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Modelling the Combined Use of Long-Lasting Insecticidal Nets and Insecticides Zooprophylaxis Against the Resilience of Anopheles Arabiensis for Effective Malaria Control

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Abstract

Malaria is a significant public health concern, especially in tropical regions. It remains endemic in many areas where malaria mosquitoes are prevalent. This study investigates the viability of insecticide zooprophylaxis (IZ) in conjunction with Long Lasting Insecticidal Nets (LLINs) as a strategic approach to combat malaria transmission, particularly in regions dominated by zoophagic vectors. Through the presentation and analysis of a mathematical model that integrates IZ and LLINs for the control of *Anopheles arabiensis* (*An. arabiensis*), the research underscores IZ's role in reducing zoophagic vector populations and enhancing malaria control efforts. Notably, the study reveals that achieving comprehensive coverage of LLINs and IZ distribution systems can reduce the basic reproduction number (R_0) below 1. Furthermore, the research highlights the potential for substantial reductions in human biting rates, vectorial capacity and Entomological Inoculation Rate (EIR) when high intervention coverage encompasses all zoophagy blood sources for malaria vectors.

Keywords: Malaria; Zoophagic mosquitoes; Cattle; Insecticides, Zooprophylaxis.

Introduction

Malaria is a potentially life-threatening mosquito-borne disease in many tropical regions, particularly sub-Saharan Africa. It is caused by the Plasmodium parasite and transmitted to humans through the bites of infected female Anopheles mosquitoes. Long Lasting Insecticidal Nets (LLINs) are globally highlighted and distributed as the foremost primary tools for malaria control (WHO 2022). While Indoor Residual Spray (IRS) use for malaria control has declined, the population using LLNs continues scaling up (WHO 2022).

LLINs provide physical and chemical barriers to mosquitoes attempting to bite protected individuals. They reduce the biting frequency, density, and survival of mosquitoes attempting to feed indoors, either through killing or deterring them, thereby reducing their biting activity (Killeen and Smith 2007). The overall impact of LLINs against malaria transmission depends on achieving high net use among all age groups within the community (Killeen and Smith 2007, Okumu 2020).

The intensified and continued use of insecticide-based intervention in areas with high malaria transmission has resulted in the emergence of multiple insecticide-resistance strains among the major malaria vectors *An. funestus* (Pinda et al. 2020, Okumu and Finda 2021), *An. Arabiensis* (Pinda et al. 2020) and *An.* Gambiae (Medjigbodoet al. 2021). Also, there is an increase in outdoor feeding of *An. gambiaesis* and *An. Funestus* (Reddy et al. 2011, Okumu and Finda 2021), reflecting the scaling up of the overall effectiveness of main indoor vector control methods. Moreover, mosquitoes prefer resting outdoors (exophilic), and feeding outdoors (exophagic) and those which prefer primarily to feed on

animals (zoophagic) are important malaria vectors in many tropical countries that contribute to the current residual malaria transmission (Kreppel et al. 2020, Okumu and Finda 2021).

Human activities, specifically cattle keeping, may influence mosquito behavioural adaptations and maintain much residual malaria transmission. Keeping cattle proximity to human habitats increases the probability of zoophagic mosquitoes attracted to those cattle feeding upon nearby people (Hewitt et al. 1994) and may result in shorter periods spent during foraging, leading to lower vector mortality and more mosquitoes surviving the extrinsic incubation period (Saul 2003). The adaptable feeding habits of *An. arabiensis*, which readily targets both cattle and humans, pose significant obstacles to existing control methods (Asale et al. 2017). The behavioural versatility of *An. arabiensis* enables it to adjust its host preference in reaction to fluctuations in the availability of these two host categories and the use of LLINs by humans.

One strategy that has been proposed for controlling malaria in an ecological and epidemiological setting with zoophagic mosquitoes is zooprophylaxis. This approach aims to lure vectors towards domestic animals that serve as dead-end or decoy host (Saul 2003). Although the WHO advocated this method as a malaria control strategy in 1982 (WHO 1982), progress in its implementation has been limited due to a lack of convincing empirical evidence of consistent impact and concerns that it might actually increase risks (Hewitt et al. 1994).

Several mathematical models that predict the impact of integrated vector control measures on mosquito populations across various ecological and epidemiological contexts exist. The deterministic models by Killeen and Smith (2007), Killeen et al. (2011) and Kiware et al. (2012), who modeled malaria transmission in the presence of untreated cattle, revealed that integrated vector control interventions could reduce malaria transmission mediated by not only anthropophagic (prefers feeding on human blood) but also zoophagic vectors.

