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PARASITISM IN VIVIPAROUS VERTEBRATES: AN OVERVIEW

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GENERAL INDEX

RESUMEN

Esta tesis consiste en dos capítulos, el primero es una revisión bibliográfica que desarrolla la interacción hospedero-parásito en hembras de especies vivíparas, enfocándose en los efectos que el parasitismo tiene sobre la reproducción. El segundo capítulo describe resultados de un trabajo empírico que se realizó en colaboración con Natalia Tepox Vivar, en donde se describe la dinámica de infección de líneas isogénicas de un gyrodactílido en guppies silvestres.

La revisión se enfocó en desarrollar los rasgos generales de la viviparidad,un modo reproductivo que ha evolucionado de forma independiente en diferentes taxa donde las crías se desarrollan dentro de las hembras para asegurar la gestación. En este tipo de reproducción, las crías reciben un suministro de alimento en el huevo a través de tejidos especializados que aseguran su desarrollo gracias al intercambio específico de nutrientes y otros componentes. Sin embargo, los desafíos ambientales, como el parasitismo y las enfermedades, pueden ser una fuerza que limite los recursos del hospedero y provoque cambios fisiológicos, morfológicos y de comportamiento que representen un costo adicional, tanto para la hembra preñada como para su descendencia. Esta revisión integra literatura publicada entre 1980 y 2021 sobre el parasitismo de los hospederos vivíparos, con énfasis en las interacciones huésped-parásito. Primero, damos información sobre las características generales de la viviparidad en hembras en diferentes taxones desarrollando acerca de su origen y regulación. Esto incluye la inversión reproductiva futura de las hembras, la tasa de sexo en su descendencia, la inversión en lactancia en mamíferos, alteraciones de los intervalos entre nacimientos, la inversion reproductiva actual, variación entre entornos, respuesta del sistema immune frente a desafios immunologicos, así como factores adicionales que pueden afectar la interacción entre hembras vivíparas y parásitos. El mantenimiento del embarazo conlleva costos en el manejo de los recursos de la madre

y en la regulación de las respuestas del sistema inmunológico hacia la descendencia, manteniendo simultáneamente una actividad aceptable para combatir parásitos y patógenos en la hembra. Los parásitos podrían ser un mediador significativo de este modo reproductivo: las hembras parasitadas cambian su inversión en supervivencia y reproducción en función de su historia de vida, los factores ambientales a los que están expuestas y la diversidad de parásitos que encuentran.

El capítulo dos presenta un estudio en donde describimos la dinámica de infección de líneas isogénicas de un gyrodactílido a nivel de infrapoblación (infección en un pez individual) y nivel de suprapoblación (la infección en un grupo de peces) en guppies de una población mexicana, usando experimentos de corto y largo plazo. Además, analizamos si el lugar de origen en el hospedero afecta la dinámica del parásito posteriormente; para ello, comparamos la prevalencia de la infrapoblación de gyrodactílidos de peces parasitados con un gusano inicial desprendido de la parte anterior de un pez donante y otro con un gusano inicial desprendido de la parte posterior de un pez donante. La dinámica de infección de los guppies mexicanos fue similar a la de estudios previos sobre este sistema huésped-parásito; es decir, encontramos una alta susceptibilidad y mortalidad, siendo dos días post infección la prevalencia más baja de girodactilidos *Gyrodactylus turnbulli* Turnbull, 1956. Asimismo, la carga parasitaria y duración de las infecciones fue similar entre infrapoblaciones de peces parasitados con un gusano inicial desprendido de anterior y anterior. partes posteriores del cuerpo de los peces donantes. El presente estudio contribuye al conocimiento de la dinámica *Gyrodactylus*-guppy bajo un nuevo contexto geográfico y evolutivo. Sin embargo, se necesitan más estudios para comprender si el origen de los gusanos que se mueven de un pez previamente parasitado a un nuevo huésped está relacionado con los ciclos de vida y la dinámica de transmisión de *Gyrodactylus* nativos de Trinidad y Tobago, los guppies y sus gyrodactílidos componen uno

de los sistemas huésped-parásito más importantes para estudiar el parasitismo, el proceso epidémico y la transmisión de ectoparásitos. En la actualidad, los guppies y gyrodactílidos están muy extendidos por todo el mundo, sin embargo, falta información sobre la dinámica de infección de estas nuevas poblaciones a pesar de que representan registros invasivos más altos.

Palabras clave: Reproducción, gestante, gestación, parásito, parasitismo, infección, disyuntiva, rasgo de historia de vida, *Gyrodactylus*, ectoparásito, guppy, guppies.

PARASITISM IN VIVIPAROUS VERTEBRATES: AN OVERVIEW

ABSTRACT

Viviparity is a reproductive mode that has evolved independently in different taxa where offspring develop inside females to ensure gestation. Offspring are provided with a food supply in the egg or through specialized tissues that ensure their development thanks to the specific exchange of nutrients and other components. However, environmental challenges such as parasitism and disease can be a force that limit the host's resources causing physiological, morphological, and behavioural changes that represent an additional cost for both the pregnant female and her offspring. This review integrates the main literature published between 1980 and 2021 regarding parasitism of viviparous hosts, with an emphasis on host-parasite interactions. We first give information on the general characteristics of viviparity in females in different taxa with its origin and regulation. This includes the future reproductive investment on females, sex rate in their offspring, lactation investment in mammals, alterations of birth intervals, the current reproduvtive investment, variation between environments, the activity of the immune system facing immunological challenges, as well as additional factors that can affect the interaction between viviparous females and parasites. The maintenance of pregnancy entails costs in the management of the mother's resources and in the regulation of the immune system's responses towards the offspring, while simultaneously maintaining an acceptable activity to fight parasites and pathogens in the mother. Parasites could be a significant mediator of this reproductive mode: parasitized females change their investment in survival and reproduction based on their life history, the environmental factors they are exposed to, and the diversity of parasites they encounter. ***Key words:*** *Reproduction, pregnant, parasite, parasitism, infection, trade-off, life history trait.*

INTRODUCTION

Traditionally, life-history evolution in viviparity has been explained in terms of selective forces like predation which can directly alter mortality rates, and consequently some life history traits responded more strongly to this factor (Jennions & Telford 2002; Riesch et al. 2013; Gorini-Pacheco et al. 2018; Hagmayer et al. 2020c). However, other forces like parasitism can also confer costs that greatly affect the hosts' fitness. Because parasites are ubiquitous in nature, it is likely that parasitism has influenced different traits in organisms with viviparous reproduction. Knowledge about the influence of parasitism on traits in viviparity has focused on mammals, as they are the main exponents of this reproductive strategy, as well as their economic and ecological importance (Dubey 2009; Reichel et al. 2013; González-Warleta et al. 2014; Arranz-Solís et al. 2015). But little is known about the effects that parasitism has on life history traits in non-mammalian viviparous organisms like in elasmobranchs, teleost fishes (Kawaguchi & Sato 2018), amphibians and reptiles (Blackburn 2018), and if these changes are reflected in their fitness and confer trade-offs in the investment of resources at their traits, causing changes in the life history depending on the different environmental conditions and pressures.

The objective of this review was to integrate the information regarding viviparous reproduction and its interaction with parasitism. We summarise relevant information about viviparity and how viviparous females deal with parasites in a wide taxonomic range of vertebrates. We begin our review with some general aspects of viviparity and its origin in different taxa, we then describe general trade-offs in this reproductive mode caused by conflicts between resource allocation and the immune system. Next, we characterized host-parasite interaction in different viviparous organisms, explaining the effect of the infection on different life-history traits of reproducing females, and their offspring. Finally, we provide an overview of the main viviparous traits that evolved in females to contrapose this antagonistic interaction and how relevant parasitism could be for the evolution of this reproductive mode compared to other selective pressures.

METHODOLOGY

We performed an extended search to collect information about parasitism in five different vertebrate taxa: elasmobranchs, teleost fishes, amphibians, reptiles (Squamata) and mammals. Birds and testudines were excluded because they are not viviparous. In our search criteria, we included published and grey literature (i.e. research that is either unpublished or has been published in non-commercial form) because in some taxa, like viviparous reptiles and amphibians, there is not enough information from published indexed articles; some guidelines recommend the inclusion of grey literature to avoid bias and to not exclude valuable information (Aromataris & Pearson 2014; Sayer 2018; Nakagawa et al. 2019; Haddaway et al. 2020). The consulted databases were Web of science, Science Direct and Google Scholar. In our search, we used the following keywords and their interaction:

“viviparity”, “placenta”, “matrotrophy”, “parasite”, “parasite-host”, “immune response”, “squamate”, “mammals”, “elasmobranch”, “teleost fish”, “poeciliid”, “Poeciliidae” “fecundity”, “trade-off”, “reproductive investment”, “hormone”. We searched publications in a date range of 41 years, from 1980 to 2021; the oldest sources provided the background for the topic, whereas recent research papers represent the current state of the knowledge. Some old articles were excluded due to outdated information. We only included studies that explicitly tested how reproduction (e.g., pregnancy, lactation) interacted with a parasitic infection in females. From our initial search we identified 3,020 publications, of which 214 fulfilled the selection criteria (Figure 1).

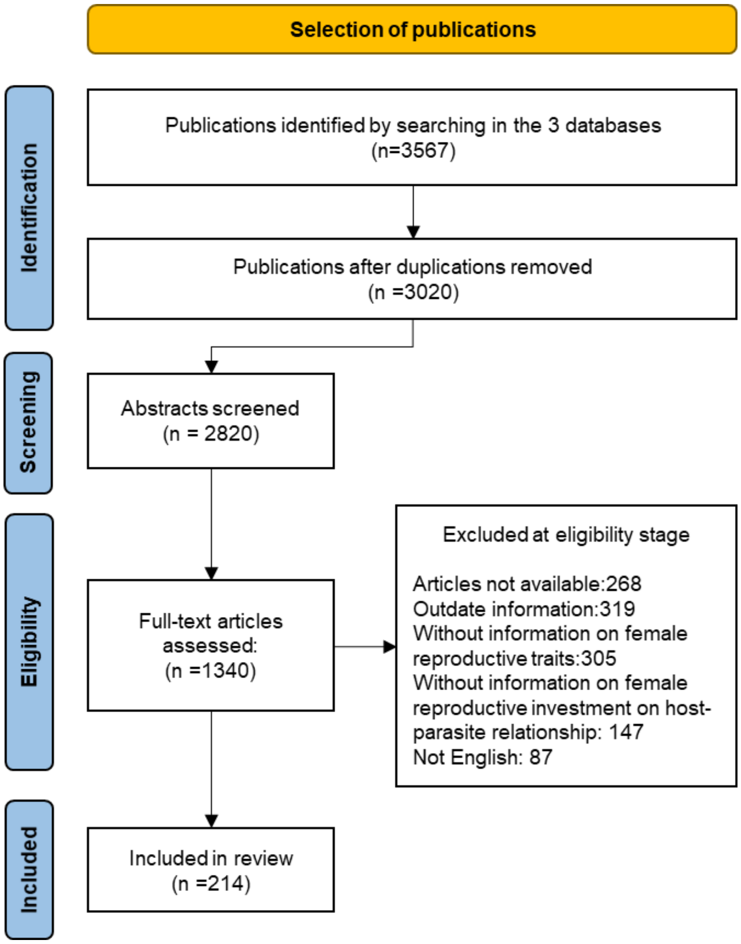

Figure 1: PRISMA Flow Diagram of the different phases of the systematic review.

VIVIPAROUS REPRODUCTION IN VERTEBRATES: ORIGIN AND CHARACTERIZATION

Viviparity is an evolutionary innovation that increases survival and improves offspring's condition by allowing the offspring to develop within the mother's body (Banet et al. 2016). This strategy is associated with internal fertilization and the retention of eggs caused by the secretion of hormones like progesterone (Custodia-Lora & Callard 2002). Additionally, viviparity entails complex physiological adaptations to support intrauterine life and to birth a young, in which the essential adaptations of the uterus include enhanced secretory function and/or oxygen exchange, expansion to accommodate the embryos, osmoregulation, waste disposal, and protection of the young (Hamlett, 1989). That is why viviparous females tend to have higher metabolic costs compared to oviparous species (Foucart et al. 2014). The functional and morphological modifications in viviparous females play a central role to understand the mechanisms that promote this reproductive mode in some taxa and the constraints for its evolution in other groups.

There are two main forms of maternal care: matrotrophy and lecithotrophy. Lecithotrophy (vitellogenesis) is the maternal investment of nutrients made prior to fertilization, where embryos acquire nutrients from the yolk sac (Wourms et al. 1988); whereas in matrotrophy the mother directly provides nutrients to the developing embryos through nutritional secretions in the uterus (histotrophic nutrition), when the embryos feed on eggs produced by the ovary (oophagy), they feed on other embryos (adelphophagy), or when there is the formation of a placenta with an intimate association of embryonic and uterine tissues that allows nutrients transmission (Reznick & Yang 1993; Hamlett et al. 2005; Sato et al. 2016; Buddle et al. 2019). Both forms of maternal provisioning are not mutually exclusive. Facultative matrotrophy species being an investment on yolk in the egg prior to fertilization and a transfer of supplementary nutrients during gestation (Figure 2) (Marsh-Matthews et al. 2005).

