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Differences in ontogenetic and diurnal microhabitat selection by sympatric live-bearing fish species with different reproductive modes

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Abstract

1. A pregnancy imposes a heavy reproductive burden on females. Some live-bearing species have evolved reproductive adaptations to reduce this burden, which may influence their ability to use specific microhabitats.
2. We investigate whether two such reproductive adaptations, placentation (embryo provisioning via a placenta) and superfetation (the ability to carry multiple broods at various developmental stages), influence microhabitat selection by five sympatric Costa Rican live-bearing fish species (family Poeciliidae). Theory predicts that placentation and superfetation should both reduce the reproductive burden of females during pregnancy, improve their body streamlining, and swimming performance, and consequently allow them to use *more performance-demanding* microhabitats.
3. Here we apply underwater visual fish surveys to test a key prediction of this hypothesis, which is that the presence of these two reproductive adaptations is correlated with the use of microhabitats in the river that are characterised by a higher-flow velocity.
4. Consistent with our predictions, we observed significant interspecific differences in daytime microhabitat use: species that had both placentation and superfetation were found in deeper and faster-flowing parts of the river, species that lacked both adaptations were confined to shallow slow-flowing areas, and species with one adaptation (i.e. only superfetation) inhabited intermediate areas. This interspecific daytime microhabitat use was strongest in reproductive adults, intermediate in immatures, and absent in juveniles (the latter of which were all found in shallow low-velocity zones), suggesting that ontogeny influences species-specific microhabitat use. Finally, at night, all fishes, regardless of the species or age-class, congregated in shallow slow-flowing waters to rest (sleep) on the river bottom.
5. Taken together, our results suggest that placentation and superfetation may be hitherto unrecognised reproductive features that help to explain differences in

ontogenetic and diurnal microhabitat preferences between sympatric live-bearing fish species living in environments characterised by large flow variation.

KEYWORDS
habitat selection, matrotrophy, placenta, Poeciliidae, superfetation

1 | INTRODUCTION

Microhabitat selection affects community assembly and structure in response to a variety of biotic and abiotic gradients (e.g. competition, predation risk, parasites, resource availability; Morris, 2003; Rosenzweig, 1991). It enables the use of a different set of local resources by different species, minimising competition with co-occurring species (Bolnick et al., 2003, 2007). Microhabitat selection results from optimisation processes involving individual fitness costs and benefits (Sibly & McFarland, 1976). For instance, in environments where patches vary in food availability, optimal foraging theory predicts that individuals should prefer habitats with high food density (MacArthur & Pianka, 1966). However, when these patches are simultaneously subject to high predation risk, individuals must balance the conflicting demands of food acquisition and predator avoidance (Sih, 1980). Different species may balance these conflicting demands (feeding vs. predator avoidance) in different ways, resulting in species-specific differences in microhabitat selection and affecting the spatial and temporal dynamics of species interactions (Morris, 2003). Microhabitat selection is therefore an important mechanism that allows for the competitive coexistence of species (Rosenzweig, 1981).

Microhabitat selection not only differs among species but can also vary within species. For instance, microhabitat use can change throughout an individual's life depending on their age, size, or developmental stage (i.e. ontogenetic microhabitat shifts). Size-dependent predation risk was shown to account for differences in habitat use between bluegill sunfish size classes (*Lepomis macrochirus*), with large bluegills preferring open-water habitats with high foraging returns and small bluegills choosing less profitable habitats close to vegetation to avoid predation (Mittelbach, 1981; Werner & Hall, 1988). Likewise, armoured catfish (Loricariidae) display size-specific spatial distributions, with small catfish preferring shallow water to reduce predation risk by piscivorous predators while large catfish avoid shallow water where they are vulnerable to avian predators (Power, 1984). In coastal lagoons, many fish species display size-related shifts from settlement habitats (larvae) to nursery areas (juveniles) and subsequently to nearby coral reefs (adults). These ontogenetic shifts in (micro)habitat use may be related to ontogenetic changes in dietary preferences or susceptibility to predation (Werner, 1984; Cocheret de la Morinière et al., 2002; Cocheret de la Morinière, Pollux, Nagelkerken, Hemminga, et al., 2003; Cocheret de la Morinière, Pollux, Nagelkerken, & Van Der Velde, 2003; Pollux et al., 2007).

Many species furthermore display pronounced day–night shifts in habitat use (diurnal microhabitat shifts). Well-known examples include the diurnal vertical migration of freshwater and marine pelagic invertebrates from deeper water during the day to avoid visually orienting predators, to shallower surface waters at night to feed (Bollens & Frost, 1989; Bollens et al., 1992; Kaartvedt et al., 2007; Sainmont et al., 2013). Juvenile Atlantic salmon (*Salmo salar* L.) show a temperature-dependent shift in diel activity and habitat use, which is probably the result of maximising feeding efficiency in summer, and reducing predation risk in winter (Fraser et al., 1993). The Eurasian lynx (*Lynx lynx*) selects open habitats at night where prey is more abundant and shifts to dense understory cover and rugged terrain during the day to avoid human activity (Filla et al., 2017). Such diel differences in activity and microhabitat use are often the result of a complex trade-off between feeding and avoiding predators (Fraser et al., 2004; Metcalfe et al., 1999; van der Vinne et al., 2019).

Finally, microhabitat selection can also change in individuals depending on their reproductive state (reproductive microhabitat shifts). Gravid and pregnant females, for example, may temporarily select *low performance-demanding* microhabitats: for example, areas where they are less prone to predation or, in stream ecosystems, where they are less exposed to strong currents. The reason is that gravidity and pregnancy may negatively affect the locomotor performance of females (Fleuren et al., 2019; Noren et al., 2011; Plaut, 2002; Seigel et al., 1987), increasing their susceptibility to predation (Pires et al., 2011; Pollux et al., 2009). This risk is compounded by the fact that predators often prefer gravid or pregnant females (Trexler et al., 1994), because they are large and (due to the presence of eggs or embryos) represent a high-quality resource that is rich in energy and nutrition. To reduce predation risk, gravid female common lizards (*Lacerta vivipara*), for instance, strongly rely on crypsis and remain motionless in the immediate vicinity of hiding places (Bauwens & Thoen, 1981). Moreover, gravid female three-spined stickle-backs (*Gasterosteus aculeatus*) remain closer to refuges than non-gravid females when inhabiting habitats with predators (Rodewald & Foster, 1998). Similarly, the Trinidadian guppy (*Poecilia reticulata*) uses habitats with lower water velocity late in pregnancy to offset some of the performance-related costs of pregnancy (Banet et al., 2016). Thus, when gravidity or pregnancy are associated with increased vulnerability to high performance-demanding conditions, this is likely to induce a shift in habitat use to less performance-demanding microhabitats.

Here, we study microhabitat selection (Allee et al., 1949) by five different live-bearing fish species belonging to the family Poeciliidae (*Poeciliopsis retropinna*, *Poeciliopsis paucimaculata*, *Poeciliopsis turrubarensis*, *Poecilia gillii*, and *Brachyrhaphis roseni*) that co-occur in rivers and streams in Costa Rica. We quantify

TABLE 1 Summary of the reproductive modes among the study species

Species	Placentation	Matrotrophy index	Superfetation[a]	Degree of superfetation	References
Poeciliopsis retropinna	✓	117	✓	4	Reznick et al. (2002) and Hagmayer et al. (2018)
Poeciliopsis paucimaculata	✓	7.8	✓	2	Reznick et al. (2002)
Poeciliopsis turrubarensis	✗	<1	✓	4	Zúñiga-Vega et al. (2007)
Poecilia gillii	✗	<1	✗	1	Pollux et al. (2009)
Brachyrhaphis roseni	✗	<1	✗	1	Pollux et al.(2009)

[a] Number of broods at different developmental stages.

differences in diurnal, ontogenetic, and reproductive microhabitat use among these species and their piscivorous predator (*Gobiomorus maculatus*). These five co-occurring poeciliid fish species are of similar size and generally prefer similar environmental conditions (Bussing, 2002; Meyer, 2015). However, they differ in the absence/presence of two reproductive adaptations (Table 1). The first reproductive adaptation is the placenta: *P. turrubarensis*, *P. gillii*, and *B. roseni* are lecithotrophic (or *yolk-feeding*), committing all nutrients required for development during pregnancy to the eggs prior to fertilisation, while *P. retropinna* and *P. paucimaculata* are placentotrophic (i.e. *mother-feeding*) provisioning nutrients to the developing embryos throughout pregnancy via a placenta (Furness et al., 2019; Pollux et al., 2014). The second reproductive adaptation is superfetation: *P. retropinna*, *P. paucimaculata*, and *P. turrubarensis* have superfetation, which means that they are able to carry multiple broods at different developmental stages, while *P. gillii* and *B. roseni* lack superfetation (Pollux et al., 2009).