Another study by Kiware et al. (2017) explores the limitations of current malaria vector control methods in achieving malaria elimination. It proposes a Vector Control Optimization Model (VCOM) to assess the impact of combined interventions on three main malaria vectors in sub-Saharan Africa: *An. gambiae s.s*, *An. Arabiensis* and *An. Funestus.* The research suggests that supplementing baseline LLNs coverage with additional interventions, including larviciding, insecticide-treated cattle (ITC), and attractive toxic sugar baits, could effectively suppress mosquito populations and aid in local malaria elimination across various transmission settings. However, specific mathematical models to account for the diverse feeding behaviours of *An. arabiensis* and assess the role of ITC in the control of malaria transmission are limited.

In light of the challenges exhibited by *An. arabiensis*, the study at hand seeks to explore the potential of an alternative method known as Insecticide Zooprophylaxis. This approach involves the application of insecticides to domestic livestock to target and kill zoophagic mosquitoes (Chaccour et al. 2018). Although originally used to control tsetse flies (Hargrove et al. 2001, Torr et al. 2007), the application of IZ to combat *An. arabiensis* and reduce the vector population that feeds on cattle represents a novel approach, especially in settings with high coverage of LLINs and IRS (Chaccour et al. 2018). By examining the additional effects of the IZ method, this study aims to contribute valuable insights into the multifaceted efforts to control malaria in regions grappling with these complex challenges.

Model framework and description

This work extends a deterministic malaria transmission model of Kiware et al. (2012) and other models that consider the anthropophagic and zoophagic feeding behaviours of *An. Arabiensis* vector v (Killeen and Smith 2007, Killeen et al. 2011). The proposed mathematical model illustrated in

1 describes the feeding process of *An. Arabiensis* in presence of ITC. Let human

$h \in H =$ {protected human (p,h), unprotected human (u,h)} and cattle $c \in C_t =$ {protected cattle (p,c), unprotected cattle (u,c)}, then a host $s \in S = \{H \cup C_t\}$. The intervention scenario Ω consists of LLINs and ITC. It is assumed that mosquito parasites, vectors and hosts are mixed within an enclosed community and host-seeking mosquitoes have equal chances of encountering protected and unprotected hosts.

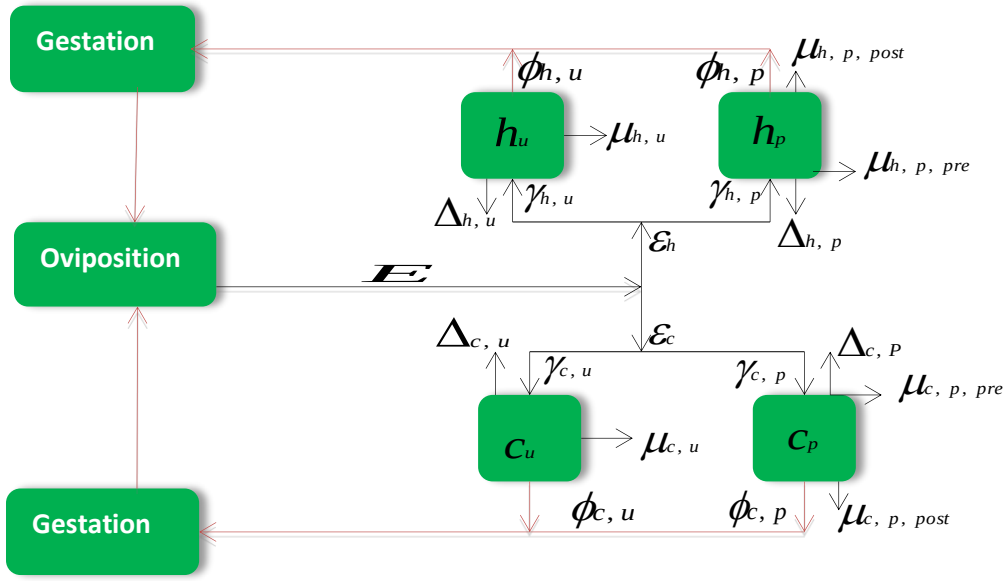

Figure 1: A cyclic mathematical model for the feeding process of *An. arabiensis*. This Figure illustrates how emerged mosquitoes E from oviposition site encounter with hosts $(\mathcal{E}_s)$ and the likelihood that they will bite (γ_s), get diverted (Δ_s), feed successfully (ϕ_s), or die (μ_s) when attempting to feed on a host s.

Figure 1 describes the mathematics related to each stage involved by host-seeking *An. Arabiensis*. A mosquito blood-feeding process is assumed to be cyclic and the feeding mechanism starts at the mosquito's emergence E. The feeding success process must pass through several stages, including host-seeking, host attack or diversion and successful blood feeding. As shown in Figure 1, mean attack availability of a host a_s is obtained as $a_s = \mathcal{E}_s\gamma_s$, where $\mathcal{E}_s$ is the rate at which $\mathcal{V}$ encounters $\mathcal{S}$ and γ_s is the probability that $\mathcal{V}$ attacks $\mathcal{S}$. The availability of host blood *per se* z_s is given by $z_s = \mathcal{E}_s\phi_s$, where ϕ_s is the probability of feeding on that host (Okumu et al. 2010). Thus, the vector will successfully gestate and move to oviposition site when $z_s = 1$. Upon mosquito host encounter, a probability of either attacking γ_s or diverting away from the host Δ_s is computed from $\gamma_s + \Delta_s = 1$.

