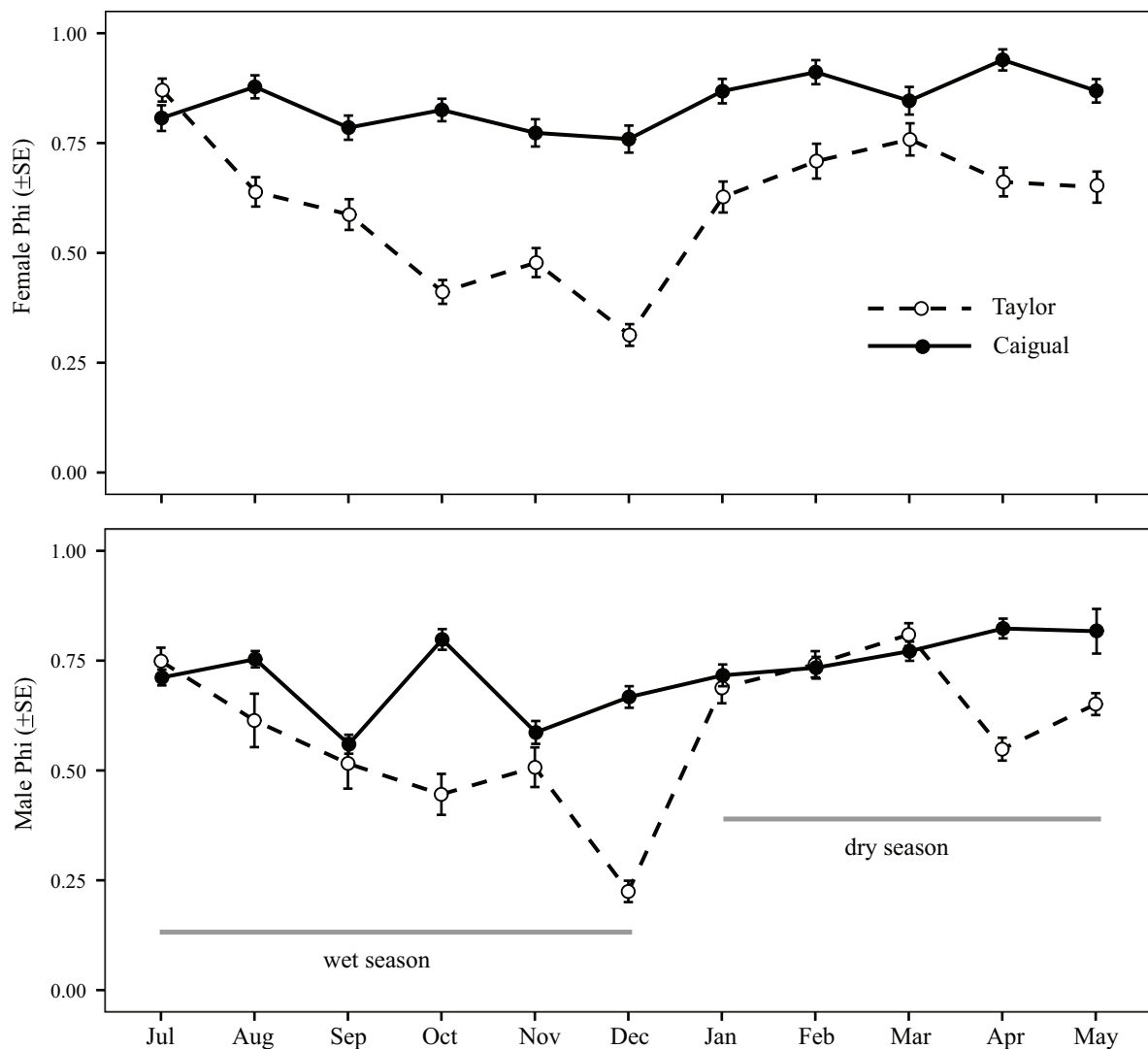
Figure 2: Female (*top*) and male (*bottom*) monthly survival estimates (estimate ± SE) for *Poecilia reticulata* in the Taylor (open circles, dashed line) and Caigual (closed circles, solid line) populations. Estimates are based on the top apparent survival model (table 1). Wet and dry seasons are indicated in gray on bottom panel. This study was conducted in two streams in the Northern Range Mountains of Trinidad between June 2009 and June 2010.

general, apparent survival probability estimates were higher overall in the Caigual River, across sex and time.