Theory predicts that (different combinations of) these two reproductive adaptations may be associated with differences in microhabitat use. The reason is that the presence of the placenta and superfetation are both thought to reduce a female's reproductive burden during pregnancy (Bassar et al., 2014; Furness et al., 2021; Hagmayer et al., 2020; Pollux et al., 2009; Reznick et al., 2007). A reduced reproductive burden has further been associated with enhanced body streamlining and improved locomotor performance of females during pregnancy (Fleuren et al., 2018, 2019; Pires et al., 2011; Pollux et al., 2009; Quicazan-Rubio et al., 2019; Thibault & Schultz, 1978; Zúñiga-Vega et al., 2010), potentially allowing the use of different stream (micro)habitats (Banet et al., 2016). Here, we test a key prediction of this hypothesis, namely that the two reproductive adaptations should be associated with a species' microhabitat use. Specifically, (1) we predict that reproductive adults of species with a placenta and/or superfetation will inhabit relatively deeper, faster-flowing sections in the middle of the river compared to species that lack both reproductive adaptations. (2) Furthermore, we know from preliminary nocturnal observations (Hagmayer, Furness, & Pollux, personal observations) that poeciliid species become inactive at night and tend to move to the shallows to rest. We therefore predict that if adults of placental species with superfetation indeed inhabit deeper, faster-flowing parts of the river during the day (see prediction 1), then they should show a far more pronounced diurnal shift at dusk towards shallower, slow-flowing microhabitats compared to species that lack both reproductive adaptations. (3) Finally, we expect that juveniles and immatures of all five species tend to avoid the faster-flowing sections of the river, because their swimming abilities are still limited (Dial et al., 2016; Lankheet et al., 2016). If true, then these younger ontogenetic stages (juveniles and to a lesser extent immatures) should display a similar habitat selection regardless of the species, with all preferring shallow, slow-velocity areas near the riverbank. By comparing microhabitat use of these five sympatric live-bearing fish species, our study provides new insights into the potential effects of reproductive adaptations on microhabitat selection and local diurnal and ontogenetic migration.

2 | METHODS

2.1 | Study species

Poeciliopsis retropinna, *P. paucimaculata*, *P. turrubarensis*, *P. gillii*, and *B. roseni* all inhabit freshwater streams in the Rio Terraba and Rio Coto drainages in the province of Puntarenas, Costa Rica (Bussing, 2002). With the exception of *Brachyrhaphis* sp., which mainly feed on ants and tiny dipterans (Pichler & Schiemer, 2008), all study species browse on detritus, ooze, and algae (Bussing, 2002). Furthermore, although adult female *B. roseni* are generally smaller than the females of the other study species, female body size does not differ between *P. retropinna*, *P. paucimaculata*, *P. turrubarensis*, and *P. gillii* (Methods 1.1 in Supporting Information; Table S1; Figure S1). However, the study species differ in the absence/presence (or degree) of two reproductive adaptations: placentation and superfetation (Table 1). The degree of placentation is quantified as the ratio of offspring mass at birth to egg mass at fertilisation, also referred to as the Matrotrophy Index (MI; Pollux et al., 2014; Reznick et al., 2002). Some live-bearing species, known as lecithotrophs (yolk-feeding), allocate all resources to eggs prior to fertilisation in the form of large fully-yolked eggs. Embryos subsequently lose dry mass over the course of gestation due to metabolic processes. Such species have an MI less than 1. Other live-bearing species, known as matrotrophs (mother-feeding), allocate nutrients to the developing offspring post-fertilisation throughout pregnancy. Such species have an MI greater than 1, indicating that embryos gain dry mass during pregnancy. Placentotrophy represents one specific type of matrotrophy that is achieved through a follicular placenta, roughly an analogue to the mammalian placenta (Pollux et al., 2009). The degree of superfetation is the number of broods at various developmental stages that are carried by a female (Turner, 1937). Females with superfetation tend to produce smaller broods, but do so more often (Reznick & Miles, 1989).

Poeciliopsis retropinna and *P. paucimaculata* are both characterised by superfetation and post-fertilisation maternal provisioning (i.e. matrotrophy). *P. retropinna* females carry up to four broods at various developmental stages and offspring increase in dry mass more than 100-fold during pregnancy (MI = 117; Reznick et al., 2002). *P. paucimaculata* females carry up to two broods at different stages and the embryos increase approximately 10-fold in dry mass during gestation (MI = 7.8; Reznick et al., 2002). *P. turrubarensis* exhibits superfetation, carrying up to four different broods (Zúñiga-Vega et al., 2007), but does not provide nutrients to the embryos after fertilisation (i.e. MI < 1). In contrast, *P. gillii* and *B. roseni* are both non-placental species and carry embryos of only a single brood (i.e. no superfetation; Pollux et al., 2009, 2014). All five live-bearing fish species commonly co-occur with *G. maculatus*, a benthic piscivorous predator found on the Pacific versant of Costa Rica (Bussing, 2002).

2.2 | Underwater visual census

In February and March (i.e. end of dry season) 2017–2019, we selected 10 sites in the province of Puntarenas in Costa Rica. The average monthly precipitation at the study sites in February and March is low (~80 mm; Fick & Hijmans, 2017), and thus, variation in water depth and velocity can be expected to be relatively small. At each site, 7–17 transects of 4–24 m were placed using two 5 mm ropes separated by 1 m (Figure S2). Each transect was divided in quadrats of 1 m, which results in 1,406 total quadrats of 1 m × 1 m, an average of 141 quadrats per site (Tables 2 and 3). Underwater visibility was high at all study sites. We recorded the occupancy (i.e. presence or absence) of juveniles, immatures, and adults of all study species including *G. maculatus* during daytime in each quadrat of each transect. Specifically, fish occurring in deep-water transects in the middle of the river were identified by means of underwater visual census while snorkelling (Pollux et al., 2007). The snorkeller began at the downstream end of the transect and slowly worked his way upstream, metre by metre, while recording the occupancy (i.e. presence or absence) of each species and size class after completing each meter mark (Figure S2). In very shallow transects (too shallow to snorkel), fish were instead identified from above while standing or sitting on the shore. Poeciliid fish can be closely approached by a snorkeller without being disturbed (e.g. without scaring them away or altering feeding behaviour). All individuals were classified into three categories based on their ontogenetic stage: adults, defined as large (potentially pregnant) females and mature males (fully developed gonopodium present); immatures, defined as small (non-pregnant) females and males that did not have fully developed gonopodia; and juveniles, defined as fish <2 cm.

Immediately following the daytime census, we measured the (1) water depth to the nearest cm by using an aluminium metre stick and (2) water velocity to the nearest 0.01 m/s with a Höntzsch Vane Wheel FA current meter (type ZS30 GFE md20 T/100-2/p10, Höntzsch Instruments) three times separately in the centre of each 1 × 1 m quadrat. In quadrats where the water depth exceeded 60 cm, the water velocity was calculated as the average between the velocities measured at 0.2 times the water depth and 0.8 times the water depth in the centre of the quadrat (Hauer & Lamberti, 2007). This ultimately yielded a mean water velocity for each 1 × 1 m quadrat, calculated as the average of the three (or six if water depth exceeded 60 cm) repeated measurements in its center.