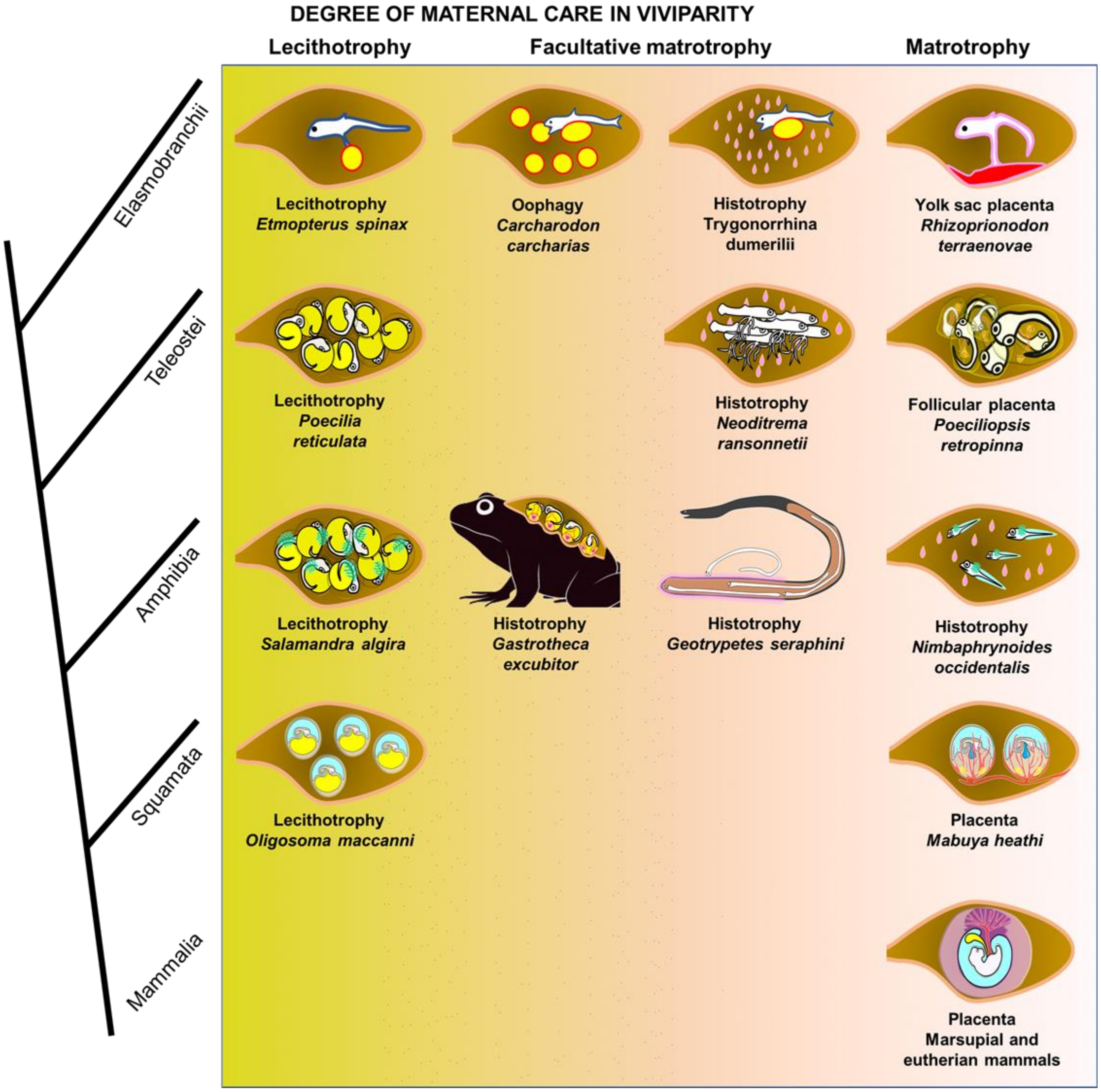

Figure 2: Diverse modes of maternal care in different taxa: The presence of different forms of maternal inversion in viviparous vertebrates is represented by a gradient that goes from lecithotrophic inversion

(left), the ancestral form of viviparity, to matrotrophic inversion (right), that can occur in a complementary way (facultative matrotrophy) or as a primary resource provisioning.

Viviparity has evolved from oviparity independently at least 150 times across nearly every major vertebrate lineage (Blackburn 2015). The presence of viviparity can be appreciated in the oldest known record of fossilized vertebrate embryos, the placoderm fish *Watsonosteus fletti,* from the Middle Devonian (Givetian) (Newman et al. 2020). This reproductive influenced the diversification rate of organisms like cartilaginous fishes (Chondrichthyes) which exhibit 7 multiple independent origins of viviparity (Dulvy & Reynolds 1997; Musick & Ellis 2005; Buddle et al. 2019; Mull et al. 2022).

Similarly, in teleost fishes like Cyprinodontiformes, viviparity also evolved independently multiple times (Reznick et al. 2002; Helmstetter et al. 2016) and this kind of reproduction appears to be much easily gained than lost in poeciliids (Pollux et al. 2009). For example, in Poeciliidae the two kind of reproductive adaptations, lecithotrophy and matrotrophy, are present (Reznick et al. 2007). Drag reduction seems to be one of the driving forces behind the evolution of a placenta in livebearers; for example, *Poeciliopsis turneri*, a placental poecilid, has an advantage in its swimming performance at the beginning of the interbrood interval compared to *Poeciliopsis gracilis,* a non-placental species (Plaut 2002; Ghalambor et al. 2004; Fleuren et al. 2018). In *Poeciliopsis retropinna,* pregnant females exposed to high predation have smaller eggs and lower reproductive allocation, suggesting that in poeciliids the degree of placentation can also be linked with the degree of predation risk (Hagmayer et al. 2020b; Furness et al. 2021). The maternal provisioning mode has shaped the evolutionary rate in this group, with the lecithotrophic linage having twice speciation than placentotrophy (Furness et al. 2019).

Not all the matrotrophic viviparous fish develop a placenta. The surfperch, *Neoditrema ransonnetii* (Embiotocidae), is histotrophic, their foetuses develop an hypertrophied hindgut to take up maternally-supplied ovarian fluid that contain fish acid glycoprotein, and transthyretin to play a role in foetal development in a similar way as thyroid hormone distributor proteins in mammals (Ueda et al. 2016; Nakamura et al. 2020). Another peculiar reproductive adaptation for viviparity in fish is present in seahorses (genus *Hippocampus,* Syngnathidae): pregnant males provide supplementary nutrition to embryos, and in this case the physiological and genetic changes facilitating male pregnancy share homology with the genes involved in the reproductive function of pregnant mammals, reptiles, and other live-bearing fish (Whittington et al. 2015). Viviparity in fishes however, is more an exception than a rule: 420 of an estimated 600-800 species of chondrichthyans are viviparous, whereas only 510 of an estimated 27,000 species of teleosts are viviparous (Wourms 1981; Wourms & Lombardi 1992; Reznick et al. 2002).

In amphibians, viviparity has been gained and lost at a lower rate than in fishes and it seems that it evolved in steps, often considered complex, since it entailed numerous physiological adaptations between the mother and offspring (Furness & Capellini 2019). They have extensive homoplasies in the evolution of viviparity, in which nearly all the forms are yolk dependent and only a few species provide maternal nutrients during the rest of gestation (Wake 2015). Most viviparous amphibians are caecilians (order Gymnophiona), where viviparity has evolved at least four times (Gower et al. 2008). Some species provide nutrients via maternal dermatotrophy through rich lipids contained in their epidermal cytoplasm, which is considered a precursor of oviduct feeding and the ancestral state for the evolution of viviparity in caecilians (Reinhard 2014). Viviparity in caecilians allows a better maternal control of embryonic water balance and because the young are fully metamorphosed when they are born, an aquatic larval period is not required (Gower et al. 2008). That is probably why viviparity has facilitated the colonization and diversification of amphibians within a terrestrial environment (San Mauro et al. 2014). A popular example of viviparity in amphibians is given by the marsupial frog, *Gastrotheca excubitor* (Hemiphractidae), which in fact is considered an analogue of viviparity, because they incubate embryos in a pouch that is highly vascularized to accommodate the eggs; offspring use their external fused gills to absorb dissolved nutrients that crossed the eggs membranes from the pouch lumen (Warne & Catenazzi 2016). Additionally, these eggs have a larger size with significant yolk reserve and high developmental speed compared to mammals (del Pino 2018). Meanwhile, the viviparous Nimba toad (*Nimbaphrynoides occidentalis*) represent a highly matrotrophy investment in Anura with small yolk-poor eggs retained within the lower part of the oviduct with a nutrient provisioning by oviductal liquid microscopic whitish droplets, and a gestation time of nine months. The newborn Nimba toads are 15 times larger and 200 times heavier than the egg (Sandberger-Loua et al. 2017).

Viviparous Squamates, the largest order of reptiles, are predominantly lecithotrophic with some members specialized in matrotrophy provisioning like Skinks of *Mabuya* genus that exhibit a highly degree of placentotrophy and specializations for maternal–fetal nutrient transfer (Blackburn & Vitt 2002; Ramírez-Pinilla 2006; Hernández-Díaz et al. 2017). Viviparity has evolved independently in more than 100 lineages of squamate reptiles (Blackburn 2006; Blackburn 2015). The evolution of viviparity in this group was driven by cold climate and the pattern of maternal provision. The transitions to viviparity is associated with historically relatively cold climate conditions, in which hatching success increase by prolonged “uterine” (maternal-temperature) retention of eggs at high elevations in the field, and the use of thermoregulatory behaviour to shorten embryonic developmental time (Shine 2005; Ma et al. 2018; Recknagel et al. 2021). The embryonic uptake of calcium unique to squamates which differs from oviparous species primarily in the timing of uterine calcium secretion (Stewart & Ecay 2010). In live-bearing squamates, the total reproductive investment per brood, offspring sizes or brood sizes relative to maternal body size is almost identical to oviparous species because most of the egg mass is due to components (such as water stores and the eggshell) not required for oviductal incubation (Meiri et al. 2020). However, there is a cost in reproduction, like in pregnant New Zealand skinks (*Oligosoma maccanni*), that show a high oxygen demand that decreases the upper thermal tolerance in late pregnancy, compared with other adult life-history stages, but this disappears after giving birth thanks to upregulated systems for oxygen delivery during pregnancy (Virens & Cree 2019). The reduced rates of evolution and lower diversification in some life-history traits (offspring size and mass) observed in this taxon suggest this is a potentially costly process that enhances offspring survival at an increased risk of female mortality (Zúñiga-Vega et al. 2016).

Mammals are the main representatives of viviparous vertebrates. They are divided into three major lineages that diverged from a common ancestor: monotremes (Monotremata), placentals (Eutheria) and marsupials (Metatheria) (Phillips et al., 2009). Monotremes lay eggs, while marsupials and eutherian mammals combined make up the subclass Theria, in which the young does not develop in an egg but inside the mother's uterus (Luo et al. 2011; Deakin et al. 2012). Their foetuses are carried by the mother until a relatively late stage of development. In this group, viviparity evolved before the most recent common ancestor of marsupial and eutherian, within the therian steam linage 180-150 million years ago, and is a synapomorphy (Griffith & Wagner 2017). The placenta in mammals has a wide range of functions supported by genes that evolved following gene duplication events (Carter 2012). Its evolution was driven by resource allocation conflict in a rapid antagonistic coevolution between the female and its offspring's demand of resources (Mess et al. 2003).

The placenta exhibits a high degree of structural diversity because of the formation of cell layers that improve oxygen transfer; in addition, high-affinity foetal haemoglobins play a key role in placental gas exchange. In both marsupials and eutherians, the embryo implantation in the uterus is facilitated by inflammatory reactions, which is an evolutionary heritage from the ancestral condition for live-bearing mammals (Mor et al. 2011); in eutherians, this process is also sustained by an extended anti-inflammatory period between implantation and parturition (Griffith et al. 2017). Many extant mammals form the chorioallantoic placenta, an endocrine organ that has direct access to the mother's blood vessels for nutrients (Strauss et al. 1996; Mess & Carter 2007; Cruze et al. 2012). Mammal reproduction is a complex process featuring extensive maternal allocation which varies in intensity through the reproductive period of gestation and feeding (Langer 2008). Even when food is sufficiently available, the direct cost of reproduction is represented by a high demand of resources during embryo development and also increased costs during lactation (Speakman 2008).

TRADE-OFFS RELATED TO VIVIPARITY AND THE IMMUNE SYSTEM

Viviparity is costly. The trade-offs presented with viviparity are given by a higher energy expenditure in females, since offspring care must be maintained for a greater duration of time and at a greater consumption of resources (Auer 2010; Olsson et al. 2016; Tobler & Culumber 2018); in other words, there is a reallocation of resources that carry physiological costs when resources are limited (Rauw 2012). Females can allocate their current and future resources in reproduction or survival (Stearns 1989), depending on whether they acquire resources in advance and store them (capital breeders) or if they adjust their food intake concurrently with breeding without reliance on store (income breeders) (Jönsson & Jonsson 1997). Therefore, fertility and growth rate can be affected by a change in food intake. For instance, in the lecithotrophic guppy *Poecilia reticulata*, the ovarian width and volume, and gonad weight increased with food with high concentration of carbohydrates and lipids and low protein, without altering their fecundity and fertility (Dahlgren 1980). Conversely, the matrotrophic poeciliid *Heterandria formosa* produced small offspring with low access to food and large offspring with high amount of food (Reznick, 1996). This pattern is similar to what is observed in the matrotrophic reptile grass skink, *Pseudemoia entrecasteauxii*: when availability of food is low, there is a reduction of offspring developmental success, placental nutrient transport, offspring size, maternal growth and body condition (Van Dyke et al. 2014). Both strategies, capital or income breeders, show particular trade-offs, and in fluctuating environments lecithotrophic strategy is more likely to occur, compare with matrotrophic strategies that benefit more with the constant access to food sources (Molina-Moctezuma et al. 2020).

This resource reallocation of limited resources to different life history traits during pregnancy proposes a competition with the immune system (Schmid-Hempel 2003). In different vertebrates, the regulation by hypothalamic-pituitary-gonadal (HPG) axis ensures the close cooperation between body energy status, reproductive activity, and immune function; the evolution of viviparity shaped this neuroendocrine-immune relationship (Segner et al. 2017). The protection of the foetus and foetal membranes from the mother's immune system is mediated by the regulation or inhibition of the immune response (Abrams & Miller 2011; Erlebacher 2013), the participation of complement system (Sunyer & Lambris 1998) and the continued participation of sex steroid hormones like oestrogen, which can affect the function of the innate and adaptive immune systems (Nadkarni & McArthur 2013). Indeed, a basic component of the immune system regulation is given by sex hormones, like in the cottonmouth (*Agkistrodon piscivorus*), in which an elevated concentration of progesterone maintains uterine tissue, ovum, and embryos, and a following reduction in plasma bacteria lysis capacity (Graham et al. 2011).

In the viviparous fire salamander (*Salamandra salamandra*), the levels of immunosuppression in pregnant females are higher compared with non-pregnant salamanders, immunoglobulin M (IgM) and α2-macroglobulin seem to be responsible for the immunosuppression during pregnancy (Badet 1984). In the viviparous lecithotrophic nurse shark (*Ginglymostoma cirratum*): the eggs are provided with Immunoglobulin G (IgG) for protection, reduced risk of infections and successful parturition (Haines et al. 2005). The participation of cytokines like interleukin-1 (IL-1) in the lecithotrophic lizard *Zootoca vivipara* plays a role in the immunoregulatory processes, allowing the establishment and maintenance of pregnancy (Paulesu et al. 2005). The expression of classical and non-classical MHC-1 in marsupial and eutherian mammals regulates the survival of the mammalian foetus at the maternal-foetal interface (Buentjen et al. 2015)

In the Atlantic sharp-nosed shark (*Rhizoprionodon terraenovae*) the presence of the lymphoid aggregates in the shark placenta plays a role in maintaining pregnancy during all stages of gestation and the presence of placental cells resemble the mammalian uterine NK cells and melanomacrophages (Haines et al. 2006). In mammals, to ensure a robust pregnancy and placentation, the presence of CD4 regulatory T cells are essential to inhibit effector immunity, contain inflammation and support vascular adaptation facilitating trophoblast invasion and placental access to maternal blood supply (Robertson et al. 2018).

In European bats (*Myotis daubentoniid*), there is a clear influence of the female reproductive state, pregnant and lactating, on both humoral and cellular immune parameters with increased IgG concentrations and enhanced haemolysis during lactation (Ruoss et al. 2019). In some cases, like in Brandt's voles (*Lasiopodomys brandtii*), the immune response was not supressed in lactating females, and particularly in mothers with larger litter size, this response was even increased, for example, in their total IgG (Xu et al. 2012).

No matter what the outcome of parasitism is for viviparous females, their immune system defies a double challenge: to tolerate the foreign growing foetus and to fight off infections that could affect both the mother and the foetus (Nahmias et al. 2011). Because pregnant females are limited in resources as they invest in multiple systems to maintain reproduction, they face significant challenges when their body condition is altered by external stressors. That is why pathogens and parasites generate trade-offs for resource allocation between the mother, her investment in the immune system and the maintenance of her offspring.