Additionally, model selection results revealed strong support (91% of the weight of evidence) for the most general model in transition probability between fin-rot states (table 1). Although all factors interacted in the top model, individuals from the Taylor River showed a higher probability of transition from fin-rot absent to fin-rot present state than the Caigual River over time in both sexes (fig. 3). The disparity in transition probability between populations was greater in females than in males. Probability of transition in the opposite direction (infected to healthy) did not differ between streams (fig. B1).

Discussion

Deviations from repeated patterns of parallel evolution may arise when selection pressures differ between what otherwise appear to be similar environments (Kaeuffer et al. 2011). We find that fine-scale environmental variation results in nonparallel low-predation environments and is associated with differences in mortality and life histories between neighboring guppy populations. Specifically, we find that differences in mortality (fig. 2) and life history (Torres-Dowdall et al. 2012) are associated with seasonal changes in rainfall and flooding, as well as indicators of disease. We therefore hypothesize that the higher levels of
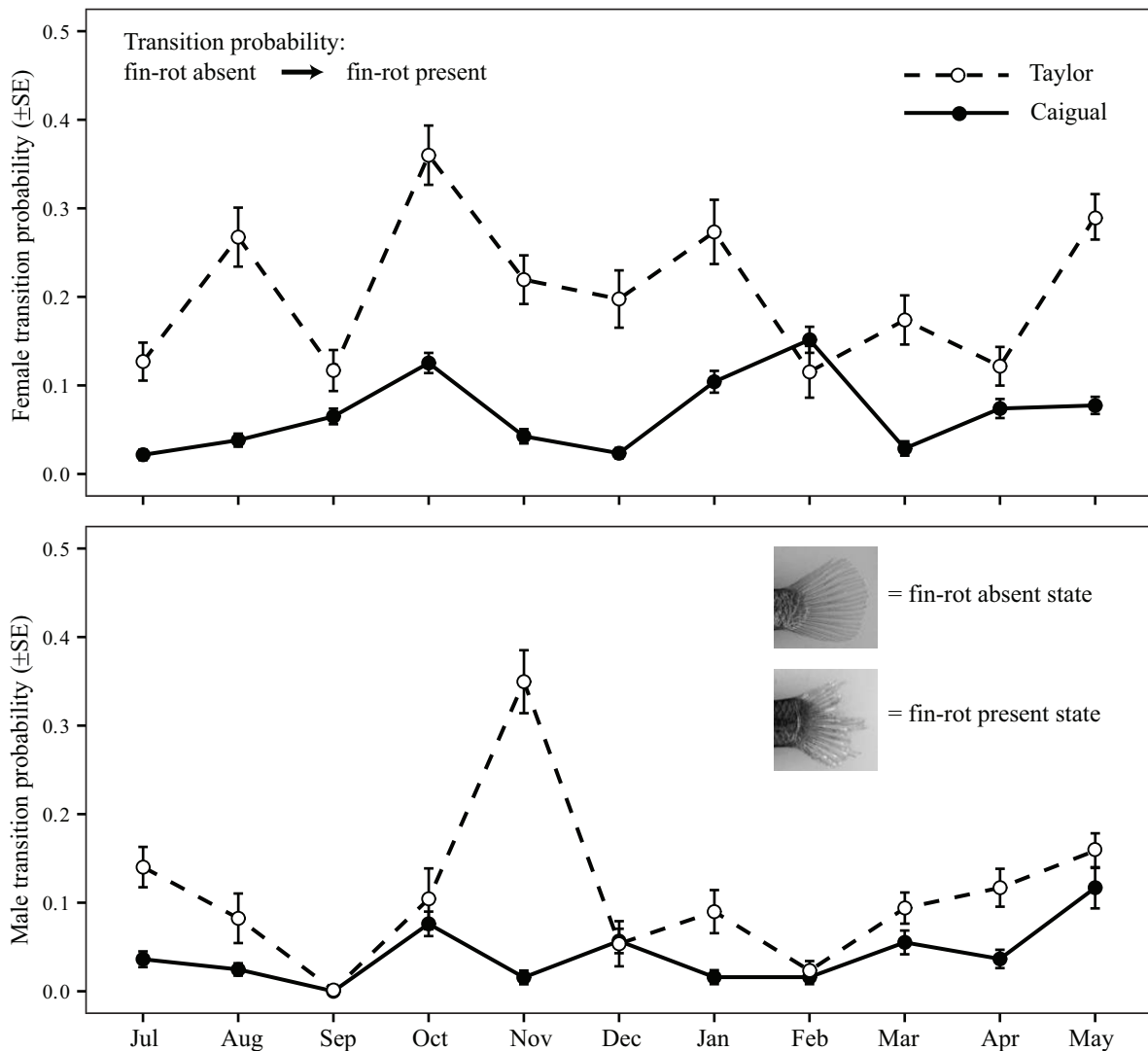
Figure 3: Female (*top*) and male (*bottom*) monthly estimates of transition from a fin-rot-absent to a fin-rot-present state (estimate ± SE) for *Poecilia reticulata* in the Taylor (open circles, dashed line) and Caigual (closed circles, solid line) populations. Estimates are based on the best-supported transition probability model (table 1). Images on bottom panel illustrate differences between the fin-rot-absent and the fin-rot-infected caudal fin of the same individual caught on two occasions.