Finally, to quantify diurnal (day–night) shifts in microhabitat use, each transect was censused a second time that same night (as described above; Figure S2). For this, we used a 2000 Lumen ThorFire S1 underwater lamp to identify fish occurring in deep-water transects while snorkelling and headlamps for identifying fish in the

TABLE 2 Study locations (plus coordinates), study species present (PR: *Poeciliopsis retropinna*; PP: *Poeciliopsis paucimaculata*; PT: *Poeciliopsis turrubarensis*; PG: *Poecilia gillii*; BR: *Brachyrhaphis roseni*; GM: *Gobiomorus maculatus*), census dates, and number of transects (n_t) at each site

River	Species	Coordinates	Census date	n_t
Rio Pedregoso	PR, PP	N 09°21′, W 83°43′	12.03.2017	7
Rio Balsar	PR, PG, GM	N 08°59′, W 83°31′	27.03.2018	11
Rio Tinoco	PR, PG, BR	N 08°54′, W 83°22′	27.03.2018	9
Rio Corredor	PR, BR	N 08°40′, W 82°54′	28.03.2018	14
Rio Esquinas	PR, PP	N 08°44′, W 83°10′	29.03.2018	15
Rio Union (downstream)	PR, PP, PG	N 09°15′, W 83°34′	09.02.2019	17
Rio Nuevo	PT, GM	N 08°31′, W 83°21′	12.02.2019	16
Rio Agujas	PR, PT, PG, BR, GM	N 08°34′, W 83°23′	13.02.2019	17
Rio Union (upstream)	PP, PG	N 09°17′, W 83°32′	14.02.2019	16
Rio Pacuar	PR, PP, PG	N 09°21′, W 83°44′	15.02.2019	15
Rio Corredor	PR, BR	N 08°40′, W 82°54′	19.02.2019	6
Total				143

TABLE 3 Study locations, mean and range of water depth (m) and velocity (m/s), number of quadrats (n_q), and percentage of occupied quadrats at day and night at each site

River	Mean depth [min, max]	Mean velocity [min, max]	n_q	% Occupied day	% Occupied night
Rio Pedregoso	0.26 [0.04, 0.60]	0.23 [0.00, 1.28]	98	20	44
Rio Balsar	0.37 [0.05, 1.20]	0.10 [0.00, 0.78]	110	48	40
Rio Tinoco	0.26 [0.05, 0.55]	0.05 [0.00, 0.37]	73	95	88
Rio Corredor	0.20 [0.05, 0.60]	0.20 [0.00, 1.03]	133	89	62
Rio Esquinas	0.29 [0.01, 0.80]	0.37 [0.00, 1.35]	132	40	31
Rio Union (downstream)	0.38 [0.05, 0.80]	0.16 [0.00, 0.95]	169	75	31
Rio Nuevo	0.28 [0.05, 0.95]	0.21 [0.01, 0.76]	160	61	26
Rio Agujas	0.24 [0.05, 0.65]	0.22 [0.00, 0.89]	168	61	40
Rio Union (upstream)	0.29 [0.05, 0.85]	0.21 [0.00, 0.78]	158	65	44
Rio Pacuar	0.20 [0.01, 0.55]	0.11 [0.00, 0.58]	150	79	64
Rio Corredor	0.23 [0.05, 0.80]	0.11 [0.00, 0.42]	55	93	75
Total			1,406		

shallow shore transects. To ensure the same transect positions between day and night census, the transects placed during the day were left in place until we returned the same night.

2.3 | Data analysis

The habitat preference by the different species was quantified using the Bayesian programming environment JAGS (Plummer, 2003) in R v 3.5 (R Core Team, 2020).

For this, we quantified (1) the occupancy probability of a given age-class of a species as a function of water depth and velocity, as well as (2) the preferred mean water depth and velocity for a given age-class of a species.

For (1), the occupancy (i.e. presence or absence) of a given age-class of a species per quadrat was fitted in a Bernoulli generalised linear mixed model as a function of the three-way interaction between water depth, age, and day–night cycle, and the three-way interaction between water velocity, age, and day–night cycle. Additional variables included the second order polynomials of water depth and velocity. The model estimates species-specific slopes on each of the parameters and quadrat-, transect-, and site-specific random intercepts to account for pseudo-replication and between-transect/site variation, respectively. In the case of *G. maculatus*, information about age is not available. Thus, occupancy per quadrat was fitted as a function of the two-way interaction between water depth and day–night cycle, and the two-way interaction between water velocity and day–night cycle. The quadrat, transect, and site identity were fitted as additional intercepts (see above), and the second order polynomials of water depth and velocity as additional slopes.

For (2), the water depth and velocity of the occupied quadrats only (i.e. quadrats with occupancy = 1) were fitted as a function of the three-way interaction between age, day–night cycle, and species in a bivariate Gaussian model allowing for the covariance between the residuals of both responses. In the case of *G. maculatus*, the water depth and velocity of the occupied quadrats were fitted in a bivariate Gaussian model as a function of the day–night cycle only.

Convergence was assessed by visual examination of the traces and by checking that $\hat{R} < 1.01$. The model fits were assessed using posterior predictive checks on the model predictions. The JAGS code for the models including the priors, number of MCMC chains, iterations, burnin, and thinning is given in the Supporting Information.

3 | RESULTS

3.1 | Ontogenetic microhabitat use during daytime

During the day, adults of all species occupied deeper, faster-flowing water than immatures, and immatures occupied deeper, faster-flowing water than juveniles (Table S2; Figure 1: left panels, Figure 2). This ontogenetic habitat use was most pronounced in *P. retropinna* and *P. paucimaculata*, intermediate in *P. turrubarensis*, and least obvious in *P. gillii* and *B. roseni* (Tables S3 and S4; Figure 1: left panels). In other words, adults of species that have a placenta and superfetation (*P. retropinna* and *P. paucimaculata*) tend to inhabit deeper, faster-flowing parts in the middle of the river compared to adults of species that lack both reproductive adaptations (*P. gillii* and *B. roseni*). *P. turrubarensis*, which has superfetation but lacks a placenta, inhabits intermediate water depth and velocity. Moreover, juveniles (and to a lesser extent immatures) display a similar habitat selection regardless of the species. Specifically, they prefer shallow, slow-velocity areas near the riverbank (Table S2; Figure 1: left panels).

3.2 | Ontogenetic microhabitat use disappears at night

At night, the ontogenetic microhabitat use observed during daytime disappears. At night fall, all age-classes, regardless of the

