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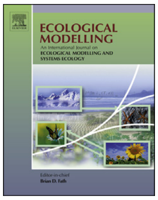

A myiasis model for *Philornis torquans* (Diptera: Muscidae) and *Pitangus sulphuratus* (Passeriformes: Tyrannidae)

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ABSTRACT

The genus *Philornis* comprises neotropical parasitic flies that parasites bird nestlings in their larval stage. The ecology of most species of these parasitic flies is largely unknown. Here we present an epidemiological model that describes the behavior of parasite and host populations. The model was validated with real data of nestlings of the bird community present in a 30 ha area in Santa Fe, Argentina. It consists of two weakly coupled population models, one for the larval population and the other for the nestling population. It takes into account, among other things, the importance of age structure for both populations, the immune response rate on the host and larval survivor rate, the incidence of larval load on host death rate, along with others. This work presents a simple and intuitive way to represent the behavior of this complex biological system and it is a good starting point for future studies.

1. Introduction

Myiasis are parasitic diseases caused by larvae of dipterans. They may represent great economic losses for livestock industry (e.g. species of *Lucilia* Wall, 2012), public health concern (e.g. *Dermatobia hominis* Guimar aes, 1999), or contribute to wildlife species declines (e.g. *Philornis downsi* Wiedenfeld and Jiménez-Uzcátegui, 2008). The ecology of myiasis has singular aspects that need consideration. The majority of infectious agents wait passively the contact with their host (e.g. a nematode egg must be accidentally ingested when the host forages) or are transmitted by a vector (e.g. malaria is transmitted by mosquitoes). In the transmission of myiasis, the gravid female fly actively seek for the host its larvae will feed on, even over relatively long distances. The ecology of myiasis has not been approached through theoretical studies Serra et al. (2007).

Mathematical models are very important for understanding the underlying mechanism behind a disease. They are synthesized upon assumptions about biological mechanisms influencing temporal and spatial characteristics of the parasite spread (Rosà, 2003). They make the model formulation transparent and unambiguous since all the assumptions used to build it must be defined from basic theoretical knowledge in order to properly address the mechanism comprised in the system Hudson and Dobson (1995). Analysis and simulation of these models can identify important combination of parameters, essential aspects or variables of the model that allow either understand the infectious diseases and find potential ways and means to control it.

Anderson and May (1978) define two types of parasites with different epidemiological characteristics. On one hand microparasites such as bacteria and viruses increase rapidly in number when introduced into a susceptible host and there is no advantage on considering the number of infective agents. In this case, compartmental models are traditionally used and individuals are classified into susceptible, infected or immunized populations. On the other hand, macroparasites such as worms are parasitic species

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Fig. 1. Nestling infested with larvae.

for whom reproduction usually occurs trough transmission of immature stages that pass from one host to the next. Host mortality and morbidity increase with the number of parasites (Gulland, 1995). In this kind of models is important to consider not only the prevalence of infection, the parasite burden and the whole distribution of parasites among hosts since fertility, mortality and behaviour of host population depend on parasites distribution among hosts. Reinfection process is an important event in the interaction of hosts and parasites (Hudson and Dobson, 1995; Gulland, 1995; Grenfell and Dobson, 1995). In these studies, much about understanding of interactions between parasites and hosts is based on the models introduced by Anderson and May (1978), May and Anderson (1978). The authors show the importance of host heterogeneity in the dynamics of host-parasite interaction. These models have been the basis of a large development of empirical and theoretical literature (Hudson and Dobson, 1995; Grenfell and Dobson, 1995; Kelehear et al., 2012; Albon et al., 2002; Paterson and Lello, 2003; Gokhale et al., 2013). Some of the factors considered in this kind of models are: (i) seasonality (White et al., 1996), (ii) multi-species and/or trophic levels (Begon and Bowers, 1995), (iii) immunity (Woolhouse, 1992), (iv) spatial structure and (v) genetic diversity (Grenfell and Dobson, 1995).

