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Insecticide-treated Nets and the Diversion of Anopheles Biting to Livestock: A Critical Narrative Review of Zooprophylaxis in Malaria Vector Control

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Author's contribution

The sole author designed, analyzed, interpreted and prepared the manuscript.

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Review Article

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Abstract

Insecticide-treated nets (ITNs) remain the dominant tool for malaria prevention across endemic Africa and Asia, yet residual transmission persists where dominant vectors feed outdoors, early in the evening, or on non-human hosts. Zooprophylaxis, the practice of exploiting livestock as alternative blood-meal sources to divert Anopheles mosquitoes from humans, has been proposed for almost a century as a low-cost complement to net-based control, and a specific hypothesis has gained renewed attention: that ITN scale-up itself, by excluding mosquitoes from human sleeping spaces, increases the relative attractiveness of livestock and thereby amplifies passive zooprophylactic diversion. This critical narrative review synthesises entomological, epidemiological, theoretical and intervention literature bearing on this hypothesis, with particular attention to Anopheles arabiensis, the vector for which host diversion is most plausible. The evidence indicates that host diversion is real but conditional: it depends on vector species composition, the spatial placement of livestock relative to human dwellings, and the density ratio of animals to people, and it can reverse into zoopotentiation when livestock are housed close to or within sleeping areas. Direct tests of the ITN-livestock interaction

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remain scarce, and the clearest entomological demonstration reports a modest, species-specific reduction in human biting associated jointly with net coverage and cattle presence rather than a large, generalisable push-pull effect. Mathematical models show that whether livestock protect or endanger a population depends critically on mosquito mortality while host-seeking, a parameter rarely measured in the field. Converting passive diversion into a lethal event, through insecticide-treated livestock or systemic endectocides, has produced consistent entomological gains in trials but has not yet been validated against clinical malaria endpoints at scale. The review concludes that zooprophylaxis should not be promoted as a standalone control measure, that its interaction with ITNs is ecologically plausible but empirically under-demonstrated, and that insecticide-treated or endectocide-treated livestock represents the more defensible avenue for translating host diversion into measurable transmission reduction, contingent on further cluster-randomised evidence.

Keywords: Zooprophylaxis; insecticide-treated nets; Anopheles arabiensis; residual malaria transmission; livestock; human blood index; zoopotentiation; vector control.

1. Introduction

Malaria control since the year 2000 has rested overwhelmingly on two indoor-directed tools: insecticide-treated nets (ITNs), including long-lasting insecticidal nets (LLINs), and indoor residual spraying (IRS). Both interventions depend on a specific behavioural assumption about the vector: that Anopheles mosquitoes seek blood indoors, at night, from human hosts, and rest indoors afterwards, thereby bringing themselves into prolonged contact with an insecticide-treated surface. Where this assumption holds, as it largely does for Anopheles gambiae sensu stricto and Anopheles funestus sensu stricto across much of West and Central Africa, ITNs and IRS have driven substantial reductions in transmission. Where it does not hold, control has stalled even as coverage has expanded.

The vector for which the assumption breaks down most consistently is Anopheles arabiensis, a member of the An. gambiae complex that is more plastic in its host choice, its biting location and its resting location than its sibling species. An. arabiensis will feed on cattle when cattle are available, will bite outdoors or before residents retire under a net, and will rest outdoors after feeding, behaviours that place a substantial fraction of its bites beyond the reach of indoor-targeted tools (Kitau et al., 2012; Sougoufara et al., 2020). As ITN and IRS coverage has expanded, several longitudinal entomological studies have documented a shift in vector species composition and behaviour consistent with selection against the more strictly anthropophilic and endophilic phenotypes, leaving the more opportunistic An. arabiensis, and in places An. funestus populations with increased zoophagy or exophily, as a growing share of residual transmission (Kitau et al., 2012; Kreppel et al., 2020; Limwagu et al., 2024). A systematic review and modelling analysis of mosquito biting behaviour across Africa estimated that only 79% of bites by the major vectors occur while people are typically in bed, and that the proportion of bites occurring at times when people are protected by nets has fallen by roughly ten percentage points since 2000, translating into an estimated 10.6 million additional malaria cases annually under universal ITN and IRS coverage relative to what would be expected if all biting occurred indoors during sleeping hours (Sherrard-Smith et al., 2019). This body of evidence establishes both the scale of the residual-transmission problem and the specific relevance of livestock, since the same opportunistic host-seeking behaviour that permits outdoor and early-evening biting also permits feeding on cattle, goats and other domestic animals in place of humans.