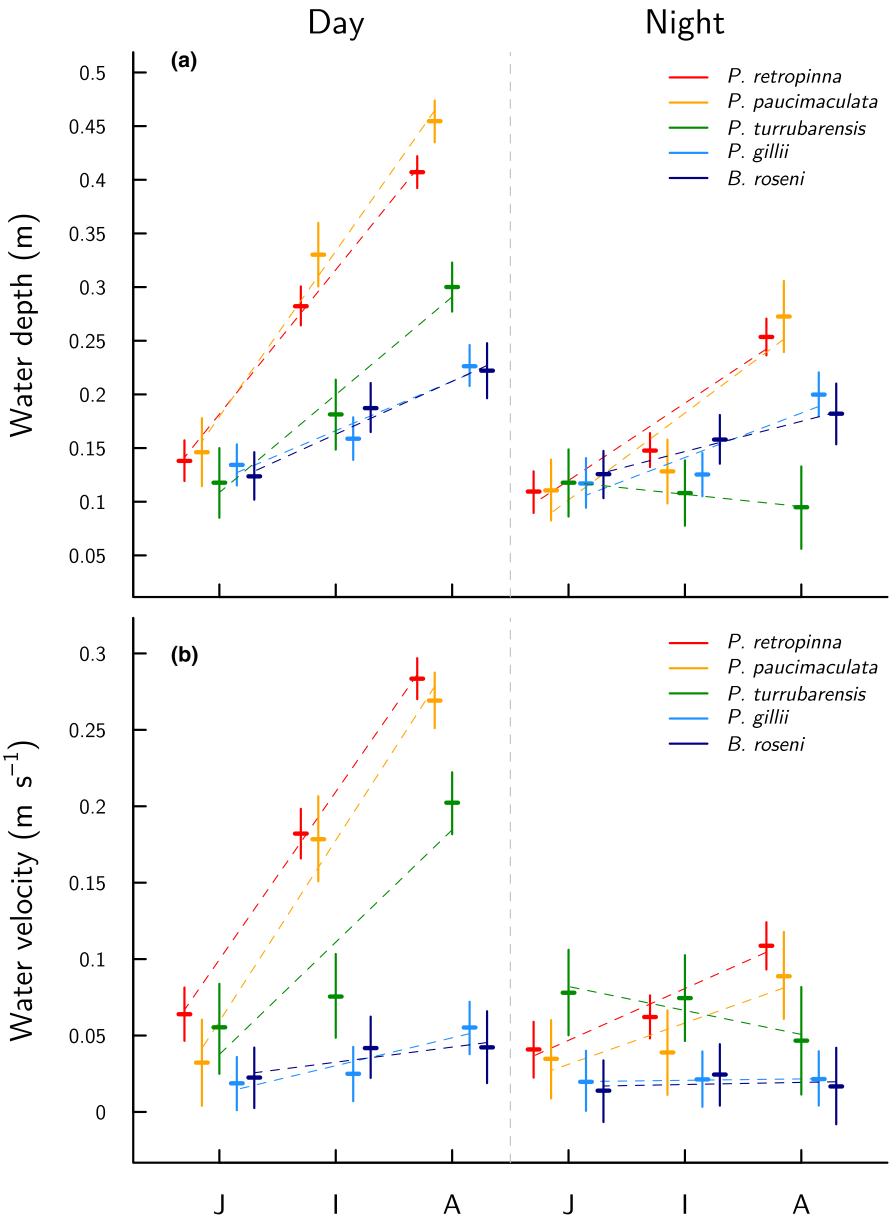


FIGURE 1 (a) Mean water depth and (b) velocity (±95% posterior density confidence interval) occupied by a given age-class of a species during day and night. Dotted line corresponds to a linear fit throughout the posterior samples of a given species at day or night, respectively. J: juvenile, I: immature, A: adult. red/orange: placental species with superfetation; green: non-placental species with superfetation; blue: non-placental species without superfetation

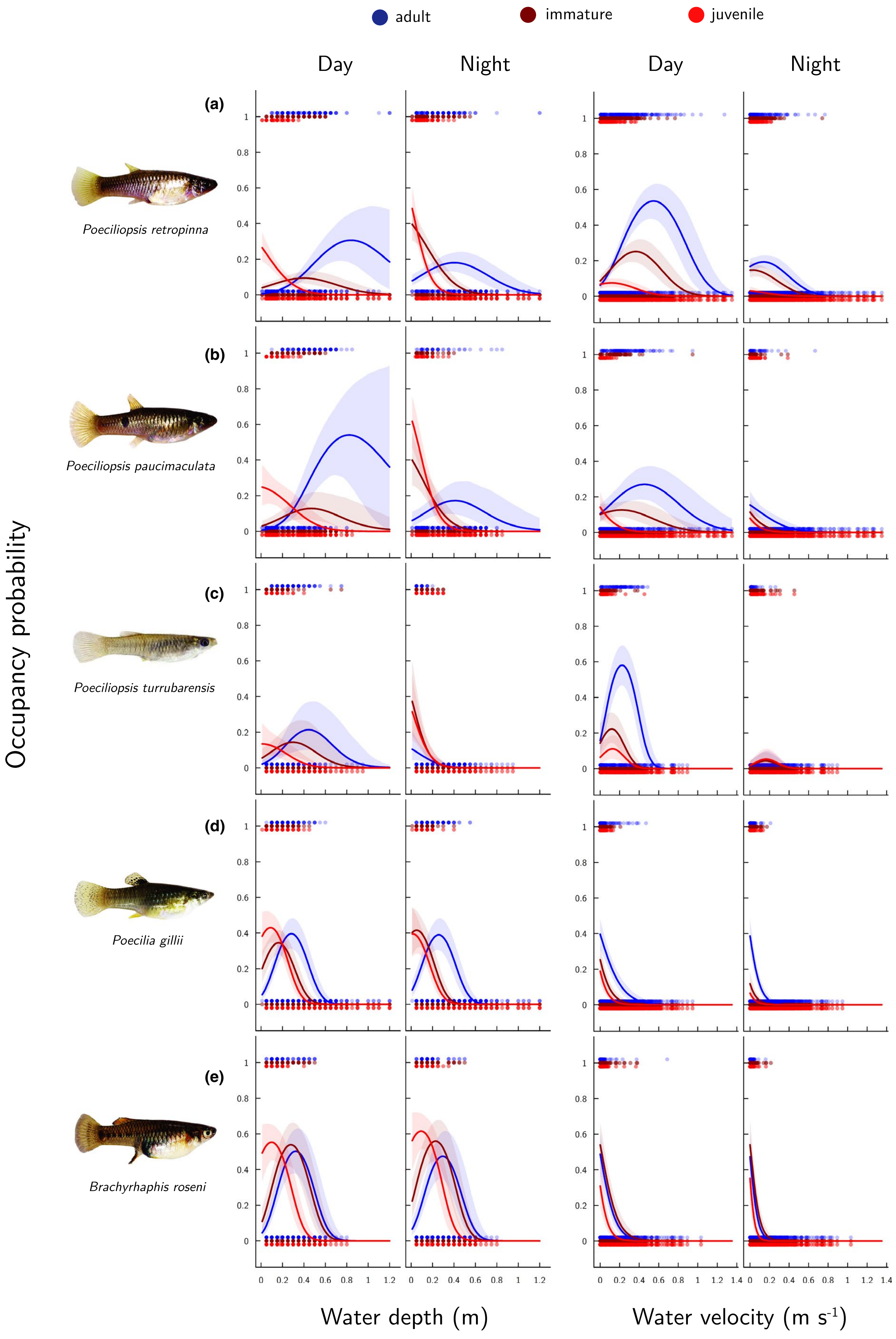
species, either remain in or move towards the shallow river shore where they congregate in the slow-flowing waters presumably to sleep (Table S2; Figure 1: right panels, Figure 2). As a result, adults of species that have a placenta and superfetation (*P. retropinna* and *P. paucimaculata*) show a far more pronounced diurnal (day–night) migration towards shallower, slow-flowing microhabitats compared to species that lack both reproductive adaptations (*P. gillii* and *B. roseni*). *P. turrubarensis*, which has superfetation but lacks a placenta, displays an intermediate diurnal microhabitat shift (Tables S3 and S4; Figure 1). Interestingly, the piscivorous ambush predator *G. maculatus* likewise moves to the slower-flowing and shallower areas at night (depth: $\beta_{\text{post.mean}}$ = 0.111, 95% confidence interval = 0.046–0.175, p_{MCMC} = .002; velocity: $\beta_{\text{post.mean}}$ = 0.063, 95% confidence interval = 0.005–0.118, p_{MCMC} = .035; Figures 3 and 4).