PARASITISM IN VIVIPAROUS FEMALES

Parasitism is an ecological interaction considered a powerful selective force, where the parasite benefits from the resources of one or more hosts, while the host is harmed by having additional costs generated by the parasite (Poulin 2007). The parasite-host interaction is a coevolutionary arms race relationship that generates a long-term series of fixation events occurring sequentially or even in parallel in both hosts and parasites (Poulin & Morand 2000; Rabajante et al. 2015; Gösser et al. 2019). Parasitism facilitates the maintenance of sex and it strongly influences the evolution of reproductive traits (Hamilton 1980; Milinski & Bakker 1990; Jokela et al.

2009; Arakelyan et al. 2019). In a host-parasite interaction, host resistance to infection is associated with their individual variation in immune response, and their relative condition exert significant impacts on parasite prevalence and infection intensity (Scott & Anderson 1984). For instance, in guppies when body condition of the host is high, the parasite burden of *Gyrodactylus turnbulli* increases (Tadiri et al. 2013). The type of parasite (ecto- or endoparasite) that infects the host is another factor that influences the course of an infection (Rubenstein & Hohmann 1989; Gooderham & Schulte-Hostedde 2011).

In the same species, the sexes can show different responses to parasite infestations, and this is evident across a range of taxa. For example, males of yellow-necked mice *(Apodemus flavicollis*) have high parasite intensity of intestinal roundworm (*Heligmosomoides polygyrus*) and their behaviour influences the dissemination of infective stages of the parasite, leading to increased rates of ingestion, and a weak immune response compared with females that have a better response to the infection decreasing their parasite burden (Ferrari et al. 2007). Male pipefish (*Syngnathus typhle*) have a more active immune system than females, a sign that the sex with higher investment in reproduction has more cells from the adaptive immune system with a more specific immune response (Roth et al. 2011). Parasitism has usually been studied in males to evaluate its effect on their body condition (Kennedy et al. 1987; Houde & Torio 1992; Buchholz 1995; Moore & Wilson 2002; Ezenwa & Jolles 2008) and sexual behaviour (Polak & Starmer 1998; Kolluru et al. 2009; Ezenwa & Snider 2016). A clear difference between males and females is the main sex hormones produced. In males, testosterone exerts immune suppressive effects, thereby increasing the susceptibility to diseases. In females, oestrogens at levels of ovulatory phase or pregnancy suppress cytotoxicity of natural killer cells to regulate the activity in the inflammatory process of pregnancy (Giefing-Kröll et al. 2015; Klein & Flanagan 2016).

Viviparous females show a variety of mechanisms to improve defences against parasites, including changes in their physiology and behaviour that can affect life-history parameters (Minchella 1985). Females gain fitness through increased longevity, that is why they invest relatively more in immune functions in order to increase their survival probability (Rolff 2002), releasing immune cells like macrophages and components like cytokines, which perform many specific functions at the defence and at the maternal-foetal interface (Pulendran 2004; Renaud & Graham 2008; Ueda et al. 2016). The difference in female investment may vary between ectotherms that invest more in innate immune system, and endotherms that invest more in adaptive immune system (Sandmeier & Tracy 2014). The growing studies in infected pregnant females in nature reveals range evidence with different effects in reproduction (Table 1).

Table 1: Studies of the effects of parasitism on viviparous females across different taxa

TAXON	SPECIE	MATERNAL CARE	PARASITE(S) / IMMUNOLOGICAL CHALLENGE	EFFECTS	REFERENCES
ELASMOBRANCH	Brown lantern shark *Etmopterus unicolor*	Lecithotrophy	Mesoparasitic barnacle *Anelasma squalicola*	Reduced and irregular egg Reduced mature eggs	Yano & Musick 2000
	Atlantic sharp-nosed shark *Rhizoprionodon terraenovae*	Facultative matrotrophy	Nematode	Damage to gonads and reproductive passageways	Borucinska & Adams 2013
TELEOST FISH	Poeciliid *Poeciliopsis retropinna*	Matrotrophy Placenta	Trematode *Uvulifer*	Reduced offspring size and condition Eggs not affected in fertilization	Hagmayer et al., 2020

	Mosquitofish *Gambusia affinis*	Facultative matrotrophy	Acanthocephala *Neoechinorhynchus*	Reduced litter size Tissue damage (Liver)	Deaton 2011; Carpenter & Herrmann 2020a
			Nematode *Eustrongylides ignotus*	Reduced litter size Reduced fertility	Deaton 2011
			Cestode *Schyzocotyle acheilognathi*	Increased litter size	(Carpenter & Herrmann 2020b)
			Trematode *Uvulifer*	Increase female size Increased fertility	(Cureton et al. 2011)
SQUAMATA	Spotted skink *Carinascincus ocellatus*	Facultative matrotrophy	Reptile mite *Ophionyssus natricis*	Symptoms of anaemia Stillbirth offspring	Atkins & Wapstra 2004
	McCann's skink *Oligosoma maccanni*	Lecithotrophy	Chigger mite *Odontacarus lygosomae*	Symptoms of anaemia Stillbirth offspring	Hare et al. 2010
	viviparous garter snake *Thamnophis elegans* Rapid-life ecotype	Facultative matrotrophy	Trematode *Alaria*	Increased litter size and weight Reduced immune system function	Palacios & Bronikowski 2017
	viviparous garter snake *Thamnophis elegans* Slow-life ecotype	Facultative matrotrophy	Trematode *Alaria*	Reduced immune system function	Palacios & Bronikowski 2017
MAMMAL	Asian elephant *Elephas maximus*	Matrotrophy Placenta	Nematode *Paramphistomum*	Increased immune system function	Lynsdale et al. 2017
	Grey squirrels *Sciuris carolinensis*	Matrotrophy Placenta	Flea *Orchopaeus howardii* Louse *Neohaematophinus sciurinus* Apicomplexa *Eimeria* Nematode *Trypanoxyuris (Rodentoxyuris) sciuri* Nematode *Trichostrongylus retortaeformis* Nematode *Trichuris*	Increased energy reserve and body fat	Scantlebury et al. 2010
	Franklin's ground squirrels *Poliocitellus franklinii*	Matrotrophy Placenta	Flea *Oropsylla (Opisocrostic) bruneri*	Increased production of female offspring in highly infected females	Pero & Hare 2018
	Bank voles *Myodes glareolus*	Matrotrophy Placenta	Nematode Mastophorus muris	Increased parasite load	Grzybek et al. 2015
	Wild mice *Mus musculus*	Matrotrophy Placenta	Nematode *Heligmosomoides polygyrus*	Increased offspring size	Kristan 2004

CONTINUED

MAMMALS	Sundevall's jird *Meriones crassus*	Matrotrophy Placenta	Flea *Xenopsylla ramesis* *Parapulex chephrenis*	Increased offspring weight in small litter Increased weight of male offspring	Warburton et al. 2017
	Cairo spiny mouse *Acomys cahirinus*	Matrotrophy Placenta	Flea *Xenopsylla ramesis* *Parapulex chephrenis*	Without modifications	Warburton et al. 2017
	Deer mice *Peromyscus maniculatus*	Matrotrophy Placenta	Trematode *Schistosomatium douthitti*	Increased offspring weight Decreased mother survival	Schwanz, 2008
	Red deer *Cervus elaphus*	Matrotrophy Placenta	Helminth *Elaphostrongylus cervi* Trematode *Fasciola hepática*	Increased levels of specific antibodies against helminths Increased parasites load Increased interbirth interval	Albery et al. 2020 Albery et al. 2021
	Soay sheep *Ovis aries*	Matrotrophy Placenta	Gastrointestinal nematodes	Increased parasite load	Leivesley et al. 2019
	Dall's sheep *Ovis dalli dalli*	Matrotrophy Placenta	Nematode *Marshallagia marshalli*	Reduced fetus size and weight Increased production of male offspring in heavily infected females	Aleuy et al. 2020
	Spotted hyena *Crocuta crocuta*	Matrotrophy Placenta	Nematode *Ancylostoma*	Increased parasite load	East et al. 2015
	Gelada monkey *Theropithecus gelada*	Matrotrophy Placenta	Platyhelminthe *Tenia*	Increased interbirth interval Increased female mortality	Nguyen et al. 2015
	Mandrill *Mandrillus sphinx*	Matrotrophy Placenta	Simian retrovirus Protozoa *Plasmodium*	Increased activity in immune system cells	Dibakou et al. 2020
	Baboon *Papio cynocephalus*	Matrotrophy Placenta	Helminth *Trichuris trichiura* *Abbreviata caucasica* *Streptopharagus pigmentatus*	Reduced fertility Increased parasite load Increased interbirth interval	Akinyi et al. 2019
	Chacma baboons *Papio ursinus*	Matrotrophy Placenta	Roundworm *Oesophagostomum* Nematode *Protospirura* Roundworm *Trichuris*	Increased parasitic load	Habig et al. 2021
	Chimpanzee *Pan troglodytes schweinfurthii*	Matrotrophy Placenta	Helminth *Oesophagostomum* Amoeba *Iodamoeba*	Increased parasitic load Increased time resting Decreased feeding time	Phillips et al., 2020
	Human *Homo sapiens*	Matrotrophy Placenta	Protozoa *Plasmodium falciparum*	Alteration in blood flow of the umbilical and uterine artery Increased intrauterine growth restriction Reduced offspring weight Premature birth Loss of the fetus Symptoms of anaemia	Desai et al. 2007; Griffin et al. 2012; Rogerson et al. 2018
			Nematode *Ascaris lumbricoides*	Decreased interbirth intervals	Blackwell et al. 2015
			Hookworm Ancylostoma	Increased interbirth intervals Late age at first birth	Blackwell et al. 2015

The mere presence of parasites may cause significant tissue damage in females, carrying negative consequences for reproduction, either directly or indirectly. Some parasites can affect the development of reproductive organs, like in females brown lantersharks (*Etmopterus unicolor*) infected with a mesoparasitic barnacle (*Anelasma squalicola*), in which infected females have a smaller and irregular ovum and the number of ova is lower compared with non-parasitized females (Yano & Musick 2000). The presence of a nematode parasite can interfere with reproduction by damaging the gonads and/or reproductive passageways in the Atlantic sharp-nosed shark (*Rhizoprionodon terraenovae*) (Borucinska & Adams 2013).

Parasitism usually modifies the host's behaviour and its resource allocation (Giorgi et al. 2001), causing a reduction in activity level to decrease the pathology caused by the infection (Li et al. 2020). Most importantly, parasites can directly affect their host's reproduction; these costs are measured in terms fertility loss (Lin et al. 1990; Heins & Baker 2014) and field observations indicate a strong relationship between reproductive effort and prevalence of parasitism (Festa-Bianchet 1989). Parasitized females sometimes reduce their current reproductive effort. For instance, in the placental livebearer *Poeciliopsis retropinna,* a heavily infection by a trematode parasite (*Uvulifer* spp) produces smaller offspring and in worse condition at birth, while egg size and quality at fertilization remain unaffected (Hagmayer et al., 2020). Facultative matrotrophy female western mosquitofish (*Gambusia affinis*), with a yolk deposited in oocytes and a degree of nutrient transfer from maternal tissues (Marsh-Matthews et al. 2005), decrease brood size as a consequence of liver damage by Acanthocephala *Neoechinorhynchus*; when mosquitofish females are infected with the nematode *Eustrongylides ignotus*, females reduce brood size and some females even do not develop any brood, decreasing their fecundity (Deaton 2011). Females of the spotted skink (*Carinascincus ocellatus*), a viviparous species endemic to Tasmania, decrease their condition with symptoms of anaemia and their offspring are stillbirth when they are heavily parasitized with reptile mites, *Ophionyssus natricis* (Atkins & Wapstra 2004); the same effect is observed in McCann's Skinks (*Oligosoma maccanni*) infected with chigger mites, *Odontacarus lygosomae* (Hare et al. 2010).

The difference between the reproductive responses of hosts to parasitism could be tied to differences in their life-histories (Minchella 1985; Agnew et al. 2000). For example, the viviparous garter snake (*Thamnophis elegans*) has two life-history strategies, the fast-living lakeshore ecotype and the slow-living meadow ecotype; gravid females of both ecotypes show lower immune function, i.e. lower t-lymphocyte proliferation, than non-reproductive females, but those with the fast life-history invest more in current reproduction producing larger and heavier litters (Palacios & Bronikowski 2017). Two rodents of the family Muridae, the solitary females Sundevall's jird (*Meriones crassus*) and the social Cairo spiny mouse (*Acomys cahirinus*), have different responses to parasitism that seem to be related to their parental investment. While in the Cairio spiny mouse there does not seem to be a change in the reproductive investment due to flea infection, in Sundevall's jird the reproductive investment changes depending on the size of the litter. Offspring from small litters gain more body mass compared to large litters that gain less body mass in infected females (Warburton et al. 2017). For larger mammals with greater longevity, the commitment to fight parasites is greater for the senescence (Kirkwood & Rose 1991; Nussey et al. 2012), and because they have more chance of being infected multiple times and become susceptible to mortality more frequently than animals with shorten lifespan (Castle et al. 2007). In roe deer (Capreolus capreolus) infected with gastrointestinal strongyles and Trichuris spp, the innate and adaptive immune response showed senescence in older adults (> 7 years) with increased parasite load due to decreased adaptive immune system and decreased functional innate immune traits (phagocytic capacity of neutrophils and activity of leukocytes) (Cheynel et al. 2017).

A modification of female reproductive investment can directly affect offspring sex ratio. Females in better body condition are more likely to have sons, like in the nailtail wallaby, *Onychogalea fraenata*, in which condition appears to improve with age, and older, more experienced mothers are able to devote more resources to produce more males than females (Fisher 1999). Females in poor condition tend to produce more females than males, for example, in Franklin's ground squirrels (*Poliocitellus franklinii*), females with low ectoparasite load of the flea *Oropsylla* (*Opisocrostic*) *bruneri* produce higher proportion of male offspring in comparison with highly infected females (Pero & Hare 2018). Pregnant females Dall's sheep, *Ovis dalli dalli*, infected with the nematode *Marshallagia marshalli*, produce lighter and smaller foetuses; however, contrary to what is usually expected, females in good body condition, which typically have low parasite intensity, are more likely to carry female than male foetuses (Aleuy et al. 2020).

