



Contents lists available at ScienceDirect

International Journal for Parasitology: Parasites and Wildlife

journal homepage: www.elsevier.com/locate/ijppaw

Temporal and demographic blood parasite dynamics in two free-ranging neotropical primates



Gideon A. Erkenwick^{a, b, *}, Mrinalini Watsa^{b, c}, Alfonso S. Gozalo^d, Nicole Dmytryk^a, Patricia G. Parker^{a, e}

^a Department of Biology and Whitney R. Harris World Ecology Center, University of Missouri-St. Louis, One University Blvd., Saint Louis, MO 63121, USA

^b Field Projects International, 7331 Murdoch Ave, Saint Louis, MO 63119, USA

^c Department of Anthropology, Washington University in St. Louis, One Brookings Drive, Saint Louis, MO 63130, USA

^d Comparative Medicine Branch, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Bethesda, MD 20892, USA

^e WildCare Institute, Saint Louis Zoo, One Government Dr., Saint Louis, MO 63110, USA

ARTICLE INFO

Article history:

Received 18 November 2016

Received in revised form

8 March 2017

Accepted 10 March 2017

Keywords:

Co-infection

Blood parasites

Cooperative breeding

Longitudinal sampling

Callitrichidae

ABSTRACT

Parasite-host relationships are influenced by several factors intrinsic to hosts, such as social standing, group membership, sex, and age. However, in wild populations, temporal variation in parasite distributions and concomitant infections can alter these patterns. We used microscopy and molecular methods to screen for naturally occurring haemoparasitic infections in two Neotropical primate host populations, the saddleback (*Leontocebus weddelli*) and emperor (*Saguinus imperator*) tamarin, in the lowland tropical rainforests of southeastern Peru. Repeat sampling was conducted from known individuals over a three-year period to test for parasite-host and parasite-parasite associations. Three parasites were detected in *L. weddelli* including *Trypanosoma minasense*, *Mansonella mariae*, and *Dipetalonema* spp., while *S. imperator* only hosted the latter two. Temporal variation in prevalence was observed in *T. minasense* and *Dipetalonema* spp., confirming the necessity of a multi-year study to evaluate parasite-host relationships in this system. Although callitrichids display a distinct reproductive dominance hierarchy, characterized by single breeding females that typically mate polyandrously and can suppress the reproduction of subdominant females, logistic models did not identify sex or breeding status as determining factors in the presence of these parasites. However, age class had a positive effect on infection with *M. mariae* and *T. minasense*, and adults demonstrated higher parasite species richness than juveniles or sub-adults across both species. Body weight had a positive effect on the presence of *Dipetalonema* spp. The inclusion of co-infection variables in statistical models of parasite presence/absence data improved model fit for two of three parasites. This study verifies the importance and need for broad spectrum and long-term screening of parasite assemblages of natural host populations.

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1. Introduction

The surveillance of parasites and pathogens in wildlife populations has received international attention, since wildlife conservation outcomes can be affected by parasitic infections (van Riper et al., 1986; Levin et al., 2013), and since wildlife are increasingly found to host pathogens that can infect humans (Guberti et al., 2014). Parasite-host associations are dictated by characteristics intrinsic to the host, the parasite, and the

environment. Although associations can vary, parasitism is frequently correlated with host density (Poulin, 2004; Fernandes et al., 2012), age (Sol et al., 2003; Clough et al., 2010; Parr et al., 2013; Leclair and Faulkner, 2014) sex (Poulin, 1996; Schall et al., 2000; Clough et al., 2010; MacIntosh et al., 2010), and dominance status (Muehlenbein and Watts, 2010). Meta-analyses across species indicate that parasitism positively correlates with group size (Vitone et al., 2004; Rifkin et al., 2012), but this is modulated by the mode of transmission and mobility of the parasites in question (Cote and Poulin, 1995). In addition to these host-specific factors, when longitudinal data are available, studies of parasite prevalence in diverse taxa demonstrate temporal effects of season (Huffman et al., 1997; Raharivololona and Ganzhorn, 2010) and year

* Corresponding author. Department of Biology, University of Missouri-St. Louis, 8223 Research Building, One University Blvd., St. Louis, MO 63121, USA.

E-mail address: gaet4b@umsl.edu (G.A. Erkenwick).

(Bakuza and Nkwengulila, 2009; Clough et al., 2010; Moreno et al., 2013).

In nature, animals almost always exhibit infections by several different parasites at the same time and in succession (Pedersen and Fenton, 2007; Telfer et al., 2008, 2010). Since parasites can bring about distinct changes to host hematology, body condition and immune investment (Budischak et al., 2012; van Wyk et al., 2014), it follows that even disparate parasites can boost (Monteiro et al., 2007b; Knowles, 2011; Thumbi et al., 2014) or suppress one another (Moreno et al., 2013) via their influences on host immune function (Cox, 2001; Ulrich and Schmid-Hempel, 2012). Although the logistics and economics of collecting long-term, individual-based infection data are challenging, these data are critical to study the effects of age, social structure, life history, time, seasonal variation, and co-infection on disease dynamics (Clutton-Brock and Sheldon, 2010). For example, with repeat sampling we can assess how particular parasites influence host susceptibility to other parasites (Telfer et al., 2008), and if concomitant parasite infections reduce or increase host fitness overall (Balmer et al., 2009). While long-term studies on human populations are numerous (Weil et al., 1999; Bloch et al., 2011), comparable monitoring of wild animal populations are rare (Telfer et al., 2008; Tompkins et al., 2010); however, such studies are critical in the case of long-lived hosts, such as the primates, with complex social organization.