Zooprophylaxis, understood as the deliberate or incidental use of non-human animals to divert blood-seeking vectors away from humans, is not a new idea. It was recognised as a plausible malaria-control mechanism well before the era of synthetic insecticides, and international guidance has periodically endorsed livestock-based diversion as a candidate low-cost intervention (Bøgh et al., 2001). The concept, however, carries an internal tension that has structured the empirical literature for decades. Introducing additional blood-meal hosts can reduce human exposure by satiating host-seeking mosquitoes on animals rather than people, but it can equally increase local mosquito density and survival by improving overall blood-meal availability, and it can increase human exposure directly if livestock are kept close enough to human sleeping quarters to attract more vectors into the immediate vicinity of the house. The first outcome is conventionally termed zooprophylaxis; the second and third are collectively termed zoopotentiation (Donnelly et al., 2015; Saul, 2003; Sota & Mogi, 1989). Whether a given livestock-keeping arrangement falls on one side of this line or the other has been shown, across a heterogeneous body of field studies, to depend on vector species composition, the spatial distance between animal shelters and sleeping areas, the relative density of animals to humans, and the presence or absence of complementary personal protection such as ITNs (Asale et al., 2017; Donnelly et al., 2015).

It is this last contingency, the interaction between livestock-mediated diversion and net-based protection, that has generated the specific hypothesis addressed by this review. As ITN coverage excludes mosquitoes from the immediate vicinity of sleeping humans, the argument runs, host-seeking mosquitoes that would previously have fed on humans indoors are increasingly likely to encounter and feed upon livestock kept nearby, converting a passive ecological association into an active, ITN-dependent push-pull system in which the net "pushes" mosquitoes away from the protected host and livestock "pull" them toward an alternative, epidemiologically inert blood meal (Iwashita et al., 2014). This mechanism, if real and generalisable, would represent a naturally occurring amplifier of ITN effectiveness in livestock-keeping communities and would carry direct implications for the siting of livestock relative to housing in vector-control planning. If, conversely, the mechanism is weak, inconsistent across vector species, or reversible into zoopotentiation under common husbandry practices, then policy or community messaging that encourages livestock-keeping near homes as a malaria-control measure would be actively counter-productive.

A second and closely related strand of literature asks whether passive diversion, even where demonstrable, is the most defensible way to exploit the zoophagic tendencies of vectors such as An. arabiensis. Because livestock are not competent hosts for human Plasmodium species, a mosquito that feeds on an untreated animal is diverted but not killed, and it survives to seek another blood meal, potentially from a human, on a subsequent night. Treating livestock with topical or systemic insecticides, or with endectocides such as ivermectin and eprinomectin that are lethal to mosquitoes after ingestion in a blood meal, converts this diversion into a lethal event and has become an active area of intervention research operating under the labels insecticide-treated livestock (ITL) and endectocide-based vector control (Chaccour et al., 2018; Poché et al., 2015; Ruiz-Castillo et al., 2022). This strand of evidence is mechanistically distinct from passive zooprophylaxis, but it shares the same underlying ecological premise, namely that a meaningful fraction of An. arabiensis and related vectors can be intercepted at the point of livestock feeding, and it has been proposed repeatedly as a complement to ITNs specifically because it could address the same outdoor, zoophagic residual transmission that ITNs cannot reach (Killeen & Thomas, 2007; Yakob et al., 2017).

