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Interplay between insecticide-treated bed-nets and mosquito demography: implications for malaria control



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HIGHLIGHTS

- A malaria model with decaying bed-net efficacy, mosquito demography and feeding bias is presented.
- Assuming constant bed-net efficacy and unbiased feeding patterns misrepresents true disease risk.
- The existence of a backward bifurcation suggests additional effort is required for malaria elimination.
- Understanding mosquito demography, e.g., parasite-modified biting patterns, can inform policy.
- Bed-nets are useful in controlling malaria, but alone may be insufficient in highly endemic regions.

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ABSTRACT

Although malaria prevalence has witnessed a significant reduction within the past decade, malaria still constitutes a major health and economic problem, especially to low-income countries. Insecticide-treated nets (ITNs) remain one of the primary measures for preventing the malignant disease. Unfortunately, the success of ITN campaigns is hampered by improper use and natural decay in ITN-efficacy over time. Many models aimed at studying malaria transmission and control fail to account for this decay, as well as mosquito demography and feeding preferences exhibited by mosquitoes towards humans. Omitting these factors can misrepresent disease risk, while understanding their effects on malaria dynamics can inform control policy. We present a model for malaria dynamics that incorporates these factors, and a systematic analysis, including stability and sensitivity analyses of the model under different conditions. The model with constant ITN-efficacy exhibits a backward bifurcation emphasizing the need for sustained control measures until the basic reproduction number, R_0 , drops below a critical value at which control is feasible. The infectious and partially immune human populations and R_0 are highly sensitive to the probability that a mosquito feeds successfully on a human, ITN coverage and the maximum biting rate of mosquitoes, irrespective of whether ITN-efficacy is constant or declines over time. This implies that ITNs play an important role in disease control. When ITN-efficacy wanes over time, we identify disease risks and corresponding ITN coverage, as well as feeding preference levels for which the disease can be controlled or eradicated. Our study leads to important insights that could assist in the design and implementation of better malaria control strategies. We conclude that ITNs that can retain their effectiveness for longer periods will be more appropriate in the fight against malaria and that making more ITNs available to highly endemic regions is necessary for malaria containment.

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1. Introduction

Malaria is a life-threatening parasitic, mosquito-borne disease affecting predominantly low-income regions of the world. Currently, five species of *Plasmodium* parasites cause malaria in humans, with *Plasmodium falciparum* resulting in the most severe symptoms and greatest morbidity and mortality. The World Health Organization (WHO) estimated that there were 214 million cases

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of malaria in 2015, resulting in roughly 438 thousand deaths, 305 thousand of which were among African children below the age of five (World Health Organisation, 2015). While these statistics represent an improvement upon previous years and can be attributed to resolute control efforts, these numbers remain staggeringly high, and African children bare the brunt of the burden (World Health Organisation). Several forms of intervention exist to combat malaria, including antimalarial drugs, insecticides, larvicides, and intermittent preventive treatment. One of the simplest forms of malaria control is the use of insecticide-treated bed-nets (ITNs), i.e., both long lasting insecticide-treated bed-nets (LLIN) and insecticide-treated ordinary bed-nets, to shield humans from mosquitoes and to kill mosquitoes that land on the nets. Female *Anopheles* mosquitoes require blood-meals to produce viable eggs, and it is through these blood-meals that mosquitoes can infect humans with *Plasmodium* parasites, and likewise, humans can infect mosquitoes (Klowden, 1995; Attardo et al., 2006). Because some species of mosquitoes, e.g., *Anopheles gambiae sensu stricto* blood-feed predominantly at night, proper use of insecticide-treated bed nets can be an effective means of reducing contacts between mosquitoes and humans, thereby reducing the likelihood of disease-transmission.

Inability of at-risk populations in hyper-endemic or holo-endemic malaria regions to afford ITNs, and improper use of ITNs when they are available (Minakawa et al., 2008; Kayedi et al., 2008; Honjo et al., 2013; McLean et al., 2014) remain major limitations to the success of ITN campaigns, and hence malaria control. In 2013, about 44–54% of sub-Saharan African households owned at least one ITN, marking a 2% decrease from the number of households in 2012, (World Health Organisation, 2014). Despite this decline, a substantial number of sub-Saharan African households have embraced ITNs as a malaria control measure, with about 86% of households with access to ITNs in 2013, actually sleeping under the ITNs compared to less than 35% in previous years (World Health Organization, 2013). For effectiveness, ordinary nets require regular re-coating with insecticides every six months (Schellenberg et al., 2001; Lengeler et al., 2004), which might not be cost-effective, while LLINs, currently recommended by WHO, can retain their effectiveness for about three years (WHO, 2011). In addition to the fact that the efficacy of LLINs wanes naturally over time, LLINs hardly attain their prescribed lifespans because of inappropriate use and handling by humans, e.g., some sub-Saharan African inhabitants' wash and/or expose ITNs to sunlight frequently or use them for other purposes such as fishing (Minakawa et al., 2008; Kayedi et al., 2008; Honjo et al., 2013; McLean et al., 2014).