4 | DISCUSSION

4.1 | Ontogenetic (age-related) microhabitat use during daytime

We found that adults generally tend to prefer faster-flowing and deeper water during the day than immatures, and that immatures

FIGURE 2 Occupancy probability (±95% posterior density confidence interval) of a given age-class of a species as a function of water depth (water velocity kept constant at zero), velocity (water depth kept constant at mean, i.e. 0.29 m), and day–night cycle (left panels: day; right panels: night). red: juvenile, brown: immature, blue: adult. (a) *Poeciliopsis retropinna*, (b) *Poeciliopsis paucimaculata*, (c) *Poeciliopsis turrubarensis*, (d) *Poecilia gillii*, and (e) *Brachyrhaphis roseni*. Data points correspond to the raw data (i.e. whether a quadrat is occupied by a given age-class of a species or not)



● adult
● immature
● juvenile
Day
Night
Day
Night
(a)
Poeciliopsis retropinna
(b)
Poeciliopsis paucimaculata
(c)
Poeciliopsis turrubarensis
(d)
Poecilia gillii
(e)
Brachyrhaphis roseni
Occupancy probability
0
0.2
0.4
0.6
0.8
1
0 0.2 0.4 0.6 0.8 1 1.2
0 0.2 0.4 0.6 0.8 1 1.2 1.4
Water depth (m)
Water velocity (m s-1)

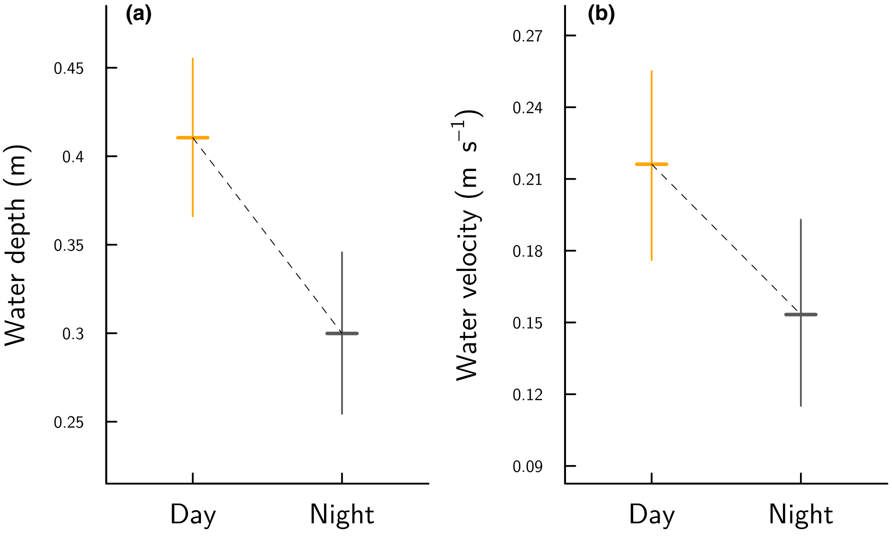


FIGURE 3 (a) Mean water depth and (b) velocity (±95% posterior density confidence interval) occupied by the predator species *Gobiomorus maculatus* during day (yellow) and night (grey). Dotted line corresponds to a linear fit throughout the posterior samples of the day–night cycle

prefer faster-flowing and deeper water than juveniles. This is probably due to the positive association between fish size (and thus, indirectly, age or ontogenetic stage; Reznick et al., 1996) and swimming capability in Teleost fish (Gibb et al., 2006). Newborn poeciliid fish have relatively poor swimming abilities (Dial et al., 2016; Lankheet et al., 2016). They are physically incapable of maintaining their position in fast-flowing water and thus seek refuge in low-velocity areas of the river near the shore. An added benefit for these small juveniles is that here they can inhabit very shallow water (sometimes less than 1 cm deep) where they are out of reach of piscivorous predators. The subsequent growth of fish is associated with physical ability and better control of the locomotor system (Fuiman & Higgs, 1997; Gibb et al., 2006; Lankheet et al., 2016), leading to an increase in swimming ability with increasing body length (Gibb et al., 2006). This allows larger and physically stronger adults to inhabit the relatively faster-flowing parts of the river.

The above may explain why only adult individuals *are physically able* to swim in the fast flow. However, it does not explain why some would *want* to move to the fast-flowing parts of the river in the first place, considering that there they are exposed to high drag forces (Quicazan-Rubio et al., 2019) making it energetically expensive for them to swim. We tentatively propose that some adults may move to deeper water to avoid avian predation. Together with various other piscivorous birds (e.g. herons), the southern Pacific region of Costa Rica is inhabited by four species of kingfisher (Garrigues & Dean, 2014), which mainly feed on fish (Fry et al., 1999). Piscivorous birds are very effective predators in shallow shore water or close to the surface (Kramer et al., 1983; Whitfield & Cyrus, 1978), where they show a preference for larger fish (Power, 1984; Trexler et al., 1994). This means that large adult poeciliids are more vulnerable to avian predation in shallow water than small juveniles. At the same time, piscivorous fish are presumably feeding in deeper water to prevent avian predation (Power, 1984). Indeed, we found that the piscivorous predator *G. maculatus* inhabits relatively deeper water during the day (i.e. when most piscivorous birds are active in the shallows). It has furthermore been shown that larger prey fish are able to perform faster escape responses, making them less vulnerable to predation by piscivorous fish (Gibb et al., 2006). Thus, one could argue that the mortality risk of live-bearing fish during daytime is highest for adults in shallow habitats from piscivorous birds, and highest for juveniles in deep habitats from piscivorous fish (Power, 1984; Schlosser, 1988). If true, then it would be advantageous for juveniles to inhabit shallow waters near the shore, while it would be beneficial for larger adults to move to deeper water as they outgrow the vulnerability to piscivorous fish (Power, 1984). Collectively, these findings suggest that the observed ontogenetic microhabitat preference in live-bearing fish during daytime may be an adaptive response to predation risk.

4.2 | Diurnal (day–night) shifts in microhabitat use

Many fish exhibit diurnal shifts in microhabitat use (Helfman, 1986; Lowe-McConnell, 1975), which have been attributed to shifts in foraging activity (Piet & Guruge, 1997), the use of shallow water as refuge from predation (Arrington & Winemiller, 2003; Copp & Jurajda, 1993), or the use of slow-flowing areas to reduce energy expenditure while resting at night (Matheney IV & Rabeni, 1995; Sempeski & Gaudin, 1995). In our study, we found that at dusk all fish, regardless of their ontogenetic stage (juvenile, immature, or adult), tend to move to shallow waters near the shore, where they sleep lying on the bottom in low-velocity areas. Occasionally, large adult individuals (particularly *P. retropinna* and *P. paucimaculata*) can be found sleeping while wedged into crevices or behind stones in deeper and faster flowing stretches of the river. Interestingly, *G. maculatus*, the most common piscivorous fish species in our study sites, is primarily a nocturnal sit-and-wait bottom predator (Swing, 1992). The finding that this piscivorous predator also moves towards shallow water at night, suggests that the observed diurnal microhabitat shifts in poeciliid fish towards shallow water are not related to predator avoidance. Instead, it is more likely that the day–night shifts are driven by a preference for low-velocity areas in the river to avoid being washed away while resting at night.

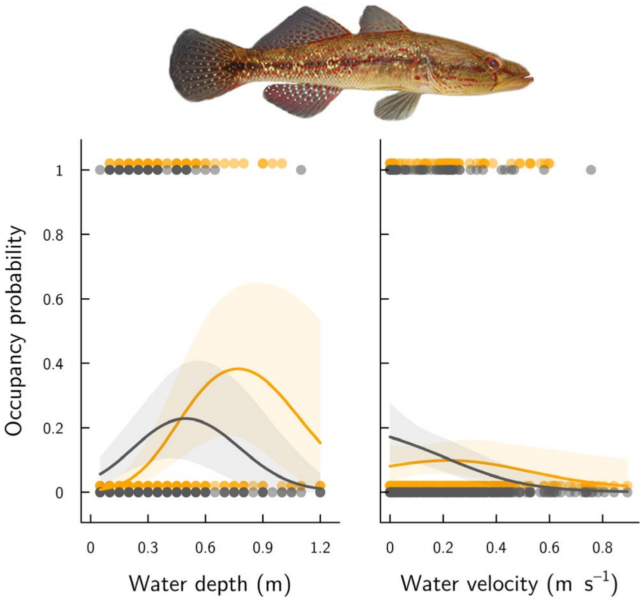


FIGURE 4 Occupancy probability (±95% posterior density confidence interval) of the piscivorous predator fish *Gobiomorus maculatus* as a function of water depth (left panel: water velocity kept constant at zero), velocity (water depth kept constant at mean, i.e. 0.28 m; right panel), and day–night cycle (yellow: day; grey: night). Data points correspond to the raw data (i.e. whether a quadrat is occupied by a given age-class of a species or not). Photo: Fredy Nugra

4.3 | Differences in diurnal and ontogenetic microhabitat use among poeciliid species with different reproductive adaptations

All five studied poeciliid species occur sympatrically in freshwater streams in Costa Rica (Bussing, 2002), yet show remarkable differences in ontogenetic and diurnal microhabitat use. This appears to be correlated with the absence/presence of the two reproductive adaptations. During daytime, adult *P. retropinna* and *P. paucimaculata* (which both have a placenta and superfetation) can be found in very fast-flowing water (of up to 1.3 m/s), while adult *P. gillii* and *B. roseni* (which both lack a placenta and superfetation) are confined to shallow and slow-flowing areas. Adult *P. turrubarensis* (which lacks a placenta but has superfetation) notably prefers an intermediate habitat. At night these differences in ontogenetic microhabitat segregation among species disappear when all ontogenetic stages (juveniles, immatures, and adults) of all five species move towards shallow waters presumably to sleep in low-velocity areas.