mortality in the Taylor River likely selected for faster life histories compared to the neighboring low-predation population in the Caigual River. Below, we discuss how disease and flooding may be overlooked ecological correlates of mortality in the evolutionary ecology of stream fishes, and place these results in the context of past work showing parallel evolution in guppies.

Disease is a potentially powerful selective agent driving life-history evolution (Lafferty 1993; Webster and Woolhouse 1999; Mitchell et al. 2004; Chadwick and Little 2005; Fredensborg and Poulin 2006). However, the role of disease in the evolution of life-history traits in vertebrate hosts is

relatively unexplored (Ohlberger et al. 2011). Fin-rot is a ubiquitous condition, known to affect both marine and freshwater fish species worldwide, yet the causal infective agent is usually unknown (Ellis et al. 2008). The erosion of the epidermis, dermis, and fin rays diagnostic of fin-rot is typically attributed to bacterial or fungal infections and considered an acute, highly contagious condition, often associated with high mortality (Ellis et al. 2008). However, we are limited in our ability to directly link fin-rot to mortality in our system due to the difficulty of assessing the ultimate cause of death in the field. We use fin-rot as an easily diagnosed and well-established way to determine overall

health status of fish in the population (Latremouille 2003) but recognize this index does not necessarily inform us about individual disease dynamics. In other words, we cannot know if a fish observed with fin-rot is recovering from illness, recently infected, or the degree to which fin-rot is informative about the fate of that individual.

Nevertheless, we found that the Taylor River population, which has overall lower survival probabilities, showed a consistently higher probability of transition from fin-rot absent to fin-rot present states compared to the Caigual River population (fig. 3). A notable difference between the two low-predation streams in our study is that the Taylor River is located downstream of an agricultural plot that periodically uses chicken manure as a source of fertilizer (S. W. Fitzpatrick, personal observation), whereas the headwaters of the Caigual River are more remote and pristine. Although we cannot determine whether fin-rot is a cause of death in the population or just a sign of poor overall health condition, our data suggest that disease could contribute to the higher mortality in the Taylor River population and in turn be contributing to the divergence in life-history traits observed in the two studied streams.