Lactation is considered a high-cost component of reproduction. For example, lactation is associated with increased strongyle infection (*Elaphostrongylus cervi*) in female red deer (*Cervus elaphus*); (Albery et al. 2020). In spotted hyenas (*Crocuta crocuta*), females that are nursing twins have more parasites of the nematode *Ancylostoma* than females nursing a single young and non-reproductive females; the higher the social status, the lower the parasite load, probably because dominant females have access to more resources, including food, than subordinate females (East et al. 2015). To compensate its high cost, lactation usually requires a substantial rise in food intake. For instead, to face the cost of nursing offspring, female bank voles (*Myodes glareolus*), a small rodent that lives in woodland areas, forage more invertebrates, some of which are infected with the stomach nematode *Mastophorus muris,* so as a consequence, females increase their parasite load (Grzybek et al. 2015). In female chimpanzees (*Pan troglodytes schweinfurthii*) there is an increase in parasites shedding (counts of eggs, cysts and larvae) as a reflect of high prevalence, intensity and richness por parasites (*Oesophagostomum* and *Iodamoeba*) with pregnancy and age, and lactating females from populations with lower food availability spend more time resting and less time feeding in comparison to females with more access to food (Phillips et al., 2020). Nursing female grey squirrels (*Sciuris carolinensis*) augment their energy reserve and body mass to avoid compromising their investment in parasite defence during the energetic demands of lactation against ectoparasites flea *Orchopaeus howardii* and the louse *Neohaematophinus sciurinus*, and endoparasites coccidia (*Eimeria* sp.) oocysts and nematodes *Trypanoxyuris* (*Rodentoxyuris*) *sciuri*, *Trichostrongylus retortaeformis* and *Trichuris* spp (Scantlebury et al. 2010).

Another reproductive trait altered by parasitism is the interbirth interval, which is the period in between two consecutive births. In female red deer, survival probability is strongly affected by helminth *E. cervi* and trematode *Fasciola hepatica* stimulated the production of specific antibodies against helminths and increased interbirth interval in the year following their infection (Albery et al. 2021). Parasite richness in wild female baboons (*Papio cynocephalus*) is associated with low fecundity, higher parasite burdens and long interbirth interval; particularly, females infected with the parasitic roundworm Trichuris trichiura tend to have elevated glucocorticoids and longer gestations (Akinyi et al. 2019). This pattern is similar in gelada monkeys (*Theropithecus gelada*) infected with worms of the genus *Tenia*: parasitized females exhibit longer interbirth intervals and increased mortality than non-infected females (Nguyen et al. 2015). Interbirth interval in humans seems to also be affected by the presence of parasites, for instance, the infection with roundworms (*Ascaris lumbricoides*) in humans is associated with early age at first birth and short interbirth intervals, whereas hookworm (Ancylostoma) infection is correlated with late age at first birth and long interbirth interval (Blackwell et al. 2015). Most of these results should be carefully considered, given that association not always describes causation, and other variables like social determinants of health might be playing a strong effect in the data collected.

In humans, the prevalence of pathogens is consistent with areas of low economic resources and high congregation of people (McKenna et al. 2017; Abbaszadeh Afshar et al. 2020), and pregnancy seems to make women more vulnerable to infection (Francis et al. 2007; Doritchamou et al. 2012). For instance, in Ethiopia, pregnant women experienced more severe infections with intestinal parasites than their non-pregnant counterparts, and the infections were stronger in women who were pregnant for the first time (Derso et al. 2016). Infection with malaria in pregnant women is associated with low birthweight and it is more likely to cause serious disease, preterm birth and foetal loss (Desai et al. 2007). Furthermore, the first trimester is recognised as an important risk factor for miscarriage, foetal growth restriction and maternal anaemia (Rogerson et al. 2018). Specifically, malaria parasite in early pregnancy affects uterine and umbilical artery blood flow, altering placentation and angiogenesis, and ultimately increasing the risk of intrauterine growth restriction (Griffin et al. 2012) However, this pattern is not always the same in other primates; for example, wild mandrills (*Mandrillus sphinx*) exposed to a suite of parasites, like simian retroviruses and malaria agents, show high activity by immune cells but this does not depend on the female reproductive state, so pregnant females are not more vulnerable than non-reproductive females (Dibakou et al. 2020).

Conversely to the examples described above, parasitized females can sometimes increase the relative value of their current reproductive effort. For example, mosquitofish females infected with the trematode (*Uvulifer* spp) are larger and have higher fecundity than uninfected females (Cureton et al. 2011), and females infected with the cestode (*Schyzocotyle acheilognathi*) invest more in their current reproduction producing larger brood sizes than uninfected females (Carpenter & Herrmann 2020a). Female deer mice (*Peromyscus maniculatus*) highly infected with the trematode *Schistosomatium douthitti* decrease survival, but increase their reproductive output, producing litters of greater mass (Schwanz, 2008). In a wild population of soay sheep (*Ovis aries*), females that gave birth, and particularly those that weaned a lamb, have high gastrointestinal nematodes, representing a higher cost than when they are gestating (Leivesley et al. 2019).

PARASITISM AND ENVIRONMENTAL CONDITION

There are not many macroecological studies that allow us to integrate the relationship between parasitism level, microhabitat use and female reproductive strategies in viviparous vertebrates. However, it is acknowledged that the trade-offs between reproduction and the immune function are associated with features from the host's environment, which in turn reflect different life-history strategies in the host (Martin et al. 2008; Budischak & Cressler 2018; Downs et al. 2018). Poeciliids are the most popular livebearers both in aquaculture and in the laboratory. These fish experience great population diversity across the rivers they inhabit, however, little is known about how parasitism has influenced this diversity. For instance, the guppy has almost 80 species of parasites, and one study found 21 parasite species in 18 populations in Trinidad (Mohammed et al. 2020). In the *Gyrodactylus*-guppy interaction, the parasite does not generally show strong local adaptation to their sympatric guppy host, but guppies could be locally adapted to their sympatric parasite (Pérez-Jvostov et al. 2015). Factors such as the origin of the guppy population, the parasite strain and the size of the host may explain the variation in host survival, with larger guppies and those from the upper Aripo, a small and less genetically diverse population, showing low survival rate (Cable & van Oosterhout 2007).

Some abiotic factors such as temperature, humidity or waterfall influence parasitic infection for the hosts. For example, the diversity of parasites that infect Mosquitofish varied through time and among populations, and there is a relationship between increased waterflow and increased diversity of parasites (Carpenter & Herrmann 2020b). In Chacma baboons (*Papio ursinus*) helminth infection intensity is associated with two of the most energetically costly stages of the reproductive cycle, pregnancy and lactation; in this system, patterns of rainfall are important predictors of parasite prevalence and intensity, in which for some parasites infection intensity is greater during summer dry season (*Protospirura* and *Trichuris*), and for other parasites their intensity is greater during the wet winter months (*Oesophagostomum*) (Habig et al. 2021).

Finally, there are also biotic factors that affect parasitic infection in females such as physiological condition, feeding behaviour and diet. The deep sea shark (*Etmopterus spinax*) can host different parasites (ecto- and endoparasites) that may be more abundant depending on the abundance of prey that serves as intermediate host of parasites by its wide diet range (mainly carideans and euphausiids crustaceans, and bathypelagic fish), and larger sharks had a significantly higher prevalence of the parasite herring worm (*Anisakis simplex*) and *A. squalicola* (Isbert et al. 2015; da Rocha 2019).

EVIDENCE FROM LABORATORY MODELS

Testing animals in laboratory conditions provides evidence to understand generalized mechanisms and it also serves as a good analogue to study broad principles. Most of the results described so far in this review used wild populations to study parasitism in viviparous females, but a lot of what we know about the host-parasite interaction comes from controlled experiments carried out in the laboratory (Table 2).

Table 2: Animals used in experimental tests that evaluate reproduction in parasitized viviparous females.

LABORATORY MODELS					
TAXON	**SPECIE**	**MATERNAL CARE**	**PARASITE(S) IMMUNOLOGICAL CHALLENGE**	**EFFECTS**	**REFERENCES**
ELASMOBRANCH	Viviparous rays *Trygonorrhina dumerilii*	Matrotrophy Histotrophy	Capture/Manipulation	Decreased female weight Decreased offspring size	Guida et al. 2017
SQUAMATA	Viviparous lizard *Zootoca vivipara*	Facultative matrotrophy	Sheep red blood cells	Increased time to spent basking Reduced litter weight Increased energy spent on pregnancy	
	Viviparous snake *Sistrurus miliarius*	Facultative matrotrophy	Lipopolysaccharide	Reduced plasma bactericidal capacity Reduced litter weight Increased activity of the complementary immune system	Meylan et al. 2013
MAMMAL	Sundevall's jird *Meriones crassus*	Matrotrophy Placenta	Flea *Xenopsylla conformis mycerini* *Xenopsylla ramesis*	Increased flea immunity	Khokhlova et al. 2004
	Dunkin Hartley guinea pig *Cavia porcellus*	Matrotrophy Placenta	Protozoa *Toxoplasma gondii*	Abortions	Lopes et al. 2007; Montoya & Remington 2008; Grochow et al. 2021
	Lab mice *Mus musculus*	Matrotrophy Placenta	Protozoa *Plasmodium berghei*	Abortions Embryo resorption Reduced intrauterine growth Stillbirth offspring Reduced litter size Reduced offspring weight Postnatal mortality Reduced offspring growth	Hviid et al. 2010
		Matrotrophy Placenta	Nematode *Heligmosomoides polygyrus*	Reduced offspring size	Kristan 2002

	Lab mice BALB/c *Mus musculus*	Matrotrophy Placenta	Protozoa *Tritrichomonas foetu*	Abortions	Barbeito et al. 2008; Woudwyk et al. 2015
	Sprague dawley rat *Ratus norvegicus domestica*	Matrotrophy Placenta	Tenia *Hymenolepis diminuta*	Reduced waking time Reduced retrieval time in their offspring	Willis & Poulin 1999
	Blackface sheep *Ovis aries*	Matrotrophy Placenta	Protozoa *Neospora caninum*	Lesions in placenta and fetus Reduced reproductive performance Abortions Foetal reabsorption	González-Warleta et al. 2014

Artificial immune challenges are used to test the host's reactions to a component that activates the immune response in a specific moment or state of the organism (Poxton 1995; Spencer et al. 2006; Uller et al. 2006; Watzke et al. 2007). Low body condition females of the lizard *Zootoca vivipara* responded to an immune challenge with sheep red blood cells by increasing the time they spent basking; they also decreased litter mass and increased energetic expenditures during pregnancy, in comparison to females in good body condition (Meylan et al. 2013). Similarly, the metabolic response to an experimental immune challenge with lipopolysaccharide was costly for females of the viviparous snake *Sistrurus miliarius*, which had reduced plasma bactericidal ability; their pregnancy was associated with an increased activity of immune complements and a reduction in their litter mass (Lind et al. 2020).

The use of animal models is a common practice in medical research, they have been used extensively to address aspects on human disease, including reproductive issues (Amann 1982; Wall & Shani 2008; Hviid et al. 2010; Vargas-Villavicencio et al. 2016). For example, the use of rodents can complement studies in which placental barrier is breached by different kind of infections, studying maternal illness and long-term deleterious effects (Krishnan et al. 2013). Female mice (*M. musculus*) with malaria infection (*Plasmodium berghei*) expose striking similarities with pregnant women in placental pathology, susceptibility and the expression of variant surface antigens specific in their immune responses (Hviid et al. 2010). The Dunkin Hartley guinea pig (*Cavia porcellus*) is a suitable animal model to study human congenital toxoplasmosis. Both women and pregnant guinea pigs parasitized with a high dose of *Toxoplasma gondii* oocytes have offspring losses, particularly if this is during the first weeks of pregnancy, but a high probability of abortion continues during all the pregnancy, because if the gestational stage at infection is at the third trimester it also ends lethally for most litters (Lopes et al. 2007; Montoya & Remington 2008; Grochow et al. 2021).

The BALB/c mice is a conventional model to test the effects of parasites on reproductive traits, for example, the pathogenesis of genital trichomonosis has been studied in mice infected with *Tritrichomonas foetu*. When females are infected, increased pregnancy loss in early and middle stage of gestation, where embryo death occurs (Barbeito et al. 2008). The induction of the apoptosis is an additional mechanism involved in the pathogenesis of the early embryonic-death that occurs during *T. foetu* infection, being the increase in cell proliferation a compensatory host response (Woudwyk et al. 2015).

The spread of disease in livestock animals represents a problem, and controlled experiments can help to examine the susceptibility of pregnant females in terms of clinical and pathological parameters. For instance, female Blackface sheep (*Ovis aries*) infected with *Neospora caninum* develop placental and foetal lesions, decreasing the reproductive performance (González-Warleta et al. 2014). Also, the stage of gestation and maturity of the foetus influences the outcomes: females infected at early stages of gestation results in pregnancy loss with high parasite burden in placenta and foetal viscera, while at late stage infected females delivered viable lambs with low parasite burden (Buxton et al. 1998; Arranz-Solís et al. 2015).

The conditions in which animals used for experiments are kept may cause different immune responses, that is why the outcome of a parasite infection sometimes is different between wild and laboratory organisms of the same species. For example, when the rodent Sundevall's jird is parasitized with different flea species (*Xenopsylla conformis mycerini* and *Xenopsylla ramesis*) and its habitat is an outdoor covered circular enclosure, there is a heterospecific resistance compared with organisms kept in a laboratory (housed individually in plastic cages); interestingly, immune-naïve animals whose mothers were parasitized by fleas had some degree of immunity against fleas independently of their habitat (Khokhlova et al. 2004). In an experimental infection with, parasitized wild female mice *M. musculus* with nematode *Heligmosomoides polygyrus* increased their reproductive investment by producing larger offspring at birth, and their offspring cleared their own infection; in contrast, parasitized laboratory females with *H. polygyrus* produced smaller daughters at birth (but not male offspring) and pups has a greater infection intensity (Kristan 2002; Kristan 2004).

Controlled experiments in the laboratory are also useful to understand the effect of confounding variables, the variables that are not measured in the experiment but that influence the results of the relationships studied. For example, to carry out experiments, animals need to be manipulated, and this stressor factor can sometimes be confounded with other stressors like the presence of parasites. When pregnant viviparous rays (*Trygonorrhina dumerilii*) are captured, they exhibit a significantly reduced maternal post-partum body mass and neonatal size caused by an alteration of the immune function and the energetic cost of self-maintenance (Guida et al. 2017). It is possible that other viviparous species may similarly be affected when they are manipulated.

OTHER ELEMENTS TO CONSIDER IN THE PARASITE-VIVIPAROUS FEMALE INTERACTION

The environment and genotype of a mother can influence her offspring's phenotype in parallel with the offspring's own genotype and the environmental conditions it experiences. In that sense, mothers have substantial capacity to affect their offspring's traits (Crockford et al. 2020; Malalaharivony et al. 2021). Because of that, maternal effects can have important repercussions on the population dynamics because this an important source of phenotypic variation (Moore et al. 2019). For instance, deer mice infected with schistosome parasites wean heavier offspring and this extra mass persists until adulthood, leading to an increase of fitness through enhanced survival and reproductive success (Schwanz, 2008). Also, in Sundevall's jird infected with the flea *X. ramesis*, maternal and grandmaternal infestation status affects pre-weaning body mass gain in male pups (Warburton et al. 2019).

Controlled experiments in the laboratory have been key to understand how parasitism affects pregnant and postpartum females, particularly at a proximal level.

However, more work should integrate how parasites interact with the viviparous mode of reproduction in natural conditions so that we can ultimately recognise how selective pressures shape the evolution of the immune system. Parasites are likely to affect a small proportion of the entire population, with specific hosts being at particular risk. For larger mammals with greater longevity, the commitment to fight parasites is greater because they have more chance of being infected multiple times and become susceptible to mortality more frequently than animals with shorten lifespan. In Asian elephants (*Elephas maximus*), males, juveniles, and elderly adults are more susceptible to infection and to have high parasite burdens than pregnant females, which are at lower risk of parasite-associated mortality than non-reproductive females (Lynsdale et al. 2017).