A minority of primates exhibit social systems in which non-biological parents care for the offspring of dominant individuals in a group in a process known as alloparenting (Riedman, 1982; Sussman and Kinzey, 1984). These cooperative breeders, primarily tamarin and marmoset genera within the Callitrichidae, may exhibit greater amounts of parasitism than solitary or pair-bonded breeders due to elevated levels of sociality (Burkart, 2015), which will influence density- and frequency dependent parasite-host relationships (Anderson and May 1978; Altizer et al., 2003; Poulin, 2004; Patterson and Ruckstuhl, 2013). However, if sociality affords an overall reduction in group energy expenditure, then cooperative breeding could instead decrease parasitism by allowing improved individual host immune function (Spottiswoode, 2007; Lutermaier et al., 2013). Here, we present novel haemoparasite infection data from a longitudinal study of two free-ranging sympatric populations of cooperatively breeding primate species - the saddleback tamarin (*Leontocebus weddelli*, formerly *Saguinus fuscicollis weddelli*) and the emperor tamarin (*S. imperator*) (Matauschek et al., 2011; Buckner et al., 2015). This study explores the potential influences of intrinsic host factors, co-infection, and temporal variation on parasite prevalence via a mark-recapture program that allowed us to track the parasite infection status of individual animals across multiple years. This enabled us to control for biases due to temporal, environmental and protocol-related changes, which have been rarely addressed in studies of these species to date (Lisboa et al., 2000; Phillips et al., 2004; Wenz et al., 2009; West et al., 2013), but see (Monteiro et al., 2007a, 2007b).

We predicted four patterns of parasite prevalence would occur within this study system. Due to our observations of consistent host social group sizes through an annual mark-recapture program from 2009 to 2015 (Watsa et al., 2015), we assumed stable host populations and that parasite prevalence would exhibit only minor fluctuations between years due to random stochastic variation in the environment (Schall et al., 2000; Knowles et al., 2013). Second, although sex-biased parasitism is a topic of long debate across taxonomic orders (Morales-Montor et al., 2004) with a tendency to assign greater parasite risk to males (Poulin, 1996; Klein, 2004; Muehlenbein, 2005; Muehlenbein and Watts, 2010) we predict the opposite trend in this host system. Callitrichid sociality is characterized by stark competition among females for breeding

opportunities, with primary breeding females in return suppressing the reproduction of subdominant females behaviorally or through physiological stress (Ziegler et al., 1987; Beehner and Lu, 2013). Conversely, callitrichine males share mate access with little to no overt antagonism, and do not invest in potentially costly secondary sexual characteristics or extensive mate-guarding rituals (Hamilton and Zuk, 1982; Setchell et al., 2009). Callitrichids exhibit unusually high rates of twin offspring among primates (>80% of births) with groups usually consisting of a single female that reproduces, while all other adults assist in rearing her offspring (Sussman and Kinzey, 1984; Terborgh and Goldizen, 1985). While absolute male-female sex ratios are not skewed in this population (Watsa, 2013), operational sex ratios are biased towards males, since typically a single female reproduces in each group. Thus, if there is a parasite risk associated with maintaining social status we predict that it should be borne predominantly by the primary breeding female in a group. Third, while immunosuppression in juveniles can lead to a preponderance of infections in younger age classes (Sol et al., 2003), immunosenescence in aging adults intensifies the accumulation of parasites over a lifespan, resulting in high incidences of infection among older age classes (Shanley et al., 2009). However, although callitrichids can live up to 20 years in captivity, higher predation risks in the wild result in lower lifespan maximums of around 9–11 years (Goldizen, 1996). We therefore predict a lower parasite prevalence in adults vs. subadults or juveniles in this study system. Finally, we predict significant associations between co-infecting parasites that present ecological overlap in infection sites, host resource use, or arthropod vectors, since they are more likely to interact directly or indirectly via the host immune response (Cox, 2001).

2. Material and methods

2.1. Study area and sample collection

Sample collection took place at the Estación Biológica Rio Los Amigos (EBLA) in the Madre de Dios Department of southeastern Peru (12°34'07"S, 70°05'57"W). The 900-hectare tropical rainforest research station is located at the confluence of the Los Amigos and Madre de Dios Rivers, and is contiguous with the much larger Los Amigos Conservation Concession (~1400 km²) that lies within the buffer zone of Manu National Park (Watsa, 2013). Samples were collected annually during the dry season between May and August from 2012 to 2014. All of the primate social groups in this study inhabit a uniform area of forest with similar access to terra firme and várzea habitat. A safe animal mark-recapture program ongoing since 2009, based on the Peruvian trap model (Savage et al., 1993), was optimized to minimize the risk of harm to animals (Watsa et al., 2015). Animals were given permanent identification tags via subcutaneous microchips (Avid, Home Again®). Blood samples (<300 µl) drawn from the femoral vein under ketamine hydrochloride anesthesia (Ketalar, Pfizer Inc., New York, USA) were stored dry on Whatman FTA Micro Elute Cards, and 2 to 3 blood smears were prepared with fresh blood from each animal. All sampling protocols adhere to guidelines outlined by the American Society of Mammalogists (Sikes and Gannon, 2011) and were approved by the Institutional Animal Care and Use Committee at the University of Missouri-St. Louis (317006-2, 733363-2) and the Directorate of Forest and Wildlife Management (DGFFS) of Peru annually.

2.2. Age class and breeding status determination

Among callitrichids, age and sexual maturity can become desynchronized, particularly among females, as a result of

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