Philornis Meinert (Diptera: Muscidae) is a genus of flies that includes several parasites species, whose larvae parasitize bird nestling (Couri et al., 2009). Most parasitic Philornis spp. cause subcutaneous myiasis, with burrowing larvae tenet feed on nestlings blood, tissue and fluids (Dudaniec and Kleindorfer, 2006) (Fig. 1). These parasites harm nestlings causing mortality, reduced fitness and grow (May and Anderson, 1978; Couri, 1999). Philornis downsi was subject of extensive research because of its negative impact on Darwin's Finches. The larvae of *P. downsi* reside in the nest material and feed intermittently on blood of nestlings (Fessl et al., 2006). Recently, Philornis torquans has been object of several studies because its documented negative impact on bird nestlings, which can have sublethal effects, nestlings death or even a complete brood loss (Antoniazzi et al., 2011; Young, 1993; Arendt, 1985, 1985; Segura and Reboreda, 2011; Quiroga and Reboreda, 2012). It is also an excellent model to study the ecology of myiasis (Manzoli et al., 2013). These flies only parasite nestlings of wild birds, which remains in their nests for the whole period in which they are susceptible to be parasite. At the same time, the larvae do not migrate once they penetrate in the bird's integument. They develop underneath the point where they entered the skin, and they are easily identified. All this allows a very specific and sensitive diagnosis, providing detailed information from every single nestling present in a patch of forest, from the day they hatch until they fledge.

This paper introduces a mathematical model of Philornis larvae and Pitangus sulphuatus nestlings populations behaviour. The model is build upon two compartmental models, one for each population, coupled through a function that quantified the effect of larvae load on nestlings death rate. The effect of nestling growth process on larvae load is addressed trough the inclusion of age structure of nestlings population, which leads to a set of coupled delayed differential equations (DDE) in contrast to the ordinary differential equations (ODE) resulting from compartmental models. They represent an approximation of the population of both species. The parameters of the models were estimated using real data in combination with quasi-newton optimization methods. The importance of this approach lies mainly in the fact that, up to date, there are no mathematical models explaining the relationship between larvae that cause myiasis and their hosts. The paper is organized in the following way: Section 2 introduces the populations models justifying the implemented methodology trough the assumed hypotheses, including a brief review about the myiasis process and data processing; Section 3 provides the results of the implemented model, parameters optimization a global sensitivity analysis; conclusions are summarized in Section 4 includes descriptive graphics and figures corresponding to model's results and Appendix A include the parameters obtained in the optimization procedure.

2. Methods

2.1. The data

The data were collected in the nature reserve in the city of Esperanza, Santa Fe, Argentina (center $60°55'00''$ *W*, $31°23'08''$ *S*). Around 100 nests were revised during this process in order to collect the relevant data for the model. This data was aligned assuming that all nestlings birth happen at the same time in order to obtain the behavior of both populations (larvae and nestling) in a single brood cycle.

2.2. The model

The life cycle of Philornis flies is little known, but there is some information about they larval and pupal periods. The larvae penetrate the skin of the host and then began to grow. The larval growth process can be divided in three stages defined by their size: L_1 (up to 4 mm), L_2 (from 4 mm to 7 mm) and L_3 (larger than 7 mm). After penetrating the skin development from L_1 to L_3 takes approximately 4 to 6 days for *Philornis carinatus* (Young, 1993). Then, L_3 emerges and pupates within the nest material, which takes from 1 to 3 weeks (Young, 1993). There are several factors acting at different levels that affect the dynamics of *Philornis* abundance. At the individual level, the main driver of the parasitism are the species and the age of the host. At the micro-habitat level the main determinants of larval abundance are the average height of the forest, at the ecosystem level, the density of hosts and prior rainfall (Manzoli et al., 2013).

The model consists on two coupled sub-models, one for each population. The coupling between populations is modelled trough a function that quantified the effects of larvae load on nestlings death rate. The larval development time (approximately 6 days) is three time shorter than nestlings one (approximately 19 days). Therefore, at least two flies generations are incubated in a single nestling cycle. One unexpected behaviour detected in real data, showed in Fig. 2, is the co-existence of larvae from different developmental stages at the same time. This phenomena can be explained by the following facts: (i) larvae raise and fall from nestlings during the day, (ii) multiple infestations at different times, and (iii) migration of larvae from dead nestlings in the same nest. Another unexpected behaviour exposed by Fig. 2 is the presence of unexpected variations of L_2 and L_3 larvae populations. The L_2 larvae population is smaller than L_1 population, however, unexpected rises in L_3