Opinion piece

Epidemiological consequences of a newly discovered cryptic subgroup of Anopheles gambiae

A cryptic subgroup of Anopheles gambiae sensu stricto mosquitoes was recently discovered in West Africa. This ‘GOUNDRY’ subgroup has increased susceptibility to Plasmodium falciparum, the most deadly form of malaria. Unusual for this major malaria vector, GOUNDRY mosquitoes also seem to bite exclusively outdoors. A mathematical model is developed to assess the epidemiological implications of current vector control tools, bednets and indoor residual spray, preferentially suppressing the more typical indoor biting mosquitoes. It is demonstrated that even if the GOUNDRY mosquitoes have a decreased preference for human blood, vector controls which select for increased GOUNDRY abundance relative to their indoor biting counterparts risks intensifying malaria transmission. Given the widely observed phenomenon of outdoor biting by major malaria vectors, this behaviour should not be ignored in future modelling efforts and warrants serious consideration in control programme strategy.

Keywords: malaria; vectorial capacity; Lotka–Volterra model

A Lotka–Volterra logistic model of two-species competition is used to explore the epidemiological implications of a recently discovered cryptic subgroup of Anopheles gambiae sensu stricto [1]. This ‘GOUNDRY’ subgroup spatially coexists with the more ubiquitous, indoor-biting (endothelc ‘ENDO’) subgroup. Importantly, GOUNDRY has increased susceptibility to malaria and appears to be strictly outdoor-biting (exophilic) which is highly uncharacteristic of A. gambiae s.s. [2]. Concern was voiced by Riehle et al. [1] over current prevailing vector control strategies, bednets and indoor residual spray, preferentially removing the endophilic subgroup. Here, disease transmission dynamics are modelled for vector populations experiencing suppression through indoor control tools, and implications of this epidemiological analysis are described.

\[
\frac{dE}{dt} = r_E E\left(1 - \frac{E + \alpha_E G}{K}\right) - (\mu^* E) \quad (1)
\]

and

\[
\frac{dG}{dt} = r_G G\left(1 - \frac{G + \alpha_G E}{K}\right). \quad (2)
\]

The equations describe population dynamics of ENDO, ‘E’, and GOUNDRY, ‘G’, A. gambiae s.s. mosquitoes. Because of the highly arid nature of the savannahs of West Africa where these mosquitoes were found, the population bottleneck is assumed to be the availability of larval breeding sites, with the imposed population carrying capacity denoted ‘K’. ‘r’ is the population growth rate and ‘\(\alpha\)’ is the level of competition imposed by larvae of the other subgroup relative to larvae of like-subgroup. These rates are mosquito subgroup specific as denoted by their subscripts. The equation describing ENDO dynamics has the additional parameter, \(\mu^*\), denoting the rate at which the endophilic population of mosquitoes are killed by indoor control tools. Using the formulation of Yakob et al. [3], it is assumed that vector control efficacy decays as a function of time [3]:

\[
\mu^* = \mu \times \exp(-\tau^2 \times 0.00005). \quad (3)
\]

Here, \(\tau\) is time (in days) since insecticide application and \(\mu\) is the daily mortality rate (0.025) of the mosquito population at maximum insecticide potency. This parametrization ensures that, after an initially gradual decline, greater than 99 per cent of the insecticidal properties have decayed by six months post-application in line with World Health Organization estimates for pyrethroids [4].

To assess the epidemiological implications of distorting the relative abundances of the coexisting mosquito subgroups, the vectorial capacity (‘V’, the capacity of the mosquito population to transmit malaria) was calculated. It is assumed that (i) the enhanced transmissibility of the parasite to GOUNDRY mosquitoes as measured in the laboratory [1] is directly proportional to the increase in its true transmissibility in the field, and (ii) exophilic GOUNDRY mosquitoes are likely to have a reduced propensity for human blood meals (0 ≤ q ≤ 1). Results are presented in terms of the vectorial capacity normalized to the stable population structure of the no-control scenario, and are determined from:

\[
V = (BC_e) + (GC_q)^2. \quad (4)
\]

\(C_e\) and \(C_q\) are the rates of parasite transmission to ENDO and GOUNDRY mosquitoes, reported by Riehle et al. [1] to be 0.35 and 0.58, respectively. This representation of the vectorial capacity is analogous to that of Yakob et al. [5] in which a population of malaria vectors was subdivided according to two distinct feeding behaviours [5]. In this way, components of the vectorial capacity for which data are not available (the extrinsic incubation period, the gonotrophic cycle duration and the longevity of the mosquitoes) are assumed to be equivalent for both subgroups. If future studies discover this assumption to be violated, these additional parameters can be incorporated to recover the classic vectorial capacity formulation [6].

Sustained stable coexistence of both subgroups, as demonstrated by the presence of both ENDO and GOUNDRY in the same region across several years [1], suggests that interspecific competition is weaker than intraspecific competition [7], hence \(\alpha_e\) and \(\alpha_G < 1\). In order to model the GOUNDRY population consistently dominating A. gambiae abundance (field studies show GOUNDRY constitutes 57 per cent of the total A. gambiae s.s. population [1]), the coefficient of...
interspecific competition must be higher for GOUNDRY (\(a_g \geq a_e\)) or its rate of population growth must be higher (\(r_g \geq r_e\)). Both scenarios are modelled and the epidemiological consequences of the alternatives are contrasted in figure 1. When between-subgroup differences in interspecific larval competition produce initial conditions that recreate the empirical relative abundances, indoor vector control temporarily perturbs the system in favour of GOUNDRY, transiently increasing malaria transmission potential. Theoretically, the recovery of ENDO will always be permitted by the attenuated larval interspecific competition. If larval competitiveness is equal for both subgroups and it is differences in population growth rates that yield unequal mosquito abundances, the ENDO subgroup fails to recover following the decay in vector control efficacy, and the heightened vectorial capacity associated with increased dominance of GOUNDRY is maintained.

If the subgroups do not differ in population growth rates or larval competitive strengths, and it is just parasite transmissibility that differs between ENDO and GOUNDRY, preferentially suppressing ENDO yields results that are similar to those produced by mosquito subgroups that differ in their population growth rate (electronic supplementary material, figure S1).

This analysis highlights the need for further entomological studies in order to elucidate at least two critical ecological aspects of this newly discovered interspecific competition must be higher for GOUNDRY (\(a_g \geq a_e\)) or its rate of population growth must be higher (\(r_g \geq r_e\)). Both scenarios are modelled and the epidemiological consequences of the alternatives are contrasted in figure 1. When between-subgroup differences in interspecific larval competition produce initial conditions that recreate the empirical relative abundances, indoor vector control temporarily perturbs the system in favour of GOUNDRY, transiently increasing malaria transmission potential. Theoretically, the recovery of ENDO will always be permitted by the attenuated larval interspecific competition. If larval competitiveness is equal for both subgroups and it is differences in population growth rates that yield unequal mosquito abundances, the ENDO subgroup fails to recover following the decay in vector control efficacy, and the heightened vectorial capacity associated with increased dominance of GOUNDRY is maintained.

If the subgroups do not differ in population growth rates or larval competitive strengths, and it is just parasite transmissibility that differs between ENDO and GOUNDRY, preferentially suppressing ENDO yields results that are similar to those produced by mosquito subgroups that differ in their population growth rate (electronic supplementary material, figure S1).