Existing reviews of this literature are informative but incomplete for the present purpose. The most cited systematic treatment, a realist review by Donnelly et al. (2015), synthesised twenty empirical studies and identified vector ecology and livestock placement as the principal moderators of zooprophylaxis versus zoopotentiation, but it predates the more recent entomological literature on ITN-driven behavioural and species shifts and does not examine the ITN-livestock interaction as a distinct mechanism. A systematic review specific to An. arabiensis (Asale et al., 2017) reached similar conclusions about context-dependence but likewise stopped short of integrating the residual-transmission and insecticide-treated-livestock literatures into a single analytical frame. A short communication published in 2026 has proposed integrating zooprophylaxis, insecticide-treated livestock and ITNs within a One Health framework, but by its own description offers a conceptual and future-oriented discussion rather than a critical synthesis of the underlying primary evidence, and it does not attempt the kind of methodological appraisal, thematic synthesis or evidence-graded conclusion that a narrative review requires (Otolorin et al., 2026). No existing review, to the knowledge of the present authors, has systematically appraised the entomological, epidemiological, theoretical and intervention evidence together to ask specifically whether, and under what conditions, ITN deployment itself changes the magnitude or direction of livestock-mediated mosquito diversion, nor has any review extended the appraisal to a comparative assessment of study designs and their capacity to distinguish a genuine push-pull mechanism from confounded associations between livestock ownership, household wealth, housing quality and malaria risk.

Recent evidence further illustrates this context dependence. A cohort study in south-central Ethiopia reported lower malaria incidence among livestock-owning households, with the protective association increasing as the livestock-to-human ratio rose (Loha, 2023), whereas an urban matched case-control study in eastern Ethiopia associated livestock ownership with greater odds of malaria infection in a setting where *Anopheles stephensi* was detected (Merga et al., 2024). Concurrent entomological studies have shown that *Anopheles arabiensis* can remain a principal vector of *Plasmodium falciparum* after prolonged implementation of indoor-focused control, while vector composition and bionomic traits vary across ecological settings (Eligo et al., 2024; Esayas et al., 2024). Collectively, these findings support interpretation of livestock-mediated diversion in relation to local vector ecology, animal-husbandry arrangements, housing conditions and intervention coverage, rather than as a uniformly protective or harmful effect.

1.1 Scope, Research Gap and Objectives

This review is confined to the interaction between insecticide-treated bed nets and livestock-mediated diversion of Anopheles malaria vectors, encompassing three interlocking bodies of evidence: the vector bionomics that determine which species are susceptible to diversion; the entomological and epidemiological evidence on passive zooprophylaxis and zoopotentiation, including the specific evidence bearing on whether ITN coverage modifies these effects; and the intervention literature on insecticide-treated livestock and endectocide-based approaches that seek to convert diversion into vector mortality. The geographical focus is sub-Saharan Africa, where An. arabiensis and the An. gambiae complex dominate the relevant literature, with supporting evidence drawn from South and Southeast Asia and Central America where comparable zoophagic vectors and livestock-based trials exist. The temporal focus privileges evidence published from 1990 onward, when empirical field testing of zooprophylaxis intensified, while retaining foundational theoretical and observational work from the late 1980s where it remains conceptually necessary to the field.

The specific knowledge gap addressed is threefold. First, although the individual claims that ITNs alter vector behaviour and that livestock divert vector biting are each well supported in isolation, direct empirical tests of their interaction are few, and the single study most often cited as evidence for an ITN-driven push-pull effect reports a targeted, species-specific result that has not been widely replicated. Second, the theoretical literature establishes that the sign of the zooprophylactic effect depends on parameters, particularly host-seeking mortality, that are rarely measured alongside the entomological outcomes reported in field studies, leaving many empirical findings difficult to reconcile with modelled expectations. Third, the insecticide-treated-livestock literature has matured methodologically over the past decade, moving from laboratory and semi-field efficacy trials toward cluster-randomised field designs, but no synthesis has yet placed this trajectory in relation to the passive-zooprophylaxis evidence to ask what threshold of evidence would be required before livestock-based interventions could be integrated into vector-control policy alongside ITNs.