Not all mosquito populations attempting an attack will successfully feed, some will die before feeding including some of the diverted. The probability of successful feeding upon encountered host is given by $\phi_s = (1-\Delta_s)(1-\mu_s)$, where μ_s is the mortality rate of a mosquito attempting to feed on a host. Note that μ_s for *An. Arabiensis* attacking LLINs users and ITC are assumed to be the same.

To model the effects of LLNs and ITC on the deaths of *An. Arabiensis*, we consider chemicals that kill vectors before blood feeding and that kill vectors after blood feeding. The probability of death before feeding $\mu_{s,pre}$ caused by fast acting toxicants is considered to occur while attacking the

protected host. Thus, the probability of successful feeding upon protected host $\phi_{s,p}$ is given by $\phi_{s,p} = (1-\Delta_{s,p})(1-\mu_{s,pre})$.

Insecticidal properties of the fast acting insecticides cause additional probabilities of diversion θ_{Δ} and death before feeding $\theta_{\mu,pre}$ to a protected host. The probability of diversion before feeding upon a protected host is formulated as $\Delta_{s,p} = \Delta_{s,u} + \theta_{\Delta,S}(1-\Delta_{s,u})$, where $\Delta_{s,u}$ is the probability of diversion for *An. Arabiensis* attacking unprotected host. The probability of death before feeding on a protected host is given by $\mu_{s,pre} = \mu_{s,u} + \theta_{S,\mu,pre}(1-\mu_{s,u})$, where $\mu_{s,u}$ is the probability of death for *An. Arabiensis* attacking unprotected host. Total insecticidal-induced mortality probability $\theta_{S,\mu}$ is given by $\theta_{S,\mu} = \theta_{S,\mu,pre} + \theta_{S,\mu,post}$, where $\theta_{S,\mu,pre}$ and $\theta_{S,\mu,post}$ are the mortalities occurring before and after feeding on a host respectively. The mortality rate of a mosquito attempting to feed on a protected host $\mu_{s,p}$ is obtained from $\mu_{s,p} = \mu_{s,u} + \theta_{s,\mu}(1-\mu_{s,u})$.

This work defines crude coverage C_s as the proportion of either humans using LLNs $C_h$or cattle sprayed with insecticides C_c. The proportion of daily exposure that a non-user host would typically experience at times when a host would normally use a given protection measure is denoted as π_s (Kiware et al. 2012). The *de facto* protective coverage of any host type $D_{s,p}$ is given by $D_{s,p} = \pi_s C_s$. For ITC, $\pi_c = 1$, since insecticides are usually in use for 24 hours therefore non-user cattle are highly exposed to mosquito bites throughout the day. The total availability of any host for attack A_s is calculated as $A_s = a_s N_s \mu C_s$, where N_s is the population size of the given type of host. The total availability of all hosts for attack A is obtained from

$$A = A_{h,p} + A_{h,u} + A_{c,p} + A_{c,u}. \quad (1)$$

The total availability of blood from protected host $Z_{s,p}$ and unprotected ones $Z_{s,u}$ are given by $Z_{s,p} = z_{s,p} N_s D_{s,p}$ and $Z_{s,u} = z_{s,u} N_s (1-D_{s,p})$, respectively. Thus, the total availability of blood from all hosts Z is calculated as $Z = Z_{h,p} + Z_{h,u} + Z_{c,p} + Z_{c,u}$. Human blood index Q_h is calculated as described by Kiware *et al.*, (2012).

$$Q_h = \frac{Z_{h,p} + Z_{h,u}}{Z_{h,p} + Z_{h,u} + Z_{c,p} + Z_{c,u}}. \quad (2)$$

A parameter used to determine the zoophagic vector population is a baseline human blood index $Q_{h,0}$ (Kiware *et al.*, 2012) obtained when humans or cattle are not using any protection measure with its low values and high values representing vectors which are zoophagic and anthropophagic respectively. $Q_{h,0}$ is obtained by setting $C_h = 0$ and $C_c = 0$ of which equation (2) becomes

$$Q_{h,0} = \frac{\varepsilon_h \phi_{h,u} N_h}{\varepsilon_h \phi_{h,u} N_h + \varepsilon_c \phi_{c,u} N_c}.$$

The intermediate values of $Q_{h,0}$ represents *An. arabiensis* which merely expresses intermediate feeding preference on either human or cattle (Killeen *et al.*, 2001). The feeding cycle length f of a mosquito involves gestation period g, oviposition site-seeking interval $\eta_0 = 1/Z$ and vertebrate host-seeking interval $\eta_v = 1/A$.