This raises the question why the adults of *P. retropinna* and *P. paucimaculata*, and to a somewhat lesser extent of *P. turrubarensis* are found in fast-flowing water during daytime? It has been argued that the evolution of placentation and superfetation both reduce a female's reproductive burden during pregnancy, yet achieve this in fundamentally different ways (Pires et al., 2011; Pollux et al., 2009; Thibault & Schultz, 1978). The evolution of the placenta is associated with a shift in the timing of maternal provisioning from pre- to post-fertilisation. Non-placental live-bearers (e.g. *P. gillii*, *B. roseni*, and *P. turrubarensis*) typically produce large fully yolked eggs, committing all the nutrients required for embryo development to the egg prior to fertilisation. Placental species (*P. retropinna* and *P. turrubarensis*), by contrast, produce relatively small eggs and instead provide most nutrients to their offspring throughout pregnancy via a placenta (Pollux et al., 2009; Wourms, 1981). The shift in the timing of maternal provisioning from pre- to post-fertilisation reduces a female's reproductive burden (Bassar et al., 2014; Fleuren et al., 2018; Reznick et al., 2007). The evolution of superfetation furthermore correlates with the more frequent production of smaller broods (Reznick & Miles, 1989). By spreading reproduction more evenly over time, superfetation is thought to reduce a female's peak reproductive allotment during gestation without reducing maternal fecundity (Pollux et al., 2009). Thus, placentation and superfetation are both thought to reduce a female's reproductive burden during pregnancy (Bassar et al., 2014; Hagmayer et al., 2020; Pires et al., 2011; Pollux et al., 2009; Reznick et al., 2007; Thibault & Schultz, 1978). This is likely to cause a more slender body shape (Fleuren et al., 2018, 2019; Zúñiga-Vega et al., 2007), reduced body drag (Quicazan-Rubio et al., 2019), as well as improved sustained swimming performance (Plaut, 2002) and fast-start escape response (Fleuren et al., 2019; Ghalambor et al., 2004). Thus, one might argue that placentation and superfetation are reproductive adaptations that facilitate the use of high *performance-demanding* microhabitats (e.g. high-flow areas) in the river. Our study provides the first empirical evidence in support of one aspect of this hypothesis, namely the idea that placentation and superfetation are reproductive adaptations that can drive differences in ontogenetic, diurnal, and reproductive microhabitat use between sympatric live-bearing species.

4.4 | Other potential causes of microhabitat use

Although our findings are consistent with the idea that placentation and superfetation may shape microhabitat selection in our study species, we must entertain the notion that other factors, besides these two reproductive adaptations, could also potentially influence the observed interspecific differences in microhabitat use. For instance, larger-bodied species generally have a higher swimming capability (Gibb et al., 2006) and are therefore more likely to inhabit faster-flowing water. If co-occurring sympatric species that share similar dietary preferences have different body sizes, then spatial niche segregation (e.g. with the larger-bodied species using faster-flowing parts of the river) may reduce interspecific resource competition (Lanza, 1983). However, although adult female *B. roseni* are generally smaller than the females of the other study species, female body size does not differ between *P. retropinna*, *P. paucimaculata*, *P. turrubarensis*, and *P. gillii*. Thus, variation in female body size does not (at least not exclusively) explain the observed differences in interspecific microhabitat selection among the study species.

Furthermore, there are large sex differences in body shape in our study species. In females, pregnancy dramatically alters body shape (e.g. increase in abdominal distention and wetted surface area), significantly increasing body drag and negatively influencing swimming performance (Fleuren et al., 2018, 2019; Plaut, 2002; Quicazan-Rubio et al., 2019). By contrast, males are generally more streamlined than pregnant females (Quicazan-Rubio, 2019). If microhabitat selection was solely a function of body shape, then we should expect to find spatial segregation of the sexes within streams, with encumbered pregnant females occurring in shallow low-flow areas and the more streamlined males in the deeper faster-flowing parts of the river. We did not separately quantify microhabitat use of the sexes; however, our snorkelling observations revealed that within each species the adult males closely co-occur with adult females. So why then do males occupy similar microhabitats as females, given that they are not affected by any reproductive burden? We propose that females may be the main driver of the observed interspecific microhabitat selection and males simply follow females. Indeed, in many poeciliid species, it has been shown that males obsessively follow females in a persistent attempt to mate with them (Magurran, 2011).

5 | CONCLUSION

We report large differences in adult daytime microhabitat use between five sympatric poeciliid species, presumably associated with two reproductive adaptations (placentation and superfetation) that both improve body streamlining and swimming performance during pregnancy (Fleuren et al., 2018, 2019). The presence of these adaptations may explain, at least in part, why adult *P. retropinna* and *P. paucimaculata*, and to a lesser extent *P. turrubarensis*, inhabit deeper, faster-flowing areas during daytime, while *B. roseni* and *P. gillii* are more confined to the shallow waters near the shore. The finding that, at night, all fish (regardless of species or age-class) move to shallow, low-velocity areas to rest, lends additional support to this idea. Collectively our results suggest that a female's reproductive strategy (i.e. placentation and superfetation) may be a hitherto unrecognised biological feature that may help to understand microhabitat preferences between sympatric live-bearing fish species. Our study can be seen as a first step on which future, ideally experimental, studies can build to assess the costs of locomotion as a function of reproductive mode and pregnancy state. Future studies should furthermore focus on comparing microhabitat use in more live-bearing fish (e.g. from the family Poeciliidae, Anablepidae, Goodeidae, or Zenarchopteridae), but also other aquatic live-bearing animals (e.g. amphibians, reptiles, and mammals), to assess the generality of these findings.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from Dryad Digital Repository: https://doi.org/10.5061/dryad.xpnvx0kcg

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REFERENCES

Allee, W. C., Emerson, E., Park, O., Park, T., & Schmidt, K. P. (1949). *Principles of animal ecology*. W.B. Saunders.

Arrington, D. A., & Winemiller, K. O. (2003). Diel changeover in sandbank fish assemblages in a neotropical floodplain river. *Journal of Fish Biology*, *63*, 442–459. https://doi.org/10.1046/j.1095-8649.2003.00167.x

Banet, A. I., Svendsen, J. C., Eng, K. J., & Reznick, D. N. (2016). Linking reproduction, locomotion, and habitat use in the Trinidadian guppy (*Poecilia reticulata*). *Oecologia*, *181*, 87–96. https://doi.org/10.1007/s00442-015-3542-9

Bassar, R. D., Auer, S. K., & Reznick, D. N. (2014). Why do placentas evolve? A test of the life-history facilitation hypothesis in two clades in the genus *Poeciliopsis* representing two independent origins of placentas. *Functional Ecology*, *28*, 999–1010. https://doi.org/10.1111/1365-2435.12233

Bauwens, D., & Thoen, C. (1981). Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology*, *50*, 733–743. https://doi.org/10.2307/4133

Bollens, S. M., & Frost, B. W. (1989). Predator-induced diet vertical migration in a planktonic copepod. *Journal of Plankton Research*, *11*, 1047–1065. https://doi.org/10.1093/plankt/11.5.1047

Bollens, S. M., Frost, B. W., & Lin, T. S. (1992). Recruitment, growth, and diel vertical migration of *Euphausia pacifica* in a temperate fiord. *Marine Biology*, *114*, 219–228.