Accordingly, this review has four objectives: to characterise the vector bionomics underlying host diversion, with particular attention to the human blood index and bovine blood index as diagnostic measures; to critically appraise the entomological and epidemiological evidence on zooprophylaxis and zoopotentiation, distinguishing studies that directly test an ITN interaction from those that examine livestock effects independently of net use; to evaluate the theoretical and mathematical modelling literature that specifies the conditions under which livestock diversion protects or endangers human populations; and to appraise the intervention literature on insecticide-treated livestock and endectocide-based approaches as a mechanistically distinct but ecologically related strategy. The review excludes zooprophylaxis literature concerning non-malarial vector-borne diseases, such as tsetse-borne trypanosomiasis or sand fly-borne leishmaniasis, except where such literature is cited by primary malaria studies as methodological precedent, and it excludes larval source management and other non-host-diversion vector-control tools except where necessary for context. Because the terminology used across this literature is applied inconsistently between studies, key terms and the conceptual distinctions between them are defined in Table 1 before the evidence itself is reviewed.

Table 1. Key terms and conceptual distinctions relevant to livestock-mediated diversion of malaria vectors

Term	Definition	Distinguishing feature	Supporting references
Zooprophylaxis	A net reduction in human-vector contact, and by extension in malaria transmission risk, resulting from the availability of non-human blood-meal hosts.	Outcome-defined: requires a demonstrated reduction in human exposure, not merely the presence of animals.	Donnelly et al., 2015; Saul, 2003
Zoopotentiation	A net increase in human-vector contact or malaria transmission risk	The mirror-image outcome to zooprophylaxis, arising	Donnelly et al., 2015; Sota & Mogi, 1989

Term	Definition	Distinguishing feature	Supporting references
	resulting from the presence of non-human hosts, typically through increased local vector density, survival or attraction.	from the same ecological intervention under different spatial or ecological conditions.	
Passive zooprophylaxis	Diversion arising incidentally from pre-existing livestock husbandry practice, without deliberate insecticidal treatment of the animals.	The animal is unmodified; only its presence and placement are relevant.	Bøgh et al., 2001; Bouma & Rowland, 1995
Insecticide-treated livestock (ITL)	Deliberate topical or oral application of insecticide to livestock so that a mosquito feeding on the animal is killed or has its fecundity reduced.	Diversion is converted into a lethal or sterilising event rather than remaining epidemiologically neutral.	Poché et al., 2015; Ruiz-Castillo et al., 2022
Endectocide-based vector control	Administration of a systemic veterinary antiparasitic drug (for example ivermectin or eprinomectin) to livestock, killing mosquitoes that ingest the drug in a blood meal.	Mechanistically a subtype of ITL, distinguished by systemic rather than topical drug action and by dual veterinary and vector-control indications.	Chaccour et al., 2018; Pooda et al., 2015
Human blood index (HBI)	The proportion of identified mosquito blood meals, within a defined sample, that originate from a human host.	Measures completed host choice among fed mosquitoes; does not directly measure biting rate or vector density.	Orsborne et al., 2018
Bovine (or other animal) blood index	The proportion of identified blood meals originating from a specified non-human host species, most often cattle.	The complement of the human blood index for a named alternative host; sensitive to sampling location and method.	Muriu et al., 2008
Push-pull (livestock-mediated)	A hypothesised joint mechanism in which insecticide-treated nets exclude mosquitoes from human hosts ("push") while nearby livestock provide an alternative blood meal ("pull").	Requires a demonstrated interaction between net coverage and livestock effect, not merely co-occurrence of the two factors.	Iwashita et al., 2014

Note. ITN = insecticide-treated net; LLIN = long-lasting insecticidal net; ITL = insecticide-treated livestock; HBI = human blood index; BBI = bovine blood index; IRS = indoor residual spraying; MDA = mass drug administration