Similar selection pressures can produce different response in life-history traits. Predation and parasitism are similar because both can have coevolutionary antagonistic outcomes between host and preys on one hand, and predator and parasites on the other. However, in predation the fitness of the prey is abruptly lost due to an interruption of its survivorship; in parasitism the host is affected detrimentally but it often survives after being infected (Stevens 2010). These two selective forces, predation, and parasitism could act together generating interesting interactions. Female Sprague dawley rats, *Ratus norvegicus domestica*, an albino rat used in medical research, retrieve their pups to the safety of cover more quickly and spend less time checking for potential danger if they are infected with the tapeworm *Hymenolepis diminuta* (Willis & Poulin 1999). In the livebearer *P. reticulata,* predation has generally a more consistent and a stronger effect than parasitism on behaviour; often parasites have milder and more transient effects (Intensity and virulence) that might impose weaker selection and tend to favour plastic response (Jacquin et al. 2016). All the agents of selection can vary with different environmental conditions, for example, downstream guppy populations experience high predation and in upstream populations the high density population increased interspecific competitive ability in foraging (Reznick & Travis, 2019). It would be interesting to test whether there is an interaction between the predation gradient experience by different populations of guppies and the level of parasitism they experience.

CONCLUSIONS

Viviparism is an evolutionary innovation that increases the fitness of the females by improving their reproductive success at a higher parental investment. The placental functions and resource provisioning in fishes, reptiles and mammals are based on similar genetic pathways associated with pregnancy (Brandley et al. 2012; Whittington et al. 2015). Viviparity has independently originated in different taxa through the development of analogous structures and physiological responses that allow the interaction between the offspring and the mother. In most cases, it encourages diversification (except reptiles), and it is considered a trait that once obtained is difficult to lose due to the complexity of its function and maintenance, providing advantages in the provision of resources and offering greater security to the offspring.

The evolution of viviparity shapes the relationship that exists between the endocrine and immune systems for the maintenance of pregnancy, which involves the participation of immune cells and sex hormones. Viviparous females must deal with the continuous regulation of their own immune system to prevent the embryos from being eliminated, but also to be able to use the immune system to deal with pathogens (Figure 3). Parasitized females can either increase their investment into current reproduction by providing more for their offspring during pregnancy or postpartum, e.g., lactation and care, or parasitized females can first deal with the infection to ensure their survival by reducing their investment in reproduction. These responses are not isolated and depend on a variety of factors, for instance, food availability reduces the costs of mounting an immune response, and seasonal changes in the environment can favour the physical condition of the host, as well as the intensity of the infection and the richness of the parasites in the host population. The immune system is just one component of the diverse, interacting physiological processes that underpin the function of the whole-organism (Maizels & Nussey 2013).

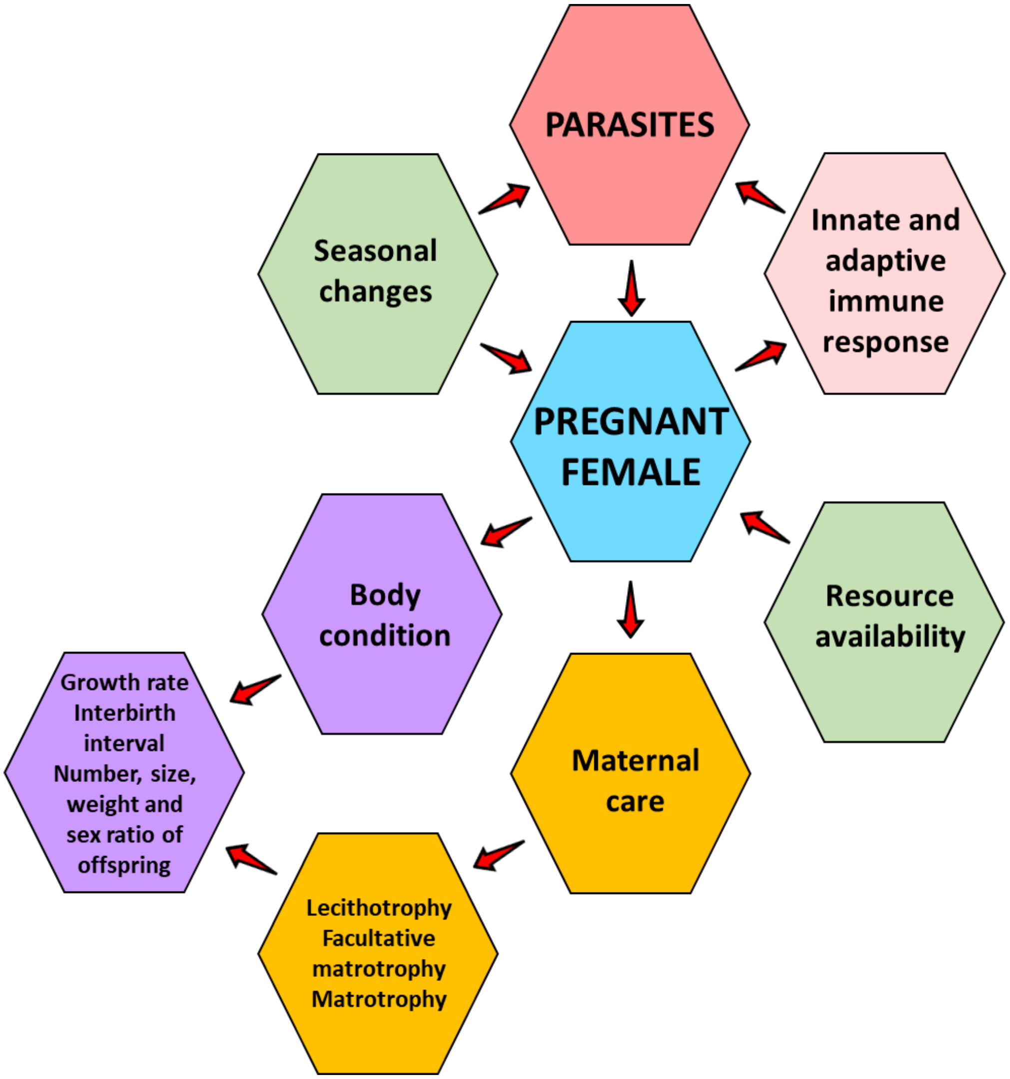

Figure 3: Schematic representation of the factors interacting during the host-parasite relationship. Pregnant females are in constant pressure by different factors that alter their reproductive investment. Their parasites, the seasonal changes in the environment and resourse availability determine how the resources are accesible and distributed for the immune system, self-maintenance and maternal care.

In this review we present a vast set of studies that describe the interaction between parasites and viviparous females in different contexts represented in a variety of taxa. Reproducing females of viviparous species frequently face increased costs under parasitic infections compared to non-reproducing females. The study of the interaction between parasitism and reproduction not only gives information on the costs that females face, but also the costs on the next generation in how offspring respond when they are infected.

Most of the research in this regard has been carried out in the laboratory, for example, mice and cattle are usually tested in preclinical research, toxicology, environmental health, and veterinary medicine (Langendam et al. 2021). However, wild animals studied under natural conditions are also valuable because they can provide more information about how the immune response is affected by trade-offs originated by infection costs that consequently alter reproductive traits in females. For humans, parasitism usually has negative effects on different reproductive traits such as fertility, changes in birth interval and higher offspring mortality, particularly earlier in pregnancy (Blackwell et al. 2015; Anderson et al. 2020).

The limitations of viviparity are related to the kind of maternal supply, lecithotrophic or matrotrophic, which can generate conflicts between the demand of resources that are required for self-maintenance or for reproduction. However, if the environmental factors are optimal and the general condition of the females is adequate, it is possible for females to deal with the infection of parasites without compromising reproduction or survival. Studying the cost of parasitism on different reproductive modes will allow us to expand our knowledge on how females deal with infections and whether each reproductive mode generates specific trade-offs during this interaction. Additionally, there is still a need to include more non-mammalian organisms in the parasite-host research and to investigate the direct and indirect effects on reproduction. For example, host-parasite interaction in amphibians is still limited to provide a few general information on how their immune system interacts with bacteria on their skin and how it resists lethal pathogens like fungus *Batrachochytrium dendrobatidis* (Bd) (Catenazzi et al. 2018; Latney & Klaphake 2020). Studies on parasitism in amphibians that include reproduction are also restricted to oviparous species, like in females corroboree frog (*Pseudophryne corroboree*) and whistling tree frog (*Litoria verreauxii*) that increase their provisioning to eggs and the size of their sex organs when they are infected (Brannelly et al. 2016).

The independent emerge of viviparity in different taxa is a striking example of an evolutionary innovation that converges in the care and maintenance of the offspring inside females, and supports the value of considering life history, immunity, and parasitism simultaneously to examine the fitness consequences of viviparity.

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EXPERIMENTAL INFECTIONS OF *GYRODACTYLUS TURNBULLI* ISOGENIC LINES ON MEXICAN WILD GUPPIES

This empirical study was carried out in colaboration with Natalia Tepox-Vivar. We planned the experiment, collected the data, analysed it and wrote the following text together. This chapter is also presented in Tepox-Vivar's master thesis (Transmission dynamics of ectoparasitic gyrodactylids (Platyhelminthes, Monogenea): An integrative review), published in December 2021.

ABSTRACT

Natives from Trinidad & Tobago, guppies and their gyrodactylids compose one of the most important host-parasite systems to study parasitism, epidemic process, and ectoparasite transmission. At present, guppies and gyrodactylids are widespread around the globe; however, there is a lack of information about infection dynamics of these new populations despite the fact that they represent higher invasive records. In this study, we describe infection dynamics of gyrodactylid isogenic lines at infrapopulation level (infection in an individual fish) and suprapopulation level (the infection in a group of fish) on wild guppies from a Mexican population, using short and long-term experiments. In addition, we compare gyrodactylid infrapopulation prevalence of parasitized fish with an initial worm detached from anterior part of a donor fish and other one with an initial worm detached from posterior part of a donor fish. Infection dynamics of Mexican guppies were similar to the ones of previous studies on this host-parasite system; that is, we found a high susceptibility and mortality, being two days post infection the lowest prevalence of gyrodactylids *Gyrodactylus turnbulli* Turnbull, 1956. Also, parasite burdens and duration of infections were similar between infrapopulations of fish parasitized with an initial worm detached from anterior and posterior body parts of donor fish. The present study contributes to the knowledge of *Gyrodactylus*-guppy dynamics under a new geographical and evolutive context. However, more studies are needed to understand if the origin of worms that move from a previous parasitized fish to a new host are related to life cycles and transmission dynamics of *Gyrodactylus*.

Keywords: monogeneans, poeciliidae, invasive species, translocation.

INTRODUCTION

The host-parasite system composed by guppies (*Poecilia reticulata* Peters, 1959) and *Gyrodactylus turnbulli/Gyrodactylus bullatarudis* Harris, 1986 has been investigated extensively to understand evolutionary patterns of parasitism (Cable and Van Oosterhout 2007a, b; King and Cable 2007; Van Oosterhout et al. 2003, 2007), ectoparasite epidemic process and their transmission dynamics (Scott 1982; Scott and Robinson 1984; Cable et al. 2002; Stephenson et al. 2017, 2019; Tadiri et al.2016, 2018, 2019). For instance, experimental infections in the laboratory show that these parasites change host features that effects their fitness, such as behaviour (Kolluru et al. 2003, 2005; Croft et al. 2011; Reynolds et al. 2018; Stephenson 2019), mate choice (Kennedy et al. 1987; Houde and Torio 1992; López 1999), and immune responses (Kolluru et al. 2003, 2005; Cable and Van Oosterhout 2003, 2007; Konczal et al. 2020a). Recently, studies in transmission dynamics investigate the effect of donor heterogeneity and host behaviour on gyrodactylid epidemic progression (Stephenson et al. 2017; Stephenson 2019) and genome analysis are determining the molecular basis of parasite adaptation at macroevolutionary scales in gyrodactylids from Trinidad (Konczal et al. 2020 a,b; Konczal 2021).

Most of these studies including those in parasite dynamics have been tested with guppies and gyrodactylids from Trinidad & Tobago (Cable and Van Oosterhout 2007a, b; Van Oosterhout et al. 2003, 2007; Schelkle et al. 2012; Stephenson et al. 2015) and commercial fish from Europe (Richards and Chubb 1996, 1998; King et al. 2009) even though guppies are widespread in at least 72 different countries across the world (Deacon et al. 2011; FIGIS 2021) and gyrodactylids are commonly kept in aquaria and found in wild populations (Trujillo-González et al, 2018; Maceda-Veiga and Cable, 2019; Rubio-Godoy et al. 2010). Mexico is not the exception since, wild guppies are found in many localities such as the Lerma-Santiago River system, the main basin of the Mexican High Plateau (Contreras-MacBeath et al. 1998;FIGIS 2021) whereas the monogenean *Gyrodactylus* is reported in several introduced exotic fish, comprising at least 12 described species in Mexican freshwater fish (Rubio-Godoy et al. 2012), new described species (Rubio-Godoy et al. 2010; García-Vásquez 2019) and several more species without taxonomic identification or catalogued by *Gyrodactylus* sp. (Salgado-Maldonado 2006).

Despite the extensive research on helminths wildlife from Mexico there is limited information about invasive helminths taxonomy (Salgado-Maldonado and Rubio-Godoy 2014) and data regarding to disease dynamics on their main hosts and native Mexican fish. Gyrodactylids were probably introduced to Mexico with their main hosts like “tilapas” and guppies (Salgado-Maldonado and Rubio-Godoy 2014) but, in recent times these parasites have been found in Mexican fishes such as *Poecilia mexicana* Steindachner, 1863 (Salgado-Maldonado and Rubio-Godoy 2014), *Poeciliopsis gracilis* Heckel, 1848 and *Pseudoxiphophorus bimaculatus* Heckel, 1848 (García-Vásquez et al. 2017) reaching a higher invasive score in Mexico (CONABIO 2014). In order to know more about parasite dynamics between guppies and gyrodactylids and to understand their evolutionary and biogeographic history, we described the infection dynamics of *G. turnbulli* on naïve guppies from a Mexican wild population using isogenic lines of worms that were isolated from commercial ornamental fish.

Isogenic lines define a group of organisms sharing the same genotype irrespective of their initial homo- or heterozygous nature (Wenzel and Foroughi-Wehr 1994). Isogenic lines are useful tools to investigate molecular bases of complex traits, as the genetic homogeneity within a line allows the repetition of measurement on the same genetic background through time and in different environments (Fraslin et al. 2020). Since gyrodactylids possess sexual and asexual reproduction with advanced progenesis (Cable and Harris 2002), isogenic lines minimize genetic variation to study their dynamics under laboratory conditions. The process traditionally consists of removing one or two gravid worms from parasitized donor individuals and then waiting for the parasite attachment on the caudal fin of a previous anesthetized recipient fish (Scott 1982). Then, an isogenic line of gyrodactylids is obtained with a single parasite as the beginner of an experimental epidemic (King and Cable 2007; King et al. 2009; Olstad et al. 2009).