It might be expected that the enhanced vectorial capacity resulting from suppressing the ENDO group (thereby selecting for the GOUNDRY group) would be offset by the fact that the exophilic GOUNDRY may have a reduced propensity to feed on humans. This property was parametrized (see equation (4)) and its epidemiological consequences are illustrated in figure 2. Even under the circumstances that GOUNDRY mosquitoes have reduced preference for human blood meals, selecting for their increased abundance relative to ENDO mosquitoes (through indoor vector control) can still result in heightened vectorial capacity. There is a threshold beyond which a reduced preference for human blood offsets the increased transmissibility of the parasite in GOUNDRY mosquitoes:

\[ q = \sqrt{\frac{C_e}{C_g}} \]  

This means that if the human biting preference for GOUNDRY is higher than the square root of the ratio of the parasite transmissibility to ENDO versus GOUNDRY mosquitoes, preferentially suppressing endophilic mosquitoes will generate an overall increase in the vectorial capacity.

This analysis highlights the need for further entomological studies in order to elucidate at least two critical ecological aspects of this newly discovered interspecific competition must be higher for GOUNDRY (\(a_g \geq a_e\)) or its rate of population growth must be higher (\(r_g \geq r_e\)). Both scenarios are modelled and the epidemiological consequences of the alternatives are contrasted in figure 1. When between-subgroup differences in interspecific larval competition produce initial conditions that recreate the empirical relative abundances, indoor vector control temporarily perturbs the system in favour of GOUNDRY, transiently increasing malaria transmission potential. Theoretically, the recovery of ENDO will always be permitted by the attenuated larval interspecific competition. If larval competitiveness is equal for both subgroups and it is differences in population growth rates that yield unequal mosquito abundances, the ENDO subgroup fails to recover following the decay in vector control efficacy, and the heightened vectorial capacity associated with increased dominance of GOUNDRY is maintained.

If the subgroups do not differ in population growth rates or larval competitive strengths, and it is just parasite transmissibility that differs between ENDO and GOUNDRY, preferentially suppressing ENDO yields results that are similar to those produced by mosquito subgroups that differ in their population growth rate (electronic supplementary material, figure S1).

It might be expected that the enhanced vectorial capacity resulting from suppressing the ENDO group (thereby selecting for the GOUNDRY group) would be offset by the fact that the exophilic GOUNDRY may have a reduced propensity to feed on humans. This property was parametrized (see equation (4)) and its epidemiological consequences are illustrated in figure 2. Even under the circumstances that GOUNDRY mosquitoes have reduced preference for human blood meals, selecting for their increased abundance relative to ENDO mosquitoes (through indoor vector control) can still result in heightened vectorial capacity. There is a threshold beyond which a reduced preference for human blood offsets the increased transmissibility of the parasite in GOUNDRY mosquitoes:

\[ q = \sqrt{\frac{C_e}{C_g}} \]  

This means that if the human biting preference for GOUNDRY is higher than the square root of the ratio of the parasite transmissibility to ENDO versus GOUNDRY mosquitoes, preferentially suppressing endophilic mosquitoes will generate an overall increase in the vectorial capacity.

This analysis highlights the need for further entomological studies in order to elucidate at least two critical ecological aspects of this newly discovered interspecific competition must be higher for GOUNDRY (\(a_g \geq a_e\)) or its rate of population growth must be higher (\(r_g \geq r_e\)). Both scenarios are modelled and the epidemiological consequences of the alternatives are contrasted in figure 1. When between-subgroup differences in interspecific larval competition produce initial conditions that recreate the empirical relative abundances, indoor vector control temporarily perturbs the system in favour of GOUNDRY, transiently increasing malaria transmission potential. Theoretically, the recovery of ENDO will always be permitted by the attenuated larval interspecific competition. If larval competitiveness is equal for both subgroups and it is differences in population growth rates that yield unequal mosquito abundances, the ENDO subgroup fails to recover following the decay in vector control efficacy, and the heightened vectorial capacity associated with increased dominance of GOUNDRY is maintained.

If the subgroups do not differ in population growth rates or larval competitive strengths, and it is just parasite transmissibility that differs between ENDO and GOUNDRY, preferentially suppressing ENDO yields results that are similar to those produced by mosquito subgroups that differ in their population growth rate (electronic supplementary material, figure S1).