Thus, $f = g + \eta_0 + \eta_v$. The probability of surviving one feeding cycle P_f is given as the combination of probability of a vector to survive a gestation period P^g, oviposition site-seeking $P_{ov}^{\eta_0}$, vertebrate host seeking $P_{ov}^{\eta_v}$ and probability of surviving host attack per complete feeding cycle $P_\gamma = 1 - \left(\frac{\mu_{h,p} A_{h,p} + \mu_{h,u} A_{h,u} + \mu_{c,p} A_{c,p} + \mu_{c,u} A_{c,u}}{A_{h,p} + A_{h,u} + A_{c,p} + A_{c,u}} \right)$. Thus, $P_f = P^g P_{ov}^{\eta_v} P_{ov}^{\eta_0} P_\gamma$.

The cumulative survival of mosquitoes P_x up to a given age x and the emergence rate of adult mosquito E are estimated as in (Killeen *et al.*, 2011) and given by $P_x = P_f^{x/f}$ and $E = \sum_{x=1}^{\infty} \frac{P_f^{x/f}}{f}$ respectively. The sporozoite infection prevalence of mosquitoes S_x at each age is given by

$$S_x = \begin{cases} S_{x-1} + \frac{kQ_h(1-s_{x-1})}{f} \text{ for x > n,} \\ 0, \text{otherwise,} \end{cases} \quad (3)$$

where k is the probability that an infected human will infect an uninfected mosquito during blood meal and n is the intrinsic incubation period (Killeen *et al.*2006). The estimated number of bites on human per life time $b_h = \frac{Q_h}{f} \sum_{x=1}^{\infty} P_x$ and the number of infectious bites on human per mosquito life time $\beta_h = \frac{Q_h}{f} \sum_{x=1}^{\infty} S_x P_x$ are as described by Killeen and Moore, (2012). The estimated number of sporozoite-infected bites on either human or cattle regardless of cattle being not susceptible to infection is given by $\beta = \beta_h / Q_h$ and overall sporozoite prevalence in the vector population is $S = \beta_h / b_h = \beta / b$, where b is the number of mosquito bites on all hosts, calculated by assuming $Q_h = 1$ in the b_h formula.

As described by Killeen *et al.* (2011), we calculate *EIR* (the mean number of infectious bites) that an average community member in a given Ω receives as $EIR_{h,\Omega} = \beta_h E / N_h$, where N_h is the size of human population. The number of people not using a protection measure who may benefit from communal protection is reflected by the relative exposure for non-users $\psi_{h,u,\Omega} = EIR_{h,u,\Omega} / EIR_{h,u,0}$. The *EIR* formula for users and non-users of LLINs is $EIR_{h,p} = z_{h,p} \beta E / Z$ and $EIR_{h,u} = z_{h,u} \beta E / Z$ respectively.

Human biting rate $B_h = Eb_h / N_h$, where E / N_h is the number of mosquitoes per human, interprets daily malaria transmission per mosquito life time per unit time. For an infected vector to transmit plasmodium, it must become infectious with the probability of surviving the infectious period $P_e = P_f^{\left(\frac{n}{f}\right)}$ (Saul *et al.*, 1990). A vectorial capacity V, estimates the expected potential of mosquito to transmit malaria from all infectious bites on an infected human per unit time usually a day (Garrett-Jones and Grab, 1964). Extending the formula by Saul *et al.*,(1990), we calculate V as $V = B_h k Q_h P_e / \ln P_f^{-1}$, where kQ_h is the probability of a vector to become infectious after a single feed on infectious individual and $1/\ln P_f^{-1}$ is the expected number of days for vectors survived incubation period. Since V is not easily quantified in the field, all infected mosquitoes are assumed to become infectious ($V \approx 1$).

A basic reproductive number R_0 is another malaria transmission index intimately connected to V and EIR which gives a clear threshold value at which elimination might be feasible. It is calculated as $R_0 = k_1 k V / r$, where r is the human recovery rate and k_1 is the probability that an infected mosquito will infect an uninfected human during biting. For low-endemicity malaria transmission system with near-perfect efficiency of transmission from mosquitoes to humans it can be assumed that $k_1 \approx 1$. To parameterize the model, a literature search was undertaken to find model input data as shown in Table 1 of Appendix A. The input parameter for excess mortality occurring before the mosquito has fed on a protected host used to calculate the feeding cycle length of an individual *An. arabiensis* over its lifetime at each level of

coverage is $\theta_{h,\mu,pre}$ = 0.8 for human and $\theta_{c,\mu,pre}$ = 0.5 for cattle.

Results and Discussion

The additional effects of ITC to the pre-existing coverage achieved by LLINs is studied by comparing the impact of LLINs in the presence of unsprayed cattle and that of ITC upon malaria vector population parameters. At low coverage, Figure 2 shows that there is a modest effect of adding ITC to LLINs. Suppose that 80% of humans uses LLINs and 80% of cattle are treated with insecticides then *An. arabiensis* takes more time to complete feeding cycle (about 4 days) than when LLINs alone are used (3.5 days) (Figure 2). Generally, at any level of intervention coverage, feeding cycle length is extended far better when cattle are sprayed with insecticides than using LLINs alone.