Bolnick, D. I., Svanback, R., Araujo, M. S., & Persson, L. (2007). Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 10075–10079. https://doi.org/10.1073/pnas.0703743104

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, *161*, 1–28. https://doi.org/10.1086/343878

Bussing, W. A. (2002). *Peces de las aguas continentales de Costa Rica* (2nd ed.). Revista de Biologia Tropical.

Cocheret de la Morinière, E., Pollux, B. J. A., Nagelkerken, I., Hemminga, M. A., Huiskes, A. H. L., & Van der Velde, G. (2003). Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef continuum: Stable isotopes and gut-content analysis. *Marine Ecology Progress Series*, *246*, 279–289. https://doi.org/10.3354/meps246279

Cocheret de la Morinière, E., Pollux, B. J. A., Nagelkerken, I., & Van der Velde, G. (2002). Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuarine, Coastal and Shelf Science*, *55*, 309–321. https://doi.org/10.1006/ecss.2001.0907

Cocheret de la Morinière, E., Pollux, B. J. A., Nagelkerken, I., & Van Der Velde, G. (2003). Diet shifts of Caribbean grunts (Haemulidae) and snappers (Lutjanidae) and the relation with nursery-to-coral reef migrations. *Estuarine, Coastal and Shelf Science*, *57*, 1079–1089. https://doi.org/10.1016/S0272-7714(03)00011-8

Copp, G. H., & Jurajda, P. (1993). Do small riverine fish move inshore at night? *Journal of Fish Biology*, *43*, 229–241. https://doi.org/10.1111/j.1095-8649.1993.tb01190.x

Dial, T. R., Reznick, D. N., Brainerd, E. L., & Marshall, D. (2016). Effects of neonatal size on maturity and escape performance in the Trinidadian guppy. *Functional Ecology*, *30*, 943–952. https://doi.org/10.1111/1365-2435.12565

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

Filla, M., Premier, J., Magg, N., Dupke, C., Khorozyan, I., Waltert, M., … Heurich, M. (2017). Habitat selection by Eurasian lynx (*Lynx lynx*) is primarily driven by avoidance of human activity during day and prey availability during night. *Ecology and Evolution*, *7*, 6367–6381. https://doi.org/10.1002/ece3.3204

Fleuren, M., Quicazan-Rubio, E. M., van Leeuwen, J. L., & Pollux, B. J. A. (2018). Why do placentas evolve? Evidence for a morphological advantage during pregnancy in live-bearing fish. *PLoS One*, *13*, 1–15. https://doi.org/10.1371/journal.pone.0195976

Fleuren, M., van Leeuwen, J. L., & Pollux, B. J. A. (2019). Superfetation reduces the negative effects of pregnancy on the fast-start escape performance in live-bearing fish. *Proceedings of the Royal Society B*, *286*, 1–9. https://doi.org/10.1098/rspb.2019.2245

Fraser, D. F., Gilliam, J. F., Akkara, J. T., Albanese, B. W., & Sunny, B. S. (2004). Night feeding by guppies under predator release: Effects on growth and daytime courtship. *Ecology*, *85*, 312–319. https://doi.org/10.1890/03-3023

Fraser, N. H. C., Metcalfe, N. B., & Thorpe, J. E. (1993). Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proceedings of the Royal Society B: Biological Sciences*, *252*, 135–139. https://doi.org/10.1098/rspb.1993.0057

Fry, H., Fry, K., & Harris, A. (1999). *Kingfishers, bee-eaters and rollers: An identification guide*. Gardners Books.

Fuiman, L. A., & Higgs, D. M. (1997). Ontogeny, growth and the recruitment process. In R. C. Chambers & E. A. Trippel (Eds.), *Early life history and recruitment in fish populations* (pp. 225–250). Chapman & Hall.

Furness, A. I., Avise, J. C., Pollux, B. J. A., Reynoso, Y., & Reznick, D. N. (2021). The evolution of the placenta in poeciliid fishes. *Current Biology*, *31*, 1–8. https://doi.org/10.1016/j.cub.2021.02.008

Furness, A. I., Pollux, B. J. A., Meredith, R. W., Springer, M. S., & Reznick, D. N. (2019). How conflict shapes evolution in poeciliid fishes. *Nature Communications*, *10*, 1–12. https://doi.org/10.1038/s41467-019-11307-5

Garrigues, R., & Dean, R. (2014). *The birds of Costa Rica: A field guide*. Cornell University Press.

Ghalambor, C. K., Reznick, D. N., & Walker, J. A. (2004). Constraints on adaptive evolution: The functional trade-off between reproduction and fast-start swimming performance in the Trinidadian guppy (*Poecilia reticulata*). *The American Naturalist*, *164*, 38–50. https://doi.org/10.1086/421412

Gibb, A. C., Swanson, B. O., Wesp, H., Landels, C., & Liu, C. (2006). Development of the escape response in teleost fishes: Do ontogenetic changes enable improved performance? *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches*, *79*, 7–19. https://doi.org/10.1086/498192

Hagmayer, A., Furness, A. I., Reznick, D. N., Dekker, M. L., & Pollux, B. J. A. (2020). Predation risk shapes the degree of placentation in natural populations of live-bearing fish. *Ecology Letters*, *23*, 831–840. https://doi.org/10.1111/ele.13487

Hagmayer, A., Furness, A. I., Reznick, D. N., & Pollux, B. J. A. (2018). Maternal size and body condition predict the amount of post-fertilization maternal provisioning in matrotrophic fish. *Ecology and Evolution*, *8*, 12386–12396. https://doi.org/10.1002/eqe.3063

Hauer, R. F., & Lamberti, G. A. (2007). *Methods in stream ecology* (2nd ed.). Elsevier.

Helfman, G. S. (1986). Fish behaviour by day, night and twilight. In T. J. Pitcher (Ed.), *Behaviour of teleost fishes* (pp. 366–387). Springer-Verlag.

Kaartvedt, S., Klevjer, T. A., Torgersen, T., Sørnes, T. A., & Røstad, A. (2007). Diel vertical migration of individual jellyfish (*Periphylla periphylla*). *Limnology and Oceanography*, *52*, 975–983. https://doi.org/10.4319/lo.2007.52.3.0975

Kramer, D. L., Manley, D., & Bourgeois, R. (1983). The effect of respiratory mode and oxygen concentration on the risk of aerial predation in fishes. *Canadian Journal of Zoology*, *61*, 653–665. https://doi.org/10.1139/z83-087

Lankheet, M. J., Stoffers, T., van Leeuwen, J. L., & Pollux, B. J. A. (2016). Acquired versus innate prey capturing skills in super-precocial live-bearing fish. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 1–9. https://doi.org/10.1098/rspb.2016.0972

Lanza, J. (1983). Microhabitat use by bisexual and unisexual fishes (*Poeciliopsis*: Poeciliidae) in an artificial stream. *Oecologia*, *57*, 142–147. https://doi.org/10.1007/BF00379571

Lowe-McConnell, R. H. (1975). *Fish communities in tropical freshwaters: Their distribution, ecology, and evolution*. Longman.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*, 603–609. https://doi.org/10.1086/282454

Magurran, A. E. (2011). Sexual coercion. In J. P. Evans, A. Pilastro, & I. Schlupp (Eds.), *Ecology and evolution of Poeciliid fishes* (pp. 209–217). The University of Chicago Press.

Matheney, M. P. IV, & Rabeni, C. F. (1995). Patterns of movement and habitat use by northern hog suckers in an Ozark stream. *Transactions of the American Fisheries Society*, *124*, 886–897. https://doi.org/10.1577/1548-8659(1995)124<0886

Metcalfe, N. B., Fraser, N. H. C., & Burns, M. D. (1999). Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *Journal of Animal Ecology*, *68*, 371–381. https://doi.org/10.1046/j.1365-2656.1999.00289.x

Meyer, M. K. (2015). *Lebendgebärende Zierfische*, Band 1. Chimaira.