Seasonal flooding could also be an important cause of mortality, as organisms experiencing high levels of environmental disturbance tend to have life-history patterns associated with high mortality (Cohen 1966; Lytle 2001; Lytle 2002; Lytle and Poff 2004). The importance of seasonal flooding events on guppy populations has received relatively little attention, but observations that guppy biomass in upstream localities significantly decreases after flooding events suggest that flooding could be an important source of mortality (Grether et al. 2001). During the wet season in Trinidad, constant rain causes high soil saturation, which leads to high amounts of storm runoff and flooding in headwater streams. The intensity of these flooding events is dependent on stream characteristics, such as the shape of the channel cross section and size of the catchment area (Allan and Castillo 2007). Flooding can affect populations by causing mortality of individuals due to physical stress or via apparent mortality due to the permanent removal of individuals from the population. In our system, the Taylor River is a smaller stream with steeper banks, resulting in a more channelized stream than the neighboring Caigual River (M. Torres-Mejia, unpublished data). In concordance with the differences in the channel characteristics, we found reduced survival probabilities during the wet season in Taylor River, but not in Caigual River, adding support to the hypothesis that floods could also be an important source of mortality driving the observed life-history patterns in the Taylor River (fig. 2).

Life-history theory predicts that an increase in adult mortality rates relative to juveniles selects for a faster life-history strategy (Gadgil and Bossert 1970). Our MSMR methods are not amenable to explicit tests of age- or size-specific mortality rates. However, we found survival differences between streams in females (the larger and longer-lived sex) to be more exaggerated and sustained throughout the year (fig. 2). In other words, the increase in mortality in the Taylor River relative to the Caigual River is larger for females than males. Typically, as is the case in the Caigual River, male guppies have lower survival rates than females (Reznick et al. 1996a; Bryant and Reznick 2004; Reznick and Bryant 2007; López-Sepulcre et al. 2013), yet within the Taylor River, both sexes have equally high mortality. Additionally, females show a consistently higher probability of transition to the fin-rot present state (fig. 3). Collectively, these results argue for sustained high mortality rates, particularly on females, in the absence of predators.

Because evolutionary responses to natural selection may be constrained genetically or by age of the population (Lande 1979), an alternative explanation to the observed patterns is that there may be nonecological factors underlying this life-history anomaly. Guppies are known to have occurred in the Taylor River since at least 1990, when an extensive survey of icthyofauna in the Heights of Guanapo watershed was conducted (Gilliam et al. 1993), suggesting there has been ample time to evolve a low-predation life-history strategy (Reznick 1997). Additionally, preliminary microsatellite analyses comparing allele frequencies between guppy populations found in the Taylor and Caigual Rivers show these populations are fixed for the same allele in 7 out of 12 loci (S. W. Fitzpatrick and W. C. Funk, unpublished data), suggesting a common founding population. Thus, age of population and genetic constraints appear unlikely to be causing the divergence in life-history strategy.

Finally, we acknowledge that a caveat in our study is that the contrast in mortality is between only two low-predation populations. In spite of this limitation, we argue that our results for the Taylor River are unique, on the basis of extensive prior research on guppies from high- and low-predation environments throughout Trinidad. Prior point estimates of mortality rates from multiple experiments executed in low- and high-predation sites (Rodd and Reznick 1991; Reznick et al. 1996a), longer-term mark-recapture data from two additional high- and low-predation localities (Reznick and Bryant 2007), plus new long-term mark-recapture results from three additional introduction sites in the vicinity of the Taylor River (López-Sepulcre et al. 2013; A. López-Sepulcre, unpublished data) all document consistently lower mortality rates in low-predation environments across a diversity of locations and time intervals. In addition, repeated comparisons of guppies from high- versus low-predation environments demonstrate consistent differences and remarkable uniformity