Most existing mathematical models aimed at assessing the impact of LLINs on malaria prevalence and control, see, for example, Killeen and Smith (2007); Gu and Novak et al. (2009); Chitnis et al. (2010); Briët et al. (2012); Agosto et al. (2013), fail to capture this decline in LLIN efficacy, although it is associated with important malaria control implications. Briët et al. (2012) utilized a stochastic simulation-based tool to evaluate, among other LLIN-effectiveness factors, the impact of physical and chemical decay and discovered that the decay rate of insecticides and the attrition rate of LLINs play big roles in assessing malaria transmission. Ngonghala et al. (2014) proposed a model that accounts for this decline and found out that ITNs designed to last longer will be more useful in combatting malaria and that uncertainty and variability in ITN coverage and the human-biting rate of mosquitoes contribute most in generating variability and uncertainty in malaria dynamics. They also demonstrated that in hyper-endemic and holo-endemic regions, ITNs need to be complemented with other interventions in order to contain malaria. This model, among others mentioned above, fail to account for mosquito feeding and reproduction patterns explicitly, as well as preferential attraction exhibited by mosquitoes to infectious humans or infectious mosquitoes to humans and the associated additional mosquito mortality risk.

Recent studies suggest that mosquito feeding preferences are affected by both the infectious status of the host and the infectious status of the mosquito. Lacroix et al. (2005) showed that children with gametocytes – sexual forms of *Plasmodium falciparum* parasites that are infectious to mosquitoes – in their blood are more attractive to *Anopheles gambiae* mosquitoes than children without gametocytes. This suggests that the presence of gametocytes in human blood can influence mosquito-feeding habit, so that they show more preference towards humans harboring gametocytaemia. Related studies in Koella et al. (1998) suggest that *Anopheles gambiae* mosquitoes carrying sporozoites – asexual forms of *Plasmodium falciparum* parasites that are infectious to humans, acquire more blood than those with no sporozoites, and are more likely to feed on more humans per night compared to their uninfected counterparts. Since ITNs are primarily used at night and anthropophilic malaria vectors like *Anopheles gambiae s.s.* bite between dusk and dawn, a study like this is very important. It is worth mentioning that other malaria vectors like *Anopheles arabiensis* that tend to bite earlier in the day, might be less anthropophilic. Smallegange et al. (2013) demonstrated that when mosquitoes are presented with a choice between a substrate with human odor and a clean substrate, both infected and uninfected mosquitoes show more attraction to the substrate containing human odor; however, the degree of attraction towards the human odors was higher in the infected mosquitoes compared with uninfected mosquitoes. Cator et al. (2013) showed that *Anopheles stephensi* mosquitoes with *Plasmodium yoelii* sporozoites were more attracted to a human host than those with non-infectious *Plasmodium yoelii* oocysts. Their findings were consistent with the overwhelming hypothesis that *Plasmodium* parasites modify the nourishment behavior of mosquitoes. See Cator et al. (2012) for a review of evidence on mosquito-behavior alteration and the importance of the alteration on the spread of malaria. This biased feeding preference exhibited by mosquitoes extends beyond humans: studies on avian malaria by Cornet et al. (2013) indicate that mosquitoes that are either infected or uninfected with malaria parasites show strong attraction to infected birds. Despite this experimental and field-study evidence, only a few mathematical models for malaria, e.g., Kingsolver (1987); Chamchod and Britton (1987) have accounted for the fact that mosquitoes exhibit a different level of attraction to infected humans compared to uninfected humans. Accounting for such biases in malaria models will lead to a better quantification of disease dynamics and hence provide an opportunity for the design and implementation of better control strategies.

There is an emerging mathematical modeling literature on the role of mosquito demography/feeding and reproduction patterns on the dynamics of malaria transmission and control (Cator et al., 2014; Chitnis et al., 2012; Ngwa, 2006; Ngonghala et al., 2012, 2014; Ngwa et al., 2014; Ngonghala et al.). Cator et al. (2014) used a mathematical model to demonstrate the potential impact of decreased feeding during the oocyst stage (one of the non-infectious stages of the malaria parasite in mosquitoes) and increased feeding during the sporozoite stage (the infectious stage of the malaria parasite in mosquitoes) on the total number of infectious bites a mosquito has during its lifetime. The authors found that even under conservative assumptions about the impact of infection status on mosquito biting-behavior, one could expect, based on laboratory-derived estimates of feeding behavior during the oocyst and sporozoite stages, at least a 50% increase in the force of infection in many transmission settings. References (Ngwa, 2006; Ngonghala et al., 2012, 2014; Ngwa et al., 2014; Ngonghala et al.) consider a dynamic modeling approach, and identify and separate the mosquitoes involved in disease transmission (adult female mosquitoes questing for blood at human habitats) from those at mosquito breeding sites (newly emerged adult female mosquitoes, together with previously fed mosquitoes that have just laid

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