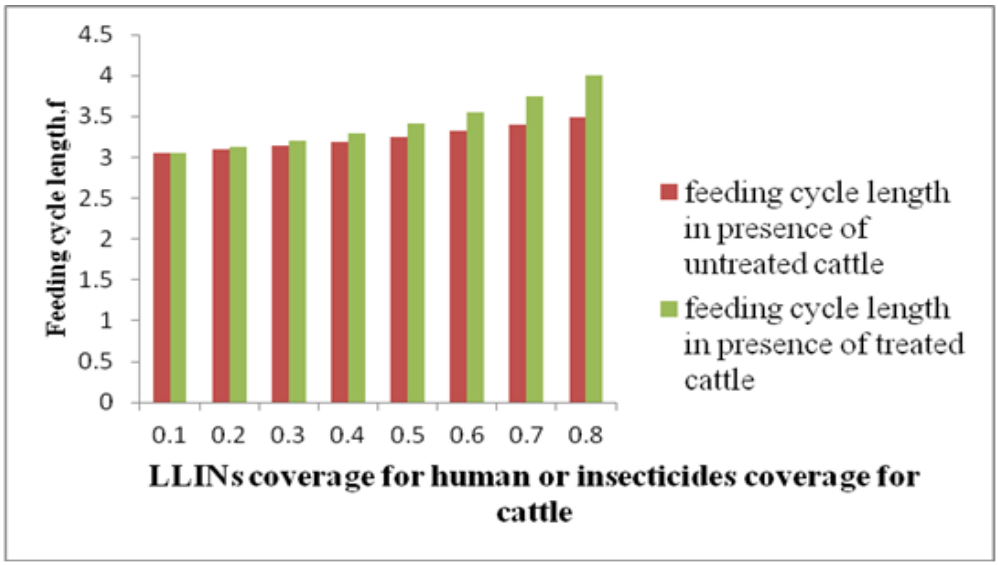

Figure 2: *An. arabiensis* feeding cycle length as a resulted of adding IZ in an existing community LLINs coverage.

Apart from the effects observed on *An. arabiensis* feeding cycle length, also a significant decrease in human biting when IZ is considered at any level of LLINs coverage is observed (Figure 3a). Biting rate is predicted to be atleast 2-fold decrease if cattle are sprayed with lethal doses than using LLINs alone (Figure 3a). If 50% of cattle in a community are treated with insecticides spray, the reduction in biting rate is almost constant at any level of LLINs coverage (Figure 3b).

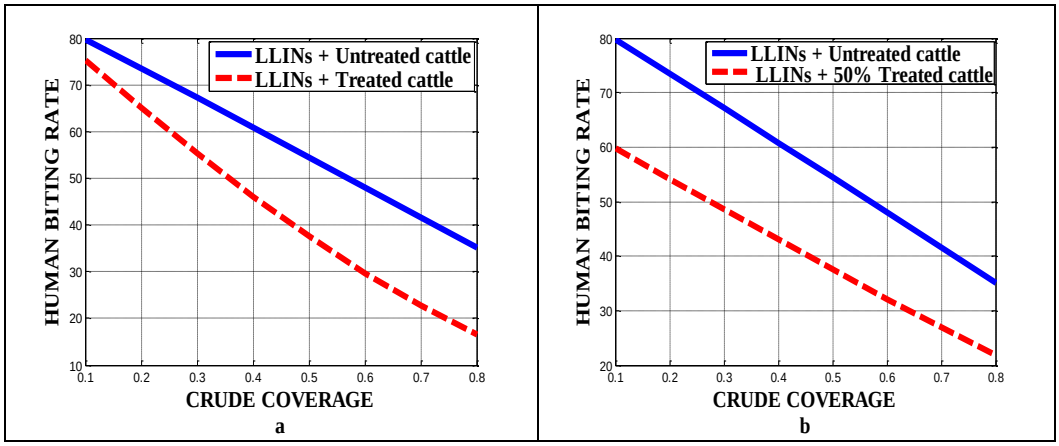

Figure 3: *An. arabiensis* human biting rate. In Figure 3a, humans and cattle have the same level of coverage at any simulation stage, while in Figure 3b, crude coverage for cattle is fixed at $C_h = 0.5$ and LLINs coverage is varied from $C_h = 0.1$ to $C_h = 0.8$.

The effects of changing the number of animals treated with insecticides or LLINs users on EIR which *An. arabiensis* would spread is shown in Figure 4. Increasing number of humans and cattle using LLINs and insecticides respectively up to 80% would lower infectious bites (Figure 4a). Similar result is observed when the number of cattle treated with insecticides is maintained at $C_h = 0.5$ while increasing the number of humans host covered with LLINs (Figure 4b). Areas with *An. Arabiensis* dominance, the coverage of $C_h = 0.8$ is required to achieve $EIR < 10$ (Figure 4a and b).