Usually, experimental infections are performed with detached worms from the posterior body part of the donor fish (e.g., caudal fin; see Stephenson et al. 2017) or areas with higher worm aggregation. However, studies on transmission dynamics suggest that as the infection progresses, gyrodactylids move from the posterior part of the caudal peduncle to the anterior part (pectoral and anal fins), which may increase the chance of transmission to other fish during the declining phase of the infection (Harris 1988). This could happen because transmission is age and stage dependent as it occurs in *G. turnbulli* on guppies (Harris, 1989) and *G. salaris* on salmon (Harris et al. 1994). These species show higher level of migration (as the movement from one region to another on the fish) and detachment of the individuals that had given birth, in contrast to most new-born parasites which move only short distances (Bakke et al. 2007). Then, it is likely that old gyrodactylids become more active and tend to move to anterior part of its host resulting in new transmission events. So far, it is unknow if experimental infections performed with detached worms from the posterior body part of the donor fish are different to those performed with worms from the anterior body part in terms of successful attachment and posterior suprapopulation growth on new infected hosts.

Early studies of gyrodactylid dynamics indicate that infection in an individual fish (infrapopulation level) starts with the parasite establishment, based on two criteria: 1) the parasite population increases above three parasites; and 2) the fish remains infected at least until day 6 post-infection (Scott and Robison 1984; Scott 1985). Then, peak population occurs on the first 4-6 days followed by a parasite population decline in the host after 10-14 days, when the fish lose their worms (Harris 1988). In other words, the duration of infection in isolated guppies lasts 14 days, when individual fish sheds all its parasites and there is no reinfection in three consecutive days (King and Cable 2007; King et al. 2009).

On the other hand, the infection in a group of fish (suprapopulation level) may depend on contact frequency between host rather than the host density; so even at low densities, the contact rates among hosts are enough to allow transmission and regulate the disease epidemic (Johnson et al. 2011) For instance, when transmission occurs in a group of 24 fish, parasite suprapopulation persists for an average of 62 days (Johnson et al. 2011). However, if the primary infected fish fails to transmit its parasites, the suprapopulation goes extinct within 4-7 days (Johnson et al. 2011). At low densities (less than 10 fish), the gyrodactylid population increases from day 0 to day 10 and then decreases to extinction between days 30 and 40 (Richards and Chubb 1998). In fact, to maintain gyrodactylid population growth in the laboratory it is recommended to add naïve and uninfected fish to the aquarium at regular intervals (Scott and Anderson 1984).

At suprapopulation level, gyrodactylid prevalence varies among populations between females and males (Martin and Johnsen 2007, Fraser and Neff 2010, Gotanda et al. 2013; Stephenson et al. 2015). For example, *Gyrodactylus* prevalence in guppies from Trinidad is higher in females than in males but only in the lower courses of the rivers (Stephenson et al. 2015) which are considered high predation sites (Magurran 2005). Also, female guppies could be super spreading hosts, responsible for many transmission events (Stein 2011), given that they tend to shoal more and therefore have more contact rate with other females than males (Johnson et al. 2011). In addition, since there is a relationship between fish size and parasite burdens, it is suggested that females support heavier parasite burdens (Cable and van Oosterhout 2007; Tadiri et al. 2013). Indeed, only one study directly compared the effects of sex on parasite epidemic dynamics on isolated and groups of guppies from Trinidad (Tadiri et al. 2016). However, more evidence is needed to know if guppies and gyrodactylids show sex-biased parasitism.

In the present study we monitored and described the population dynamics of gyrodactylid isogenic lines on individual isolated parasitized fish (infrapopulation level), and groups of parasitized guppies (suprapopulation level), which include the comparison of parasite burdens between female and male guppies at both levels.

We also tested the differences of parasite burdens and duration of infections of gyrodactylid infrapopulation initiated with a worm detached from the anterior part of donor fish and another detached from the posterior part of a donor fish.

Because gyrodactylids attached to the posterior part of donor fish (pectoral, dorsal, and anal fin) are likely older and mature than gyrodactylids from the posterior part (pectoral, dorsal, and anal fin), we hypothesize that infection abilities of worms depend on their origin from the host, resulting in differences on successful attachment, and posterior suprapopulation growth on newly infected hosts. We also expected that females support higher parasite burdens in comparison to males at supra and infrapopulation level due to greater body size and likely lower resistance of females (Dargent et al. 2015).

MATERIALS AND METHODS

Host fish population

Wild guppies were collected in 2018 and 2019 from Tepeojuma, Puebla, Mexico (grid reference 18º 45´ 12" and 98º 02´ 42"). The fish were housed at the Laboratory of Evolutionary Ecology, Facultad de Ciencias Biológicas, BUAP. Guppies were maintained under laboratory conditions, in 120 L water tanks enriched with artificial plants and gravel, at 24±1 °C on a 12 h white light (20 watts) and 12 h dark photoperiods. Although all fish were naïve to our *G. turnbulli* strain, they were dewormed with Api General Cure ™ two months before starting experimental infections.

Gyrodactylid Isogenic lines

Gyrodactylids were isolated from ornamental guppies that were bought in Puebla, Mexico, in November 2019. The process consisted of isolating 33 worms (i.e., 33 isogenic lines) and used them to infect wild guppies; 26 worms were used to conduct short-term experiments on 26 individual fish (infrapopulation level), and 7 worms to perform long-term experiments on 7 groups of guppies (suprapopulation level).

Infrapopulation level

Infrapopulation level experiments consisted of experimental infections on 26 individual isolated guppies (15 males and 11 females) in 200 ml containers. For this, one worm was transferred from an ornamental guppy with more than 10 parasites (the donor fish) to one sexually mature uninfected wild guppy (the recipient fish) (Figure 4). Donor and recipient fish were manipulated under anaesthesia (0.50 ml of 2-phenoxyethanol in 1 L water bath) in a petri dish, where the fins of the donor and recipient fish were placed next to each other until one individual parasite had transmitted from the donor to the caudal fin of recipient (Stephenson et al. 2017). If the parasite failed to attach, the procedure was repeated with a different fish (King and Cable 2007; King et al. 2009). To answer if infrapopulation prevalence of parasitized fish with an initial worm from the anterior part is different to that of parasitized fish with an initial worm from the posterior part, we conducted the described infections with 7 worms detached from the anterior body part (i.e., pectoral, dorsal, and anal fin) and 19 worms more from the posterior body part (i.e., peduncle and caudal fin) of the donor fish. We only obtained 7 experimental infections with worms from the anterior part, since most donor worms were detached from the posterior body part of donor fish.

The duration of infection, from the day of parasite establishment to the last day of observation (Richards and Chubb, 1996) was recorded in all experiments. Parasite establishment is determined when the parasite population increases above three parasites (Scott and Robison 1984; Scott 1984) and the end of infection as the absence of worms on the host for three consecutive days or when the host died (Harris 1988). Besides, the mortality of infected fish, fish that recovered from infection (i.e., fish that lost? their worms), the presence, number, and position of gyrodactylids were recorder each 48 hrs in every individual fish.

Suprapopulation level

Suprapopulation level experiments involve the isolation of two non-infected fish (one male and one female) with a fish that was infected with one worm from a donor fish (as it was described in the anterior section) in 500 ml containers (Figure 5). The procedure was replicated 7 times. After the experiment started, two new naïve fish (one female and one male) were added every 48 hrs in each group until the parasite population declined.

Here, we also registered the duration of infection, the mortality of infected fish and fish that recovered from infection each 48 hrs. Because we did not mark our fish to distinguish them (i.e., tags, photonic marks), we registered the presence, number, and position of gyrodactylids in 10 randomly fish every 48 hrs in each group of guppies.

DATA ANALYSIS

Because our aim was to describe the infection dynamics of isogenic lines of gyrodactylids in a novel wild guppy population, only descriptive statistics were conducted in the following variables, on both infrapopulation and suprapopulation levels: duration of infection, mortality of infected fish, fish that recovered from infection, number of gyrodactylids on host (parasite burden) and their position on the host through the time.

To assess if the prevalence of gyrodactylid suprapopulation initiated with a worm detached from the anterior body part is different from the one initiated with a worm from the posterior body part of a donor fish, we ran two generalized linear mixed models (GLMM) depending on error family and link function in the lme4 (Bates et al. 2015) for each variable. These are: 1) the parasite burden registered each 48 hrs and 2) the duration of infection of every parasitized fish from infrapopulation level as the response variables. Fixed effects were the body parts where worms were detached from donor fish (the posterior or anterior part) and host sex (female or male) with fish identity as a random effect. We also ran another generalized linear mixed model to test the differences in parasite burden between females and males at suprapopulation level, where the response variable was the parasite burden registered every 48 hrs on parasitized fish from suprapopulations. Fixed effects were the day of infection (0 to day 26) and sex host (female or male), and the identity of experimental group of fishes as random effects. All analyses were conducted in R v.4.1.1 (R core Team, 2021) and ggplot for plotting (Hadley, 2016).

RESULTS

Infrapopulation level

The duration of infection in infrapopulations ranged from 2 to 12 days. Mean duration of infection was 6±2 (SE) days and only 5 individuals maintained a 12-day infection. Seventeen infected fish died and 7 more were recovered from infection (they lost their worms). In general, the number of individual infected fish decreased across time (Figure 6). The parasite burden (number of worms on the host) ranged from 1 to 47 worms. The number of worms registered on each fish depended on the days of infection (Figure 7). Parasite burden data were normally distributed (Shapiro-Wilk test, p =0.60) and seemed to show a positive relationship with days of infection. Mean peak parasite burden was 10±8 (SE) worms and it was registered after 6 days of infection. Females supported a mean of 7.7±11(SE) worms while males 6.37±10 (SE) worms. These parasite loads were not different (GLMM; χ^2= 0.02, d.f=1, *p*=0.88).

Parasite burden increased with time whereas the number of infected fish decreased. Hence, parasite infrapopulation collapsed after the 6th day of infection with host deaths and high worm densities. In fact, the highest parasite loads (47 and 41 worms) were registered from two fish which also supported 12 days of infection.

All infrapopulations started with the attachment of one worm on the caudal fin of the recipient fish. Worm position did not change through time since most of the parasite loads were registered from caudal fin. We observed few migrations from caudal fin to peduncle on the second day of infection as well as, the movement to dorsal and anal fins (gonopodium for males) on the 4th and 6th day of infection.

Body parts where gyrodactylids were detached on the donor fish, anterior or posterior part did not explain parasite burdens (Figure 8. GLMM; χ^2= 0.20, d.f= 1, p=0.65) or the duration of infection at infrapopulation level (Figure 9. GLMM; χ^2= 6.54, d.f=1, p= 0.62). In other words, the prevalence of infrapopulations initiated with a worm detached from the anterior of a donor fish are similar to those initiated with a worm detached from the posterior part of a donor fish.

Suprapopulation level

The duration of infection in suprapopulations ranged from 2 to 26 days, with a mean duration time of 18 ± 9 (SE) days. Because we aggregated 2 naïve fish every 48 hrs in each group, the number of infected fish increased for 14 days. The highest number of infected fish was 19 guppies, and it was registered on the 14th day of infection (Figure 10). From 14th to 26th day, suprapopulations collapsed and declined. We registered in total 14 infected dead fish and 25 fish that recovered from infection. On average one fish died and two were free of worms in every group each 48 hrs.

Parasite burdens fluctuated from 1 to 111 worms. Nevertheless, the number of worms on the hosts varied across time in each group. The mean parasite burden peak was 46±10 (SE) worms, and the highest parasite load (111 worms) was register on the 22nd day of infection (Figure 11). On average, females supported higher parasite loads worms (19.22±24.67 SE) than males (11.61±17.15 SE) and these differences were significant (GLMM; χ^2= 82.39, d.f=1, p=<0.001).

Regarding worm position on the host, most worms were attached on the caudal fin and peduncle. However, we observed the attachment of 13±10 (SE) worms on dorsal, pectoral, and anal fins (gonopodium for males) from the day 20th to 26th of infection time.

DISCUSSION

In the present study, we parasitized wild guppies from a Mexican population with isogenic lines of *G. turnbulli* which were isolated from ornamental guppies. The prevalence of infected fish at infrapopulation level decreased over time, and only five fish supported the infection for 12 days while the number of infected fish at suprapopulation level increased for 14 days and decreased until the 26th day, even though we added new naïve fish every 48 hrs. Besides, female guppies supported higher parasite burdens than males but only at suprapopulation level. Finally, we did not find differences in parasite burdens and duration of infections of gyrodactylid infrapopulations started with worms from anterior and posterior parts of a donor fish.

On average, our guppy population maintained gyrodactylid infection for more than 6 days at infrapopulation level which is the minimum time to determine the successful establishment of *G. turnbulli* population on guppies (Scott and Robison 1984). However, early studies reported that guppies support more than 20 days of infection by *G. turnbulli* in laboratory conditions (Scott 1985). In addition, experimental infections showed that other poeciliids such as *P. picta* Regan, 1913 and *Xiphophorus maculatus* Günther, 1866 can maintain infections of *G. turnbulli* until 12 or 11 days respectively (King and Cable 2007) whereas *G. bullatarudis*, the other gyrodactylid species that parasites guppies, can maintain a prevalence of 22 days on *P. picta*, and 14 and 13 days for *P. sphenops* Valenciennes, 1846 and *X. helleri* Heckel, 1848 (King et al. 2009). On the other hand, duration of infection at suprapopulation level was the lowest reported until now (i.e., 26 days) since in groups of 10 guppies, *G. turnbulli* persist for 91 days, and *G. bullatarudis* for 40 days (Richards and Chubb 1998). Our infra and suprapopulations may have been constituted by few individuals that sustained increasing parasite burdens until they died, and several fishes that were refractory to infection and reinfection.

We suggest that the low prevalence of infected fish at both population levels may be due to the variation of immune host responses. At infrapopulation level, more than a half of infected guppies died, which could reflect a low immune competence of our guppies, resulting in low resistance to a new strain of *G. turnbulli*. However, at suprapopulation level, an average of two fish each 48 hrs managed to lose their worms, which means a higher resistance. Natural variation of resistance against gyrodactylids is reported in guppies from Trinidad since their immune competence could be innate or acquired (Madhavi and Anderson 1985; Cable and van Oosterhout 2007). For instance, guppies from sites with high predation in Trinidad show that almost half of their total variance has heritable genetic basis reaching superior innate immune response than conspecifics from low predation sites (Cable and van Oosterhout 2007). Moreover, guppies from low predation sites showed a reduction of maximum parasite loads during secondary infections, which indicated a higher acquired immunity than their conspecifics from high predation sites (Cable and van Oosterhout 2007). A similar pattern of acquired immune responses is reported in the rainbow trout *Oncorhynchus mykiss* Walbaum, 1972 infected by *G. derjavini* Mikailov, 1975 (Lindenstrøm and Buchmann, 2000).

One aspect that could explain weak immune responses in our study is stress. Because we handled the fish during experimental infections and they were isolated in small recipients, it is likely that guppies experienced high levels of stress. Even though environmental stressors have been suggested to increase host susceptibility, promoting parasite growth and reproduction (Slater and Keymark 1986; Murray et al. 1998; Krasnov et al. 2005), an alternative hypothesis indicates that environmental stress can also cause high host mortality (Agnew and Koella 1999, Jokela et al. 1999; Brown et al. 2000; Bedhomme et al. 2004; Krist et al. 2004) leading to a low parasite growth and fitness (Ebert et al. 2000, 2004; Bedhomme et al. 2004). For instance, high mortality in starved snails *Lymnaea stagnalis* Linnaeus, 1758 parasitized by *Diplostomum spathaceum* Rudolphi, 1819 causes lower reproduction of its parasite (Seppälä et al. 2008).

Parasite burdens registered in our study agree with the literature at both population levels (Scott 1982; Lyles 1990; Cable and van Oosterhout, 2007b; Schelkle et al. 2012; Tadiri et al. 2016) where guppies supported heavier parasite burdens at suprapopulation than at infrapopulation level. Contrary to previous research were at least in female guppies gyrodactylid reached higher burdens and persisted longer (Tadiri et al. 2016) we think that gyrodactylids in our study failed to grow and reproduce at infrapopulation level. The conditions within the host were unsuitable such as low body condition, early host death and the absence of naïve individuals in response to refractory host reaction-response, whereas suprapopulation level gave better conditions in terms of naïve guppies each 48 hrs. For instance, *G. turnbulli* thrives on hosts of high condition and remain on them, particularly when few hosts of high condition are available (Tadiri et al. 2013); if the body condition of the 'source' fish is high in relation to other fish in the population, the population peak parasite burden and the degree of parasite aggregations will be higher in the 'source' fish across infection time (Tadiri et al. 2013). In other words, the prevalence of gyrodactylid may depend on host condition, immune host response and good environmental conditions.

Natural parasite populations can vary substantially in wild guppies depending on their age, sex-specific and spatiotemporal distribution. For instance, *Gyrodactylus* prevalence in natural populations of Trinidadian guppy is generally, but not always, higher at higher-predation sites than at low-predation sites (Gotanda et al. 2013). Also, females maintain heavier parasite loads than males in high predation sites in Trinidad (Stephenson et al. 2015). In this study, female guppies showed higher parasite loads in comparison to males but only at suprapopulation level as it is reported in other studies of gyrodactylid epidemic. In fact, studies reported that female guppies are infected earlier than males (Richards et al. 2010; Johnson et al. 2011) since females have more social contact due to their pronounced shoaling behaviour (Griffiths and Magurran 1998; Croft et al. 2003). Nevertheless, in our suprapopulation experiments, it is unlikely that females could establish real shoals because all fish were forced to contact each other due to the small space in the containers (500 ml).

We propose females to be good resources in terms of host with better nutritive resources and a low resistance in comparison to males but only at suprapopulation level. To maximize fitness, parasites have to balance these two components as it tested in some host-parasite systems like the Alpine swift *Apus melba* Linnaeus, 1758 and the ectoparasite louse fly *Crataerina melbae* Rondadi, 1979*.* In this system, parasites have higher survival rate when they feed on intermediate host body condition, and although hosts in poor conditions have a reduced immunocompetence, parasites may have avoided them because individuals in poor condition did not provide adequate resources (Bize et al. 2008). Similar patterns are proposed experimentally in other systems such as the great tit *Parus major* Linnaeus, 1758 and hen fleas *Ceratophyllus gallinae* Schrank, 1803 (Tschirren et al. 2007), the common bully, *Gobiomorphus cotidianus* McDowall, 1975 and helminth parasites (Lagrue and Poulin 2015) and theoretically by models (Morrill and Forbes 2012).

According to our results parasite burdens is independent of sex host. However, since we did not measure host body condition, we cannot give convincing conclusions. Contrary to previous experiments where isolated male guppies reached higher parasite burdens in comparison to females, but similar parasite burdens between groups of males and females (Tadiri et a. 2016), it is likely that gyrodactylids prefer to parasite host with a high condition which not necessary is sex biased. For instance, when male guppies are raised on a high-food level (food with high levels of carotenoids) they support greater parasite population growth rates than males raised on the low-food level (Kolluru et al. 2006). Therefore, preferred host condition by parasites may be related to better host nutrients and low resistance. More studies of sex-biased parasitism are needed in the guppies- gyrodactylids system.

As with all parasites, gyrodactylid fitness depends on the transmission to a new host (Lipsitch and Moxon 1997). When transmission occurs, parasite suprapopulation of *Gyrodactylus* persists for more than 60 days but if the primarily infected fish fails to transmit, parasite suprapopulation will be extinct within 4-7 days (Johnson et al. 2011). Nevertheless, as we observed, gyrodactylid prevalence does not necessarily increase with host density. So, although we aggregated new fish every two days, suprapopulations began to decrease after 14 days. In contrast with other parasites, for example, some nematodes in mammals (Arneberg 1998), and bacteria in sea urchin (Lafferty 2004); *G. turnbulli* is not abundant with high densities of guppies. Our study supports other studies that propose that the transmission of gyrodactylids could be frequency-dependent rather than density-dependent (Johnson et al. 2011).

Contrary to our prediction, we found that the prevalence of a new parasite infrapopulation did not depend on the body origin of the worms that initiated the infection. Therefore, worms detached from the anterior part (i.e., pectoral, dorsal, and anal fin) showed similar parasite burdens and duration of infections to worms from the posterior body part (i.e., caudal peduncle and fin). Although *Gyrodactylus* does not have a specific transmission stage, its suggested that before a transmission event, gyrodactylids may migrate to specific body host parts where they can detach easily and contact a new host (Mo 1992; Soleng et al. 1999; Bakke et al. 2007). For example, *G. salaris* Malmberg, 1957 that infect *Salmo salar* Linnaeus, 1758 migrate to the dorsal, pectoral, and pelvic fins before a transmission event (Bakke et al. 2007); and *G. callariatis* Malmberg, 1957 that in heavy infections on Atlantic cod *Gadus morhua* Linnaeus, 1758 tend to move from the gill chambers to the fins for its transmission (Appleby 1996). For obligate gill parasites like *G. rarus* Wegener, 1910, such migrations are a prerequisite for transmission and must be take place at some point in the life cycle (Bakke et al. 2007).

We considered that our data were scarce to answer if there is a migration pattern before a transmission event in *G. turnbulli.* It is necessary to conduct experimental infections with significant number of worms from several body parts: head, abdomen, peduncle, gonopodium-anal, pectoral, and dorsal fins and to follow their infrapopulation prevalence through the time. If the body part where worms are detached is crucial to parasite a new host, the proposed experiments consist of crucial and innovative studies to understand more about life cycles and transmission dynamics of *Gyrodactylus*. Besides, it is likely that migration patterns and population prevalence depend on the maturity of worms rather than their body origin. Some evidence in *G. salaris* showed that worms post-1st birth are ready for transmission (Olstad et al. 2006) as well as those with a functional male reproductive system like it occurs in *G. sphinx* Dmitrieva and Gerasev, 2000 (Dmitrieva 2003) and *G. gasterostei* Gläser, 1974 (Grano-Maldonado et al. 2018). For that, we propose to compare transmission dynamics between infrapopulations started with mature and immature worms.

In conclusion, our data contribute to the knowledge of *Gyrodactylus*- guppy dynamics under a new geographical and evolutive context since, both species are not native from Mexico and they are considered invasive species. Although our data are similar to previous studies in this host-parasite system, we registered higher susceptibility and mortality of our Mexican guppy population. In addition, the prevalence of gyrodactylids *G. turnbulli* was the lowest reported until now at suprapopulation level. This information could provide new insights in studies of the coevolution of the *Gyrodactylus* and guppy system.

Human activity, migrations, and climate change have changed the geographical distribution of many species which increases rapid adaptive evolution (Carroll et al. 2014). This is the case of Gyrodactylids. For example, the translocation of different species of African cichlid fishes or “tilapias” for aquaculture has resulted in the co-introduction of *G. cichlidarum* worldwide (García-Vásquez et al. 2010, 2021; Soler-Jiménez et al.2017; Zhang et al. 2019) and the presence of guppies is related with reports of their gyrodactylid parasites in aquarium populations (Maceda-Veiga and Cable 2019). In Mexico these gyrodactylid species and more 7 are infected native freshwater fish (Rubio-Godoy et al. 2016; García-Vazquez et al. 2015) which represents a serious problem for wildlife conservation. Therefore, is crucial to continue the studies of the infection dynamics in these new and emergent host-parasite populations but also experiments that assess the potential impact of translocated gyrodactylids on native hosts.

FIGURES

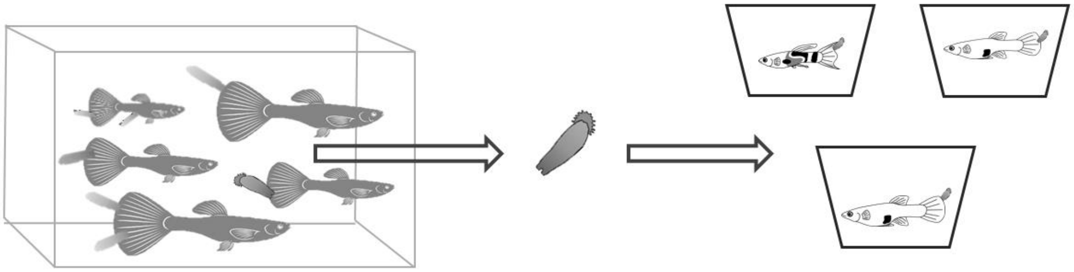

Figure 4. Gyrodactylid infrapopulations (short- term experiments) were carried out with the experimental infection of one worm from an ornamental guppy donor to one wild guppy recipient. 26 wild guppies from a Mexican population were infected and isolated in 200 ml. containers.

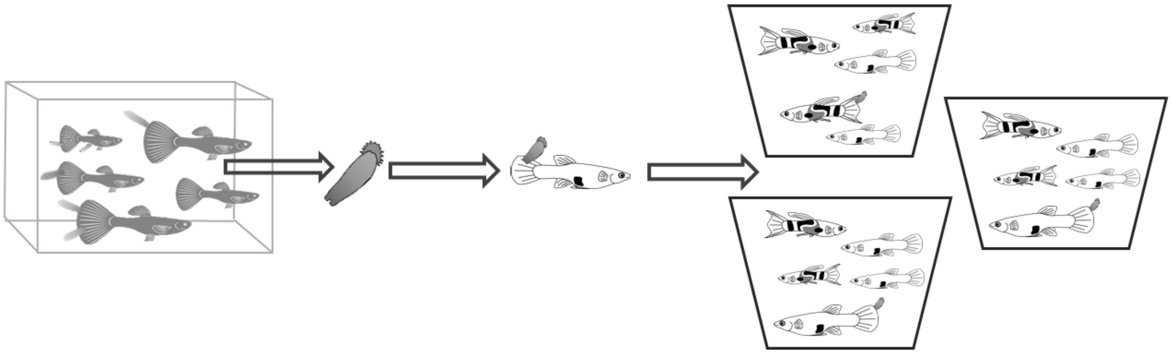

Figure 5. Gyrodactylid suprapopulations (long- term experiments) were carried out with a previous pair of uninfected Mexican guppy and one parasitized fish. Every 48 hrs, a pair of naïve guppies (one male and one female) were aggregated. The process was replicated 7 times in 500 ml containers.

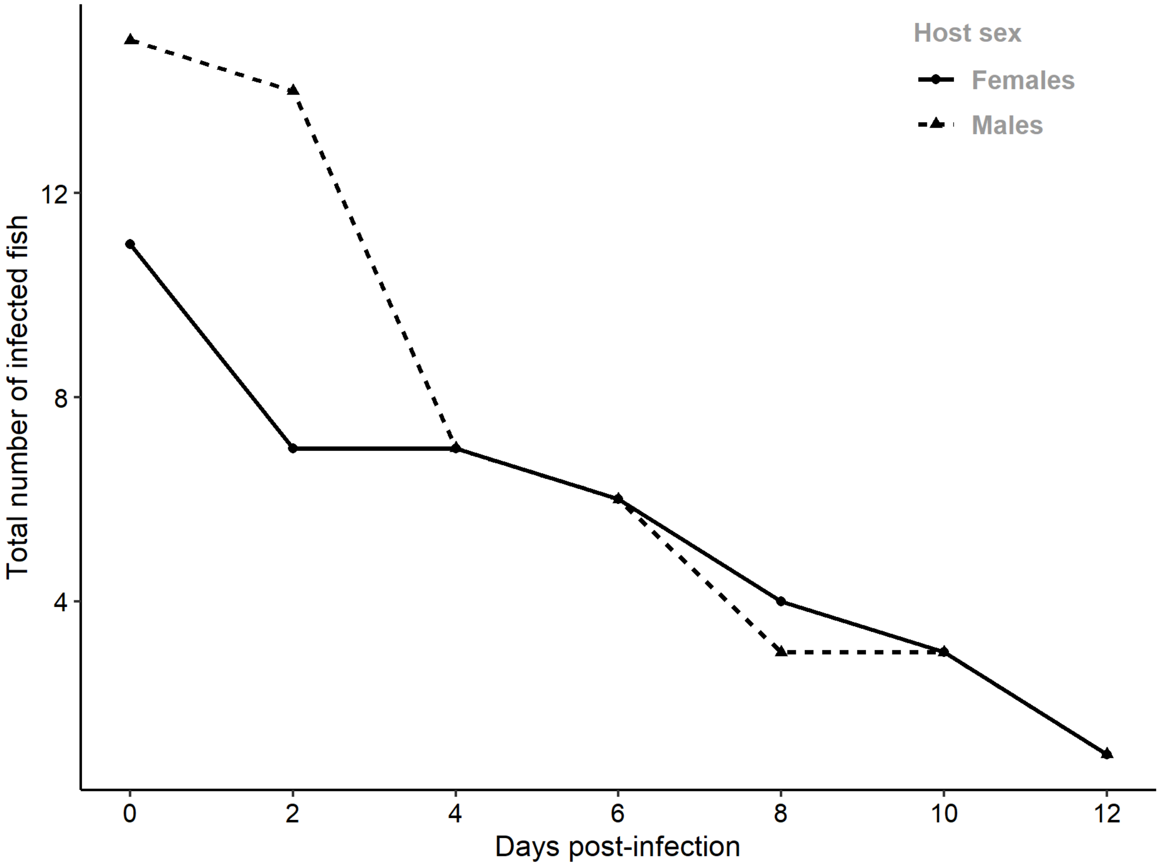

Figure 6. Relationship between the total number of wild guppies (*Poecilia reticulata*) infected with *Gyrodactylus turnbulli* and the duration of infection at infrapopulation level. Here we show the number of infected fish for 12 days where female guppies are represented with solid lines and male guppies with doted lines. The number of infected fish decreased over time.