in the life histories of guppies from low-predation environments, although magnitude of these differences can vary between drainages (Reznick and Bryga 1996). By restricting our comparisons to a single drainage, we minimize such drainage differences and were able to compare the Taylor River life history to its closest neighboring low-predation stream. Finally, we have evidence from duplicated experiments that the life histories of guppies transplanted from high- to low-predation environments will rapidly evolve to match those typical of low-predation habitats (Reznick and Bryga 1987; Reznick et al. 1990; Reznick 1997). When presented against this extensive background of a consistent association between fish communities, mortality rates, and life histories, the results for the Taylor River stand out as anomalous.

Phenotypic nonparallelisms offer an opportunity to gain a more complete understanding of the evolutionary ecology of organisms. The guppy system has proven fundamental to our understanding of how variation in predation regime can drive the parallel evolution of phenotypic divergence (Magurran 2005). However, the ubiquitous emphasis on predation regime in this system has come at the expense of potentially overlooking other relevant ecological factors. Classic examples of parallel evolution have built a consensus for natural selection as one of the primary mechanisms underlying the evolution of diversity (Jones et al. 1992; McPhail 1993; Reznick et al. 1996*b*; Huey et al. 2000; Schluter et al. 2004; Losos 2009). In turn, these well-known systems with predictable patterns of phenotypic divergence can be further utilized to explicitly investigate other fine-scale aspects of the ecological backdrop that influence phenotypic evolution (Kaeuffer et al. 2011). For example, in our study, the well-developed understanding of the predicted adaptive direction of life-history strategies across variable predation regimes highlighted a population-level anomaly, leading to one of the first studies to show that extrinsic mortality sources other than predation can shape guppy evolution in the wild. While cases of parallel evolution provide important evidence for the deterministic role of natural selection, nature is replete with "exceptions to the rule" and these complexities may be equally valuable for understanding the mechanisms underlying phenotypic evolution and diversity patterns.

APPENDIX A

Supplementary Table

Table A1: Model selection results for capture probability (p)

p model structure	AICc	ΔAICc	w	K	Deviance
Fin-rot × stream × time	15,040.01	.00	1.00	128	4,187.92
Stream × time	15,138.85	98.84	.00	117	4,309.52
Fin-rot × stream	15,149.08	109.07	.00	104	4,346.57
Fin-rot	15,164.76	124.75	.00	91	4,388.96
Fin-rot × time	15,283.36	243.35	.00	113	4,462.30
Stream	15,356.06	316.05	.00	94	4,574.10
Time	15,368.73	328.72	.00	102	4,570.33
Constant	15,419.63	379.62	.00	92	4,641.78