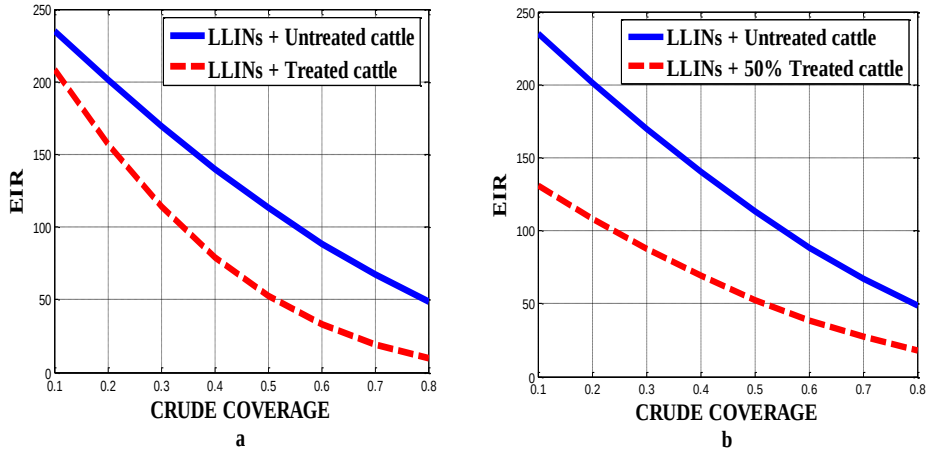

Figure 4: Impact of LLINs and IZ expressed in terms of average community member EIR.In Figure 4a, crude coverage for both humans and cattle is increased from 10% to 80% host users in the community. In Figure 4b, variation in intervention coverage is allowed to human and it is fixed at 50% for cattle.

Reducing animal accessibility to *An. arabiensis*, the disease transmission capacity reduces rapidly to minimum levels (Figure 5). Benefits of such combined tools of malaria

interventions are likely to be greater where 80% of community members use LLINs than in lower coverage (Figure 5a). It is estimated that a 50% coverage of cattle with insecticides at any level of human protection, can reduce vectorial capacity by a factor of 1 to 2 or even more (Figure 5b).

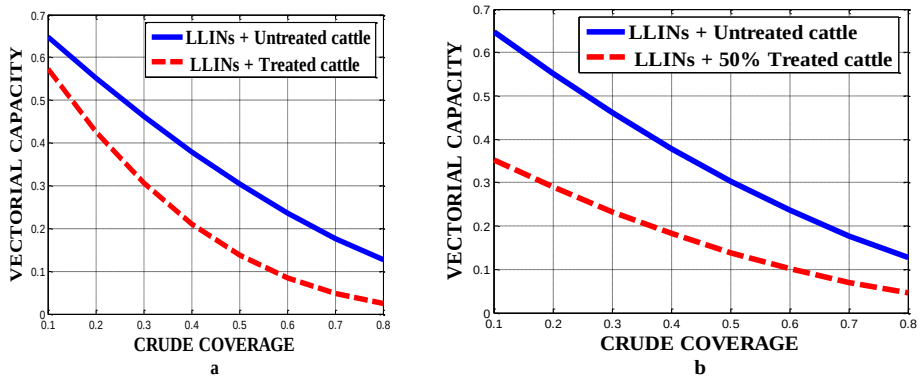

Figure 5 Impact of LLINs and IZ on the vectorial capacity of *An. arabiensis*. In Figure 5a, crude coverage for both hosts is increased from 10% to 80%. In Figure 5b, variation in intervention coverage is allowed to human only and that of cattle is fixed at 50% ITC.

The analysis that $R_0 < 1$ at high coverage of the two alternative sources of blood for *An. arabiensis* (Figure 6) indicates that practising ITC method could result into dramatic suppression of malaria transmission across the entire community. These results emphasises that, if the community could achieve 80% > coverage of animals and humans, malaria transmission mediated by *An.arabiensis* could be reduced to lower limits and eventually, malaria elimination could be achieved (Figure 6a and b).

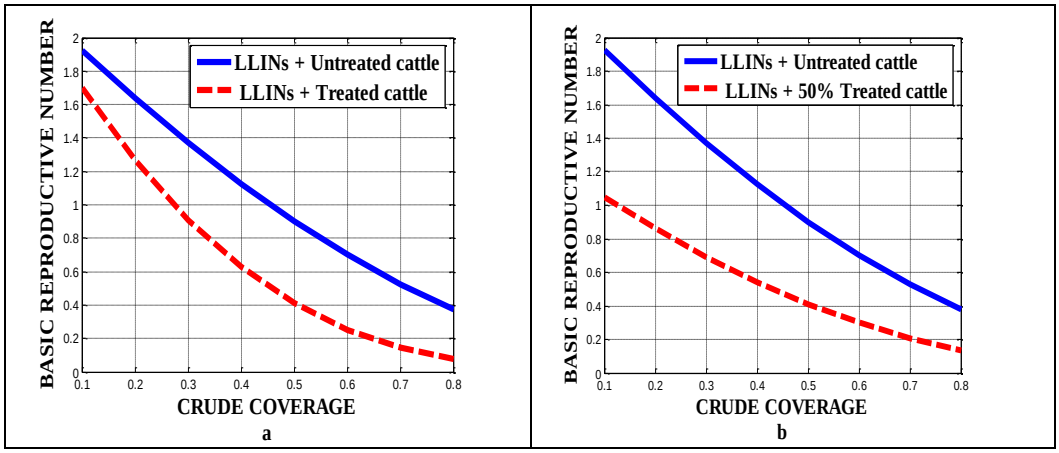

Figure 6: Impact of LLINs and IZ on basic reproductive number (R_0). In Figure 6a, crude coverage for both humans and cattle is increased from 10% to 80%. In Figure 6b, variation in intervention coverage is allowed to human only while that of cattle is fixed at 50%.

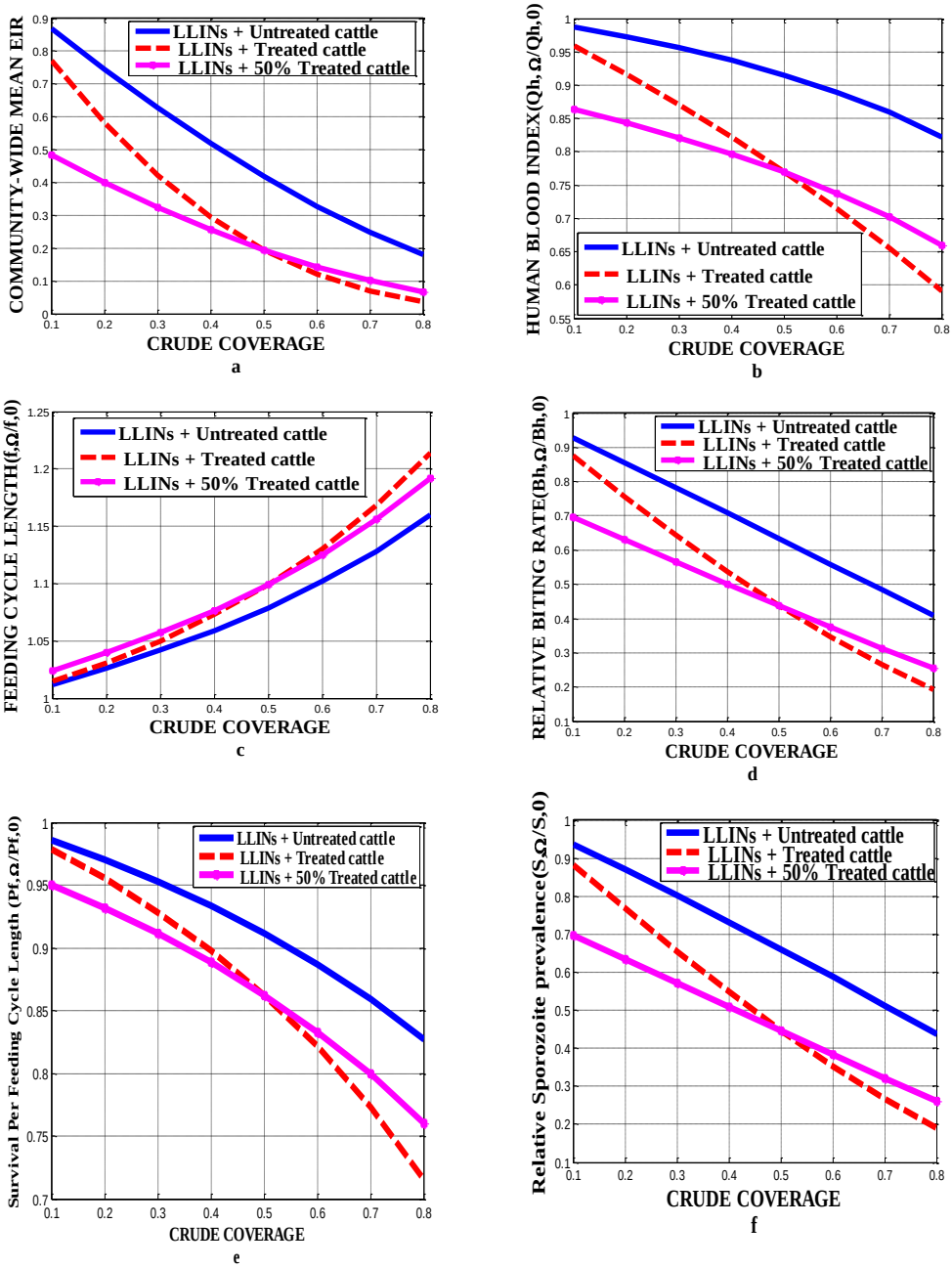

Figure a-f: Impact of LLINs and IZ upon malaria vector population parameters. Simulations are carried out by varying LLINs and ITC coverage from 10% to 80% (blue and red dotted lines). Magenta line considers 50% coverage of cattle at any level of human protection.