Mittelbach, G. G. (1981). Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. *Ecology*, *62*, 1370–1386. https://doi.org/10.2307/1937300

Morris, D. W. (2003). Toward an ecological synthesis: A case for habitat selection. *Oecologia*, *136*, 1–13. https://doi.org/10.1007/s00442-003-1241-4

Noren, S. R., Redfern, J. V., & Edwards, E. F. (2011). Pregnancy is a drag: Hydrodynamics, kinematics and performance in pre- and post-parturition bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology*, *214*, 4151–4159. https://doi.org/10.1242/jeb.059121

Pichler, C., & Schiemer, F. (2008). Ecology of fishes of Quebrada Negra, Costa Rica, a first order neotropical lowland stream. *Stapfia*, *88*, 495–505.

Piet, G. J., & Guruge, W. A. H. P. (1997). Diel variation in feeding and vertical distribution of ten co-occurring fish species: Consequences for resource partitioning. *Environmental Biology of Fishes*, *50*, 293–307. https://doi.org/10.1023/A:1007390516552

Pires, M. N., Bassar, R. D., McBride, K. E., Regus, J. U., Garland, T., & Reznick, D. N. (2011). Why do placentas evolve? An evaluation of the life-history facilitation hypothesis in the fish genus *Poeciliopsis*. *Functional Ecology*, *25*, 757–768. https://doi.org/10.1111/j.1365-2435.2011.01842.x

Plaut, I. (2002). Does pregnancy affect swimming performance of female Mosquitofish, *Gambusia affinis*? *Functional Ecology*, *16*, 290–295.

Plummer, M. (2003). JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd international workshop on distributed statistical computing*, 8.

Pollux, B. J. A., Meredith, R. W., Springer, M. S., Garland, T., & Reznick, D. N. (2014). The evolution of the placenta drives a shift in sexual selection in livebearing fish. *Nature*, *513*, 233–236. https://doi.org/10.1038/nature13451

Pollux, B. J. A., Pires, M. N., Banet, A. I., & Reznick, D. N. (2009). Evolution of placentas in the fish family Poeciliidae: An empirical study of macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 271–289. https://doi.org/10.1146/annurev.ecolsys.110308.120209

Pollux, B. J. A., Verberk, W. C. E. P., Dorenbosch, M., Cocheret de la Morinière, E., Nagelkerken, I., & Van der Velde, G. (2007). Habitat selection during settlement of three Caribbean coral reef fishes: Indications fordirected settlement to seagrass beds and mangroves. *Limnology and Oceanography*, *52*, 903–907. https://doi.org/10.4319/lo.2007.52.2.0903

Power, M. E. (1984). Depth distributions of armored catfish: Predator-induced resource avoidance? *Ecology*, *65*, 523–528. https://doi.org/10.2307/1941414

Quicazan-Rubio, E. M. (2019). *Swimming performance and morphology of pregnant fish*. Wageningen University.

Quicazan-Rubio, E. M., van Leeuwen, J. L., van Manen, K., Fleuren, M., Pollux, B. J. A., & Stamhuis, E. J. (2019). Coasting in live-bearing fish: The drag penalty of being pregnant. *Journal of the Royal Society Interface*, *16*, 1–10. https://doi.org/10.1098/rsif.2018.0714

R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Reznick, D. N., Butler, M. J. IV, Rodd, F. H., & Ross, P. (1996). Life-history evolution in guppies (*Poecilia reticulata*) VI. Differential mortality as a mechanism for natural selection. *Evolution*, *50*, 1651–1660.

Reznick, D. N., Mateos, M., & Springer, M. S. (2002). Independent origins and rapid evolution of the placenta in the fish genus *Poeciliopsis*. *Science*, *298*, 1018–1020. https://doi.org/10.1126/science.1076018

Reznick, D. N., Meredith, R., & Collette, B. B. (2007). Independent evolution of complex life history adaptations in two families of fishes, live-bearing halfbeaks (Zenarchopteridae, Beloniformes) and Poeciliidae (Cyprinodontiformes). *Evolution*, *61*, 2570–2583. https://doi.org/10.1111/j.1558-5646.2007.00207.x

Reznick, D. N., & Miles, D. B. (1989). A review of life history patterns in poeciliid fishes. In G. K. Meffe & F. F. Snelson (Eds.), *Ecology & evolution of livebearing fishes (Poeciliidae)* (pp. 125–148). Prentice Hall.

Rodewald, A. D., & Foster, S. A. (1998). Effects of gravidity on habitat use and antipredator behaviour in three-spined sticklebacks. *Journal of Fish Biology*, *52*, 973–984. https://doi.org/10.1006/jfbi.1998.0646

Rosenzweig, M. L. (1981). A theory of habitat selection. *Ecology*, *62*, 327–335. https://doi.org/10.2307/1936707

Rosenzweig, M. L. (1991). Habitat selection and population interactions: The search for mechanism. *The American Naturalist*, *137*, S5–S28. https://doi.org/10.1086/285137

Sainmont, J., Thygesen, U. H., & Visser, A. W. (2013). Diel vertical migration arising in a habitat selection game. *Theoretical Ecology*, *6*, 241–251. https://doi.org/10.1007/s12080-012-0174-0

Schlosser, I. J. (1988). Predation risk and habitat selection by two size classes of a stream cyprinid: Experimental test of a hypothesis. *Oikos*, *52*, 36–40. https://doi.org/10.2307/3565979

Seigel, R. A., Huggins, M. M., & Ford, N. B. (1987). Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia*, *73*, 481–485. https://doi.org/10.1007/BF00379404

Sempeski, P., & Gaudin, P. (1995). Size-related changes in diel distribution of young grayling (*Thymallus thymallus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *52*, 1842–1848. https://doi.org/10.1198/tech.2005.s287

Sibly, R., & McFarland, D. (1976). On the fitness of behavior sequences. *The American Naturalist*, *110*, 601–617. https://doi.org/10.1086/283093

Sih, A. (1980). Optimal behavior: Can foragers balance two conflicting demands? *Science*, *210*, 1041–1043. https://doi.org/10.1126/science.210.4473.1041

Swing, C. K. (1992). *Influences on the instream distribution of* Astyanax fasciatus *in a small river in Costa Rica*.

Thibault, R. E., & Schultz, R. J. (1978). Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). *Evolution*, *32*, 320–333. https://doi.org/10.2307/2410999

Trexler, J. C., Tempe, R. C., & Travis, J. (1994). Size-selective predation of sailfin mollies by two species of heron. *Oikos*, *69*, 250–258. https://doi.org/10.2307/3546145

Turner, C. L. (1937). Reproductive cycles and superfetation in poeciliid fishes. *Biological Bulletin*, *72*, 145–164.

Vinne, V., Tachinardi, P., Riede, S. J., Akkerman, J., Scheepe, J., Daan, S., & Hut, R. A. (2019). Maximising survival by shifting the daily timing of activity. *Ecology Letters*, *22*, 2097–2102. https://doi.org/10.1111/ele.13404

Werner, E. E. (1984). The ontogenetic niche and species interaction. *Annual Review of Ecology and Systematics*, *15*, 393–425.

Werner, E. E., & Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. *Ecology*, *69*, 1352–1366. https://doi.org/10.2307/1941633

Whitfield, A. K., & Cyrus, D. P. (1978). Feeding succession and zonation of aquatic birds at False Bay, Lake St Lucia. *Ostrich*, *49*, 8–15. https://doi.org/10.1080/00306525.1978.9633504

Wourms, J. P. (1981). Viviparity: The maternal-fetal relationship in fishes. *American Zoologist*, *21*, 473–515. https://doi.org/10.1093/icb/21.2.473

Zúñiga-Vega, J. J., Macías-Garcia, C., & Johnson, J. B. (2010). Hypotheses to explain the evolution of superfetation in vivparous fishes. In M. C. Uribe & H. J. Grier (Eds.), *Viviparous fishes II* (pp. 241–253). New Life Publications.

Zúñiga-Vega, J. J., Reznick, D. N., & Johnson, J. B. (2007). Habitat predicts reproductive superfetation and body shape in the livebearing fish *Poeciliopsis turrubarensis*. *Oikos*, *116*, 995–1005.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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