It might be expected that the enhanced vectorial capacity resulting from suppressing the ENDO group (thereby selecting for the GOUNDRY group) would be offset by the fact that the exophilic GOUNDRY may have a reduced propensity to feed on humans. This property was parametrized (see equation (4)) and its epidemiological consequences are illustrated in figure 2. Even under the circumstances that GOUNDRY mosquitoes have reduced preference for human blood meals, selecting for their increased abundance relative to ENDO mosquitoes (through indoor vector control) can still result in heightened vectorial capacity. There is a threshold beyond which a reduced preference for human blood offsets the increased transmissibility of the parasite in GOUNDRY mosquitoes:

\[ q = \sqrt{\frac{C_e}{C_g}} \]  

This means that if the human biting preference for GOUNDRY is higher than the square root of the ratio of the parasite transmissibility to ENDO versus GOUNDRY mosquitoes, preferentially suppressing endophilic mosquitoes will generate an overall increase in the vectorial capacity.

This analysis highlights the need for further entomological studies in order to elucidate at least two critical ecological aspects of this newly discovered interspecific competition must be higher for GOUNDRY (\(a_g \geq a_e\)) or its rate of population growth must be higher (\(r_g \geq r_e\)). Both scenarios are modelled and the epidemiological consequences of the alternatives are contrasted in figure 1. When between-subgroup differences in interspecific larval competition produce initial conditions that recreate the empirical relative abundances, indoor vector control temporarily perturbs the system in favour of GOUNDRY, transiently increasing malaria transmission potential. Theoretically, the recovery of ENDO will always be permitted by the attenuated larval interspecific competition. If larval competitiveness is equal for both subgroups and it is differences in population growth rates that yield unequal mosquito abundances, the ENDO subgroup fails to recover following the decay in vector control efficacy, and the heightened vectorial capacity associated with increased dominance of GOUNDRY is maintained.

If the subgroups do not differ in population growth rates or larval competitive strengths, and it is just parasite transmissibility that differs between ENDO and GOUNDRY, preferentially suppressing ENDO yields results that are similar to those produced by mosquito subgroups that differ in their population growth rate (electronic supplementary material, figure S1).

It might be expected that the enhanced vectorial capacity resulting from suppressing the ENDO group (thereby selecting for the GOUNDRY group) would be offset by the fact that the exophilic GOUNDRY may have a reduced propensity to feed on humans. This property was parametrized (see equation (4)) and its epidemiological consequences are illustrated in figure 2. Even under the circumstances that GOUNDRY mosquitoes have reduced preference for human blood meals, selecting for their increased abundance relative to ENDO mosquitoes (through indoor vector control) can still result in heightened vectorial capacity. There is a threshold beyond which a reduced preference for human blood offsets the increased transmissibility of the parasite in GOUNDRY mosquitoes:

\[ q = \sqrt{\frac{C_e}{C_g}} \]  

This means that if the human biting preference for GOUNDRY is higher than the square root of the ratio of the parasite transmissibility to ENDO versus GOUNDRY mosquitoes, preferentially suppressing endophilic mosquitoes will generate an overall increase in the vectorial capacity.

This analysis highlights the need for further entomological studies in order to elucidate at least two critical ecological aspects of this newly discovered
subgroup of *A. gambiae* s.s.: (i) why does GOUNDRY dominate in these natural populations—is it larval competitiveness, population growth rates or something not considered in this analysis? And, (ii) what is the human biting preference of GOUNDRY mosquitoes? Answering both of these questions will be integral to future epidemiological efforts to assess the impact of preferentially suppressing endophilic mosquitoes. More generally, the Lotka–Volterra type framework developed in this analysis has wider applications to malaria epidemiology in locations where multiple species (or subgroups) of vectors with different host feeding preferences and behaviours coexist.

Laith Yakob

Department of Biological Sciences, 
Saint Lucia Campus, 
University of Queensland, 
Brisbane 4072, Australia

laith.yakob@uq.edu.au