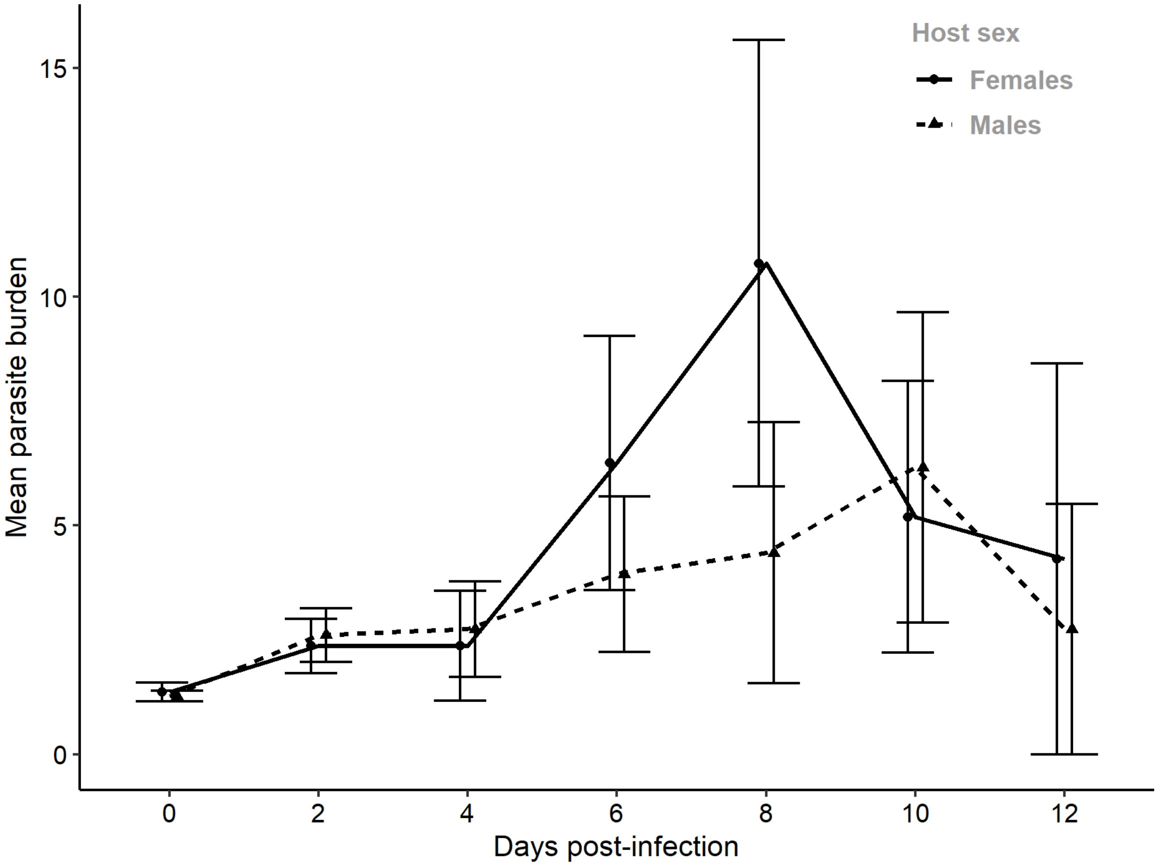

Figure 7. Mean parasite burdens of *Gyrodactylus turnbulli* registered in wild guppies (*Poecilia reticulata*) throughout the duration of infection at gyrodactylid infrapopulation level for 12 days. Female guppies are represented by solid lines and circles whereas males by doted lines and triangles. Error bars are the standard errors.

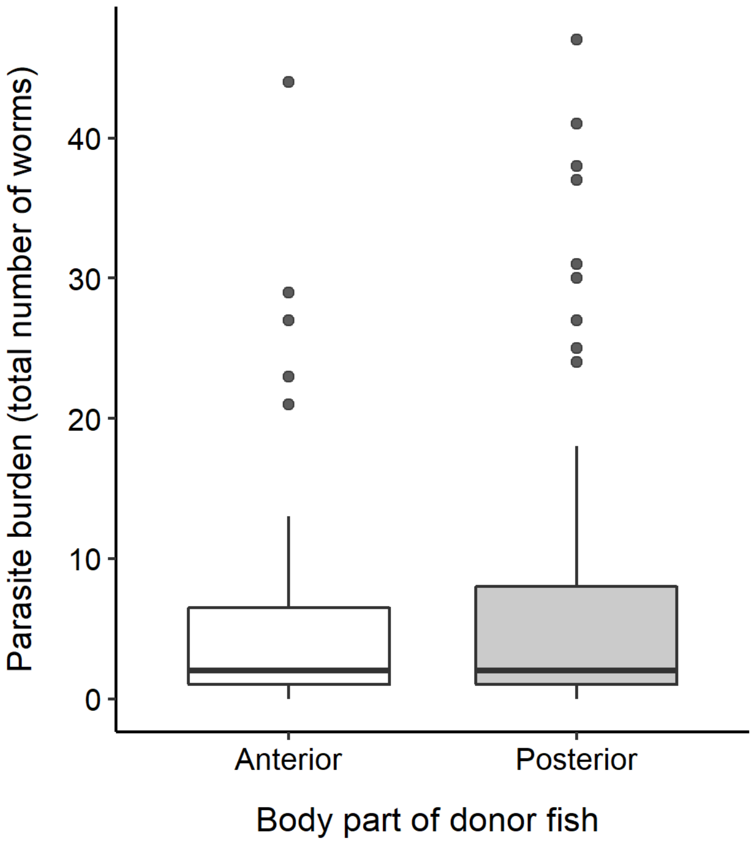

Figure 8. Boxplot of parasite burdens registered on wild guppies (*Poecilia reticulata*) parasitized with an initial worm of *Gyrodactylus turnbulli* from the anterior and posterior body part of a donor fish. No differences were observed.

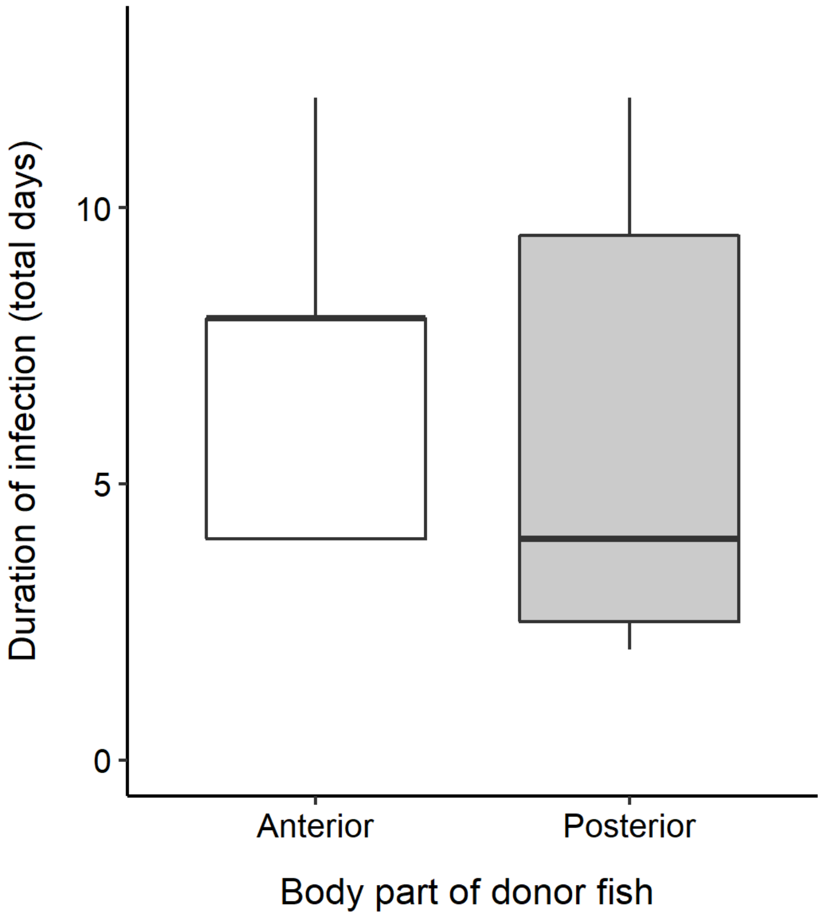

Figure 9. Boxplot of total days that wild guppies (*Poecilia reticulata*) were parasitized with an initial worm of *Gyrodactylus turnbulli* from the anterior and posterior body part of a donor fish. No differences were observed.

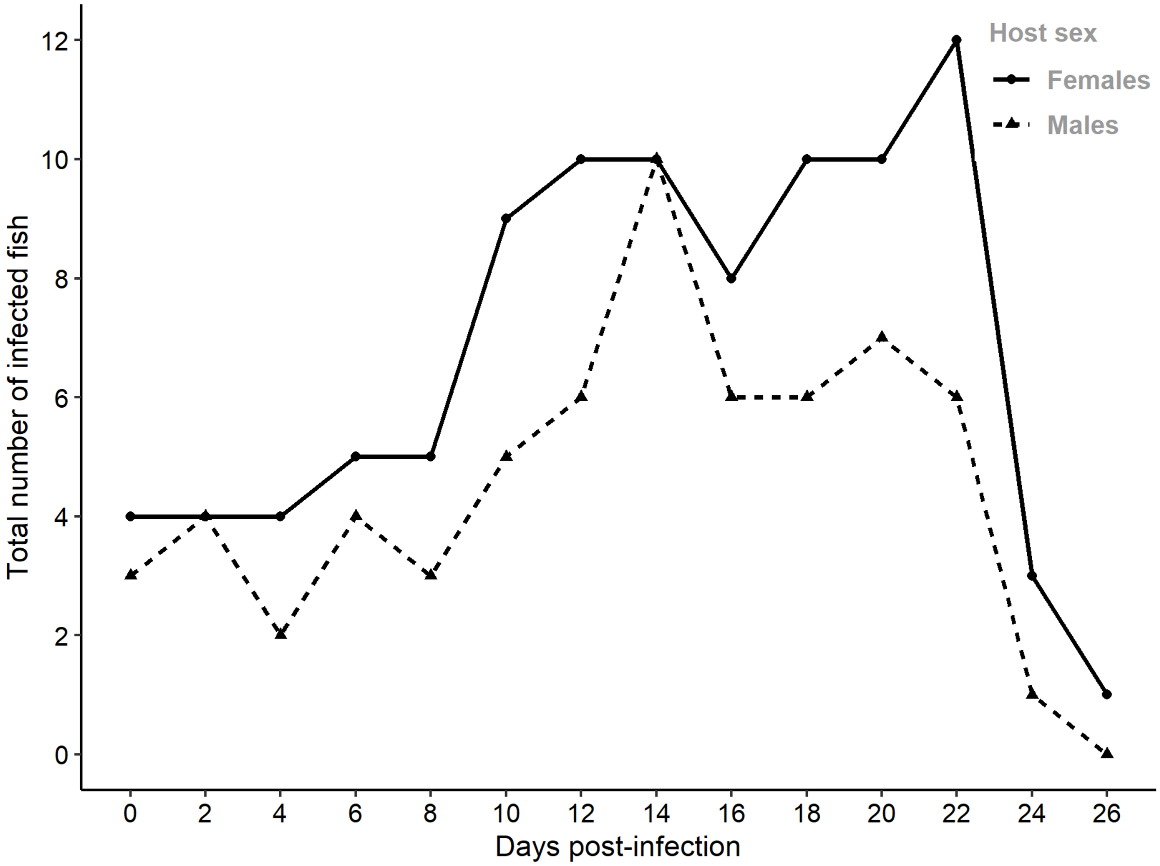

Figure 10. Relationship between the total number of wild guppies (*Poecilia reticulata*) infected with *Gyrodactylus turnbulli* and the duration of infection at suprapopulation level. Here we show the number of infected fish for 26 days where female guppies are represented by solid lines and male guppies by doted lines. The number of infected fish decreased over time.

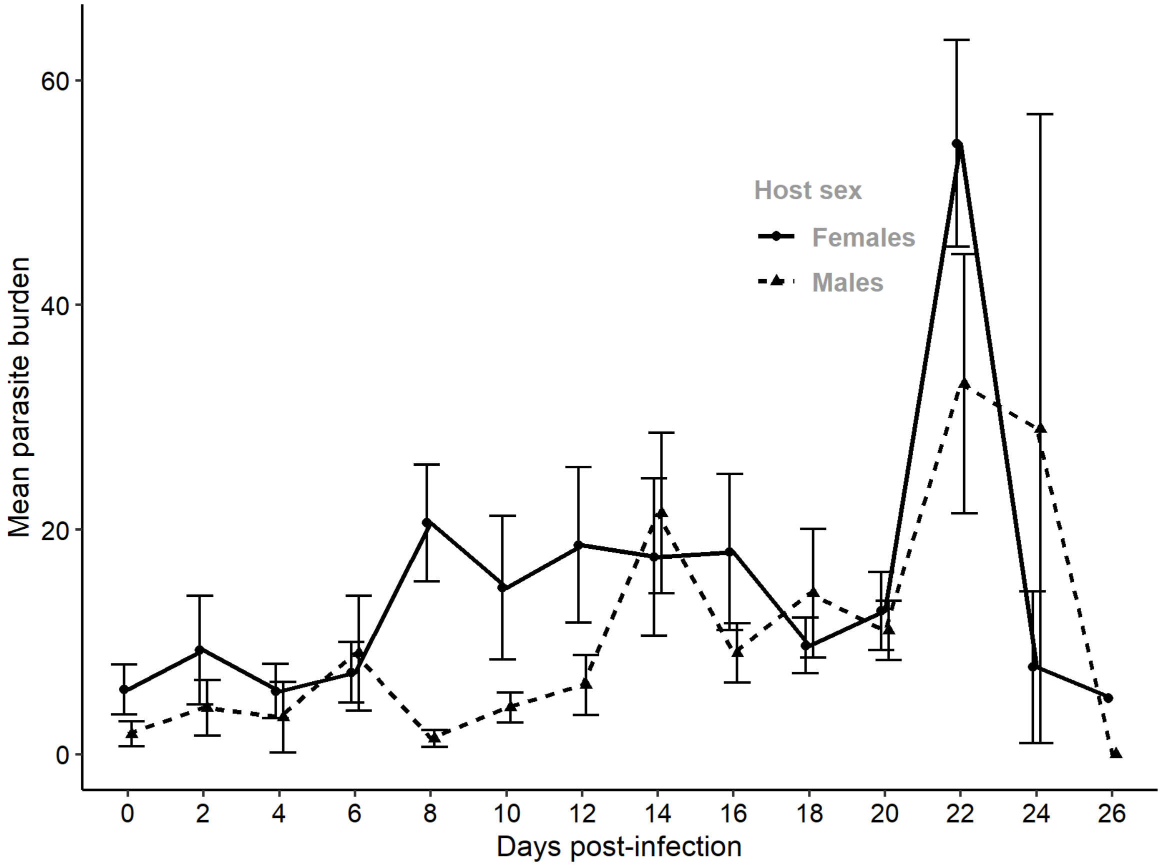

Figure 11. Mean parasite burdens of *Gyrodactylus turnbulli* registered in wild guppies (*Poecilia reticulata*) throughout the duration of infection at gyrodactylid suprapopulation level for 26 days. Female guppies are represented by solid lines and circles whereas males by doted lines and triangles. Error bars are the standard errors.

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