Note: Model structures ranked using Akaike Information Criteria corrected for sample size (AIC$_c$). Relative AIC$_c$ (ΔAIC$_c$), Akaike weight (w), model likelihood, number of parameters (K), and deviance are reported for each model. All models were run with the most general model structures for survival and transition probability: Φ(fin-rot × sex × stream × time), Ψ(fin-rot × sex × stream × time).
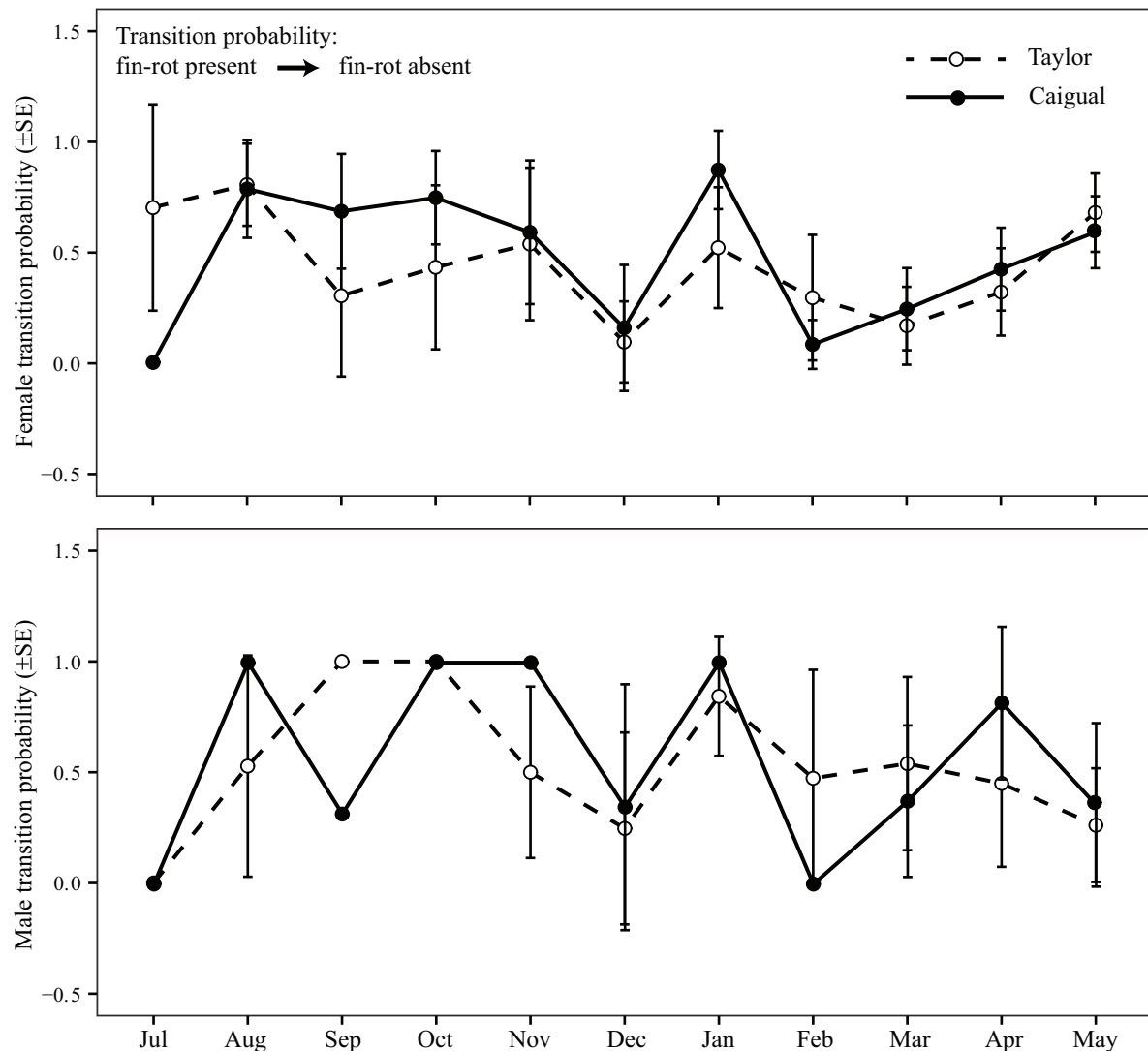
APPENDIX B

Fin-Rot-Present State to Fin-Rot-Absent State Transition Probability Estimates (Ψ)

Figure B1: Female (*top*) and male (*bottom*) monthly estimates of state transition from fin-rot present state to fin-rot absent (estimate $\pm$ SE) for *Poecilia reticulata* in the Taylor (open circles, dashed line) and Caigual (closed circles, solid line) populations. Estimates are based on the best-supported model (table 1). Taylor and Caigual populations do not show differences in the transition direction from infected to healthy states.

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Butterfly nets used to catch guppies during monthly mark-recapture surveys. Photo credit: Courtney Fitzpatrick.