As may be reasonably expected in nature, the predictions (Figure 7) show that various feeding cycle process and events that determine malaria transmission risks such as community-wide EIR is reduced when ITC method is introduced. 50% and 10% coverage of cattle with insecticides and humans with LLINs respectively lowers the EIR (Figure

7a). Also, the relative survival probability per feeding cycle is substantially reduced (Figure 7e). These results are presumably outcomes of extending the average time taken by mosquito to find alternative hosts or time of completing the feeding cycle length (Figure 7c). Mosquitoes are discouraged to bite human by diverting them to lethal doses of ITC. The effects of IZ on all malaria vector population parameters are therefore extended to the reduction of parasite transmission (Figure 7f). The benefits of combined use of LLINs and IZ to users and non-users assessed in terms of these vector population- and sporogonic stage-parameters at any level of the coverage are always far better than when only LLINs are used (Figure 7).

Although LLINs can deliver an encouraging level of protection (WHO 2082), the benefits are far better when ITC are deployed to complement and not replace LLINs. This study has shown that when the existing coverage with LLINs is 80%, treating cattle with the same range could dramatically reduce malaria risks, provided that the dominant malaria vector is both zoophagic and anthropophagic (Figures 6 and 7). While universal coverage with mosquito nets will successfully cover much of the population and dramatically reduce malaria transmission where mosquitoes feed mainly on humans, it may result in modest effects when a dominant malaria vector strongly prefers animals over humans.

The density of *An. arabiensis* may continue to increase and maintain malaria endemicity unless the other alternative blood meal is protected. This study is in agreement with other studies that suggests that the local elimination of malaria vectors achieved by LLINs and IRS (Kiware et al. 2017, Sherrard-Smith et al. 2019) can be extended to global and even elimination of the disease only if the remaining residual transmissions are controlled. Zoophagy, exophagy and exophily should be taken into serious consideration as the gaps to be reduced and eventually covered when planning for any novel means for malaria elimination.

Conclusion

The achievement gained by LLINs, IRS, and repellents should be encouraged, while also advocating for the deliberate implementation of the IZ approach for combating malaria and other diseases transmitted by pests and insects. Moreover, a routine application of insecticides for ticks and tsetse control could serve as an effective IZ in communities with any animals. The results suggest that, despite the effectiveness of LLINs in preventing human contact with malaria vectors, *An. arabiensi* should not be overlooked and left in the shadow of the enormous problem caused by other *Anopheles* mosquitoes. Instead, high levels of protective coverage greater than 80% of both blood sources are essential to substantially achieve global reduction and elimination of malaria transmission.

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Conflict of Interests:

The author declares no conflict of interest regarding this work.

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Appendix A

Table 1: Model parameters and values.

Notation	Definition and description	Value	Source
N_c	Total number of cattle	140	Okumu *et al.*, 2013
N_h	Total number of human	1000	Killeen *et al.*, 2004
$\pi_{i,h}$	Proportion of exposure during which LLIN is in use	0.79	Okumu *et al.*, 2013
$\pi_{i,c}$	Proportion of exposure during which insecticide is in use	1	This work
$\Delta_{h,u}$ or $\Delta_{c,u}$	Diversion probability from an unprotected host.	0.1	Lines *et al.*, 1987
μ_h or μ_c	Mortality probability upon attacking an unprotected host.	0.1	Lines *et al.*, 1987
$a_{h,u}$	Mean availability of individual unprotected humans	0.0012	Killeen *et al.*, 2004
$a_{c,u}$	Mean availability of individual unprotected cattle for *An.arabiensis*	0.0019	Killeen *et al.*, 2004
$A_{a,\Omega}$	Total availability of aquatic habitats	3	Killeen *et al.*, 2004
G	Duration of gestation	2	Killeen *et al.*, 2011
P	Daily survival probability while resting	0.9	Gillies, 1954
P_{ov}	Proportion of mosquitoes surviving per day while searching for source of meal and oviposition	0.85	Killeen *et al.*, 2011
N	Parasite sporogonic development period	11	Killeen *et al.*, 2011
K	Human infectiousness to mosquito	0.03	Killeen *et al.*, 2006
E	Total number of mosquitoes emerging per year	2.0×10^7	Okumu *et al.*, 2010
R	Recovery rate for human	0.01	Assumed (Smith and McKenzie, 2004)

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