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Insecticide-treated nets (ITNs) represent a powerful means for controlling malaria in Africa. This usefulness is due to the fact that the principal malaria vectors, from the Giles Anopheles gambiae and An. funestus species complexes, primarily feed indoors at night. Thus, the proportion of human exposure that occurs indoors (πi), when persons are asleep and can conveniently use ITNs, is very high (Figure 1A–D). Such estimates of πi, which take into consideration the movement patterns of persons are obtained in the field by weighting the observed indoor and outdoor biting rates at each period of the night by the proportion of humans that are typically in these two compartments at that time.

When reasonable levels of community-wide coverage are achieved, with approximately half of the population using them each night, ITNs not only confer personal protection against infectious bites but can also reduce the survival, feeding frequency, feeding success, and density of vector mosquito populations. This finding means that ITNs not only prevent malaria in protected persons, but can also reduce the exposure of unprotected persons by suppressing transmission across entire communities.

Recent evidence suggests behavioral changes by malaria mosquito populations to avoid contact with ITNs by feeding outdoors in the early evening. We adapt an established mathematical model of mosquito behavior and malaria transmission to illustrate how ITNs can achieve communal suppression of malaria transmission exposure, even where mosquito evade them and personal protection is modest. We also review recent reports from Tanzania to show that conventional mosquito behavior measures can underestimate the potential of ITNs because they ignore the importance of human movements.

Abstract. Insecticide treated nets (ITNs) represent a powerful means for controlling malaria in Africa. This usefulness is due to the fact that the principal malaria vectors, from the Giles Anopheles gambiae and An. funestus species complexes, primarily feed indoors at night. Thus, the proportion of human exposure that occurs indoors (πi), when persons are asleep and can conveniently use ITNs, is very high (Figure 1A–D). Such estimates of πi, which take into consideration the movement patterns of persons are obtained in the field by weighting the observed indoor and outdoor biting rates at each period of the night by the proportion of humans that are typically in these two compartments at that time.

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is formulated, parameterized, and applied exactly as previously described.8

Figure 1E and F show that less than half of all human exposure to An. arabiensis in urban Dar es Salaam, Tanzania occurs in times and places when using an ITNs is feasible (πi = 0.46). Based on these published field data, simulations predict only a slight suppression in personal relative rate of exposure to transmission (RRE = 0.59), equivalent to a 1.7-fold reduction (Figure 2). However, much greater decreases in exposure to transmission for ITN users (communal plus personal protection; RRE = 0.19) and non users (communal protection only; RRE = 0.32) are predicted at 50% community-wide coverage. Thus, even non-users receiving only communal protection can expect a 3.1-fold reduction of exposure to transmission and users enjoy a 5.3-fold reduction. Extrapolating this level of communal protection horizontally across Figure 2 shows that this is equivalent to the personal protection provided when mosquitoes feed predominantly at times when most resident are indoors (πi = 0.77). Once reasonably high use rates are attained, communal protection achieved is greater than personal protection because even modest reductions of mosquito survival and feeding success per gonotrophic cycle result in much larger impacts upon proportion of mosquitoes surviving the multiple blood feeds required to reach an age where they can transmit mature sporogonic-stage parasites.26–28

Conventional mosquito behavior measures5,18,24,29–32 can underestimate the potential of ITNs because they ignore the importance of human movements indoors and outdoors. Anopheles gambiae s.s. also prefers to bite outdoors in Dar es Salaam (Figure 1C),7 but surveys of human malaria prevalence confirm that ITNs confer valuable personal protection

<table>
<thead>
<tr>
<th>Parameter definitions</th>
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<tr>
<td>$P_e$ = Mean probabilities of surviving eventual host attack</td>
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<td>$\pi_i$ = Proportion of normal exposure of unprotected humans lacking nets that occurs at times and places when net users would be protected by sleeping under them</td>
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<tr>
<td>$\mu_u$ = Mortality upon attacking an unprotected host</td>
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<tr>
<td>$\mu_{u+p}$ = Overall mortality upon attacking a protected host</td>
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<tr>
<td>$a_{hu}$ = Mean availability of individual unprotected humans</td>
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<tr>
<td>$N_{hu}$ = Number of unprotected humans</td>
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<tr>
<td>$a_c$ = Mean availability of individual cattle</td>
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<tr>
<td>$N_c$ = Number of cattle</td>
</tr>
<tr>
<td>$N_{h,u}$ = Number of protected humans</td>
</tr>
<tr>
<td>$N_{h}$ = Number of humans</td>
</tr>
<tr>
<td>$A_c$ = Total availability of cattle</td>
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that the proportion of normal exposure for an unprotected individual occurring at times when insecticide-treated nets (ITNs) would be in use if they were available would be in use if they were available. This is because persons sleep indoors during peaks of mosquito activity, this location is where most human exposure occurs. This finding is due to the fact that because persons sleep indoors during peaks of mosquito activity, this location is where most human exposure occurs. Personal protection against exposure is independent of coverage in the community at large.

Plotting $\pi_i$ versus the proportion of mosquitoes that are caught indoors by conventional field methods (Figure 3) shows that in all cases, the latter consistently underestimates the former. Even for highly exophagic populations of mosquitoes, most bites (Figure 3) can be confined to times when most humans are indoors and possibly under a net. Anopheles gambiae s.s in urban Dar es Salaam, Tanzania and An. gambiae sensu lato in the rural Kilombero Valley, respectively (Figure 1). Note that although we here present a scenario in which overall ITN coverage level is set at 50%, the degree of personal protection against exposure is independent of coverage in the community at large.

Plots represent reported values of $\pi$, which is the maximum proportion of normal exposure that is directly preventable by using an insecticide-treated net. The open triangles represent the proportion of mosquitoes that are caught indoors calculated by dividing the total catch indoors across all times ($I_{0-24\text{ hours}}$) by total catch occurring outdoors ($O_{5:00 \text{am}}$) and indoors ($I_{0-24\text{ hours}}$). The filled circles represents a crude estimate of the proportion of exposure occurring indoor ($\pi_i$), obtained by dividing the total catch occurring indoor from 9:00 pm to 5:00 am ($I_{9:00 \text{pm}}$ to 5:00 am ($I_{9:00 \text{pm}}$ to 5:00 am) by itself plus the total outdoor catch from 5:00 am to 5:00 pm ($O_{5:00 \text{am}}$ to 5:00 pm).

patterns. In simple terms, it is more important that persons are asleep and can conveniently use an ITN when vector activity peaks than that the place they sleep is preferred by those mosquitoes.

We therefore caution that ITNs should not be automatically discarded as a priority vector control measure just because vector mosquitoes are observed to prefer feeding outdoors. Explicit estimates of $\pi$, values for locally relevant populations should first be obtained in the field and the potential community-level benefits, which are rarely captured by standard survey designs, should be carefully considered. Personal protection measures such as spatial repellents may be required to protect against outdoor bites in the morning or early evening, but should only be considered a supplement to ITNs unless proven otherwise. If the equitable, population-wide benefits of communal protection are ignored, potential opportunities for effective malaria control with a well-proven existing technology may be missed because the requirements for behaviorally-susceptible vector populations may be overestimated or overemphasized.
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