2. Methods for Literature Selection

2.1 Review Design and Rationale

A critical narrative review design was selected in preference to a systematic review or meta-analysis because the underlying evidence base is heterogeneous in study design, outcome measurement and ecological context, spanning experimental hut trials, paired-cohort epidemiological studies, cross-sectional surveys, semi-field insecticide efficacy trials, cluster-randomised intervention trials and deterministic and stochastic mathematical models. Pooling effect estimates across this range of designs and outcomes, as a meta-analysis would require, risks obscuring precisely the context-dependence that the literature itself identifies as the central finding, namely that the direction of the zooprophylactic effect is conditional on vector species, spatial arrangement and intervention coverage rather than a single generalisable parameter. A narrative review permits thematic organisation around these moderating conditions and allows explicit comparison of studies that test the ITN-livestock interaction directly against the larger body of studies that examine livestock effects in isolation. The narrative approach follows established guidance on the conduct of non-systematic reviews, which recommends explicit statement of search strategy, transparent eligibility criteria and structured critical appraisal even where a formal quantitative synthesis is not undertaken, so that transparency is not sacrificed for flexibility (Donnelly et al., 2015, whose realist-review methodology for the same subject area provided a template for the appraisal approach adopted here). This review differs from a systematic review in that it does not report standardised risk-of-bias scores for every included study, since a formal risk-of-bias instrument validated for entomological field trials of this kind does not exist, but it does apply consistent, stated criteria for judging methodological adequacy, which are described in Section 2.6.

2.2 Information Sources

Literature was identified through PubMed/MEDLINE, Web of Science Core Collection, Scopus, Google Scholar and OpenAlex, supplemented by backward citation searching from three recent systematic or realist reviews on zooprophylaxis (Asale et al., 2017; Donnelly et al., 2015; Otolorin et al., 2026) and forward citation searching from foundational modelling papers (Saul, 2003; Sota & Mogi, 1989). Institutional sources consulted for policy and definitional context included the World Health Organization's published guidance on integrated vector management (World Health Organization, 2017). Preprint servers were searched to identify emerging trial protocols and were cross-checked against subsequent peer-reviewed publication where available; unpublished preprints were not used as a primary evidentiary basis for any claim in this review.

2.3 Search Strategy and Search Period

Search concepts were combined using Boolean operators across four blocks: the intervention block (zooprophylaxis, zoopotentiation, insecticide-treated livestock, endectocide, ivermectin, eprinomectin, fipronil); the comparator/co-intervention block (insecticide-treated net, long-lasting insecticidal net, indoor residual spraying, push-pull); the vector and mechanism block (Anopheles arabiensis, Anopheles gambiae complex, human blood index, bovine blood index, host preference, host choice, residual transmission, outdoor biting, behavioural resistance, species shift); and the outcome block (malaria incidence, malaria prevalence, sporozoite rate, entomological inoculation rate, mosquito survival, mosquito mortality). A representative string took the form: (zooprophylaxis OR zoopotentiation OR "insecticide-treated livestock" OR endectocide) AND (Anopheles OR malaria vector) AND (cattle OR livestock OR bovine) AND ("insecticide-treated net" OR "bed net" OR LLIN OR "indoor residual spraying"). Searches were conducted across all years of database coverage; foundational theoretical and observational studies published before 1990 were retained where cited as conceptually necessary by the subsequent literature. The search end date was 21 May 2026.

2.4 Eligibility Criteria

Eligible publications were peer-reviewed original research articles, systematic or realist reviews, and methodological or theoretical papers published in indexed journals, reporting entomological, epidemiological, theoretical-modelling or intervention-trial evidence on livestock-mediated diversion of malaria vectors, insecticide-treated or endectocide-treated livestock, or the interaction between such livestock-based measures and insecticide-treated nets or indoor residual spraying. Both African and non-African settings were eligible provided the vector system involved zoophagic or opportunistic Anopheles species relevant to the mechanisms under review. Institutional reports were eligible where they provided policy context not available in the peer-reviewed literature. Excluded were studies concerning non-Anopheles vectors or non-malarial pathogens except where cited as direct methodological precedent by an included malaria study; conference abstracts without a corresponding full-text publication; non-peer-reviewed opinion pieces; and sources whose full bibliographic details, including author names, journal, year and either a verifiable digital object identifier or a stable institutional web address, could not be confirmed through at least one authoritative index. No language restriction was applied at the search stage, but only English-language, full-text-accessible sources were ultimately retained, which constitutes a limitation discussed in Section 11.

2.5 Screening, Duplicate Handling and Study Selection

Titles and abstracts returned by each database were screened for relevance to the eligibility criteria above, with full-text review conducted where relevance could not be determined from the abstract. Records retrieved from multiple databases were cross-checked by digital object identifier, and duplicate records were retained once under the earliest or most complete bibliographic entry. Where a working paper or conference report was superseded by a peer-reviewed publication, only the peer-reviewed version was retained. Because this is a narrative rather than a systematic review, no numerical screening flow diagram is reported, consistent with the guidance that a formal PRISMA-style count is appropriate to systematic reviews with a fully reproducible selection algorithm rather than to a thematically organised narrative synthesis; inaccessible sources, principally paywalled items for which neither an open-access repository copy nor sufficient abstract detail could be located, were excluded rather than cited from secondary description.

2.6 Critical Appraisal and Evidence Synthesis

Methodological quality was appraised against criteria appropriate to each study design: for entomological field studies, appropriateness of sampling method to the outcome claimed (for example, distinguishing human landing catches, which measure biting risk, from resting collections, which measure post-feeding location, and from blood-meal analysis, which measures host choice but not biting rate); for epidemiological studies, adequacy of confounding control, particularly for household wealth and housing quality, both of which correlate with livestock ownership and independently affect malaria risk; for intervention trials, the level of randomisation (village, cluster or individual) and the nature of the endpoint (entomological survival versus clinical incidence); and for modelling studies, the biological plausibility and empirical grounding of key parameters. Studies were weighted more heavily in the synthesis where they directly measured the interaction between livestock presence and ITN use rather than examining either factor alone, since this interaction is the central question of the review. Conflicting findings were retained and discussed explicitly rather than resolved by selective citation; where the literature showed a genuine split, for example between studies finding a protective association between cattle ownership and malaria risk and studies finding the reverse, both sets of findings are reported together with the contextual factors proposed to explain the discrepancy.

3. Vector Bionomics and the Biological Basis of Host Diversion

3.1 Host Preference across Anopheles Species

Diversion of a mosquito population toward livestock is possible only to the extent that the population's constituent species and sibling taxa are behaviourally capable of feeding on non-human hosts. Among the major African vectors, this capacity is markedly uneven. An. gambiae sensu stricto and An. funestus sensu stricto are, across most of their range, strongly anthropophilic and endophilic, feeding preferentially on humans indoors and showing comparatively little flexibility toward livestock even where cattle are abundant (Franco et al., 2014; Kitau et al., 2012). An. arabiensis, by contrast, is consistently described across independent field studies as an opportunistic feeder whose host choice tracks host availability rather than a fixed preference, feeding readily on cattle, goats, sheep and humans depending on what is accessible at the time and place of host-seeking (Asale et al., 2017; Main et al., 2016; Tirados et al., 2011). A blood-meal analysis of four Anopheles species in the Mwea rice-irrigation scheme of Kenya illustrates the magnitude of this species-level divergence: across 2,796 assayed blood meals, bovine blood accounted for between 56.3% and 71.4% of identified meals across all four species examined, compared with 1.1% to 23.9% for human blood, with An. arabiensis alone contributing over three-quarters of the sampled Anopheles population (Muriu et al., 2008). Within that same dataset, the bovine blood index of indoor-collected An. arabiensis (71.8%) exceeded that of outdoor-collected individuals (41.3%), while the human blood index did not differ significantly between locations, a pattern the authors attributed to local agro-ecological conditions rather than a fixed species trait, underscoring that host choice in this species is context-dependent rather than categorical (Muriu et al., 2008).

The molecular basis of this behavioural plasticity has been partially resolved. A genome-wide association study of An. arabiensis collected resting indoors and outdoors after feeding on humans or cattle in the Kilombero

Valley of Tanzania identified a significant genetic component to host choice, linked to the standard, non-inverted arrangement of the 3Ra paracentromeric chromosome inversion, which was significantly enriched among cattle-fed individuals relative to non-cattle-fed individuals (Main et al., 2016). No comparable genetic association was detected for indoor versus outdoor resting behaviour in the same dataset, suggesting that host choice and resting location, while often discussed together as components of a single "behavioural resistance" phenotype, may be under partially independent genetic and environmental control. This distinction matters for the present review because it implies that selection pressure from ITNs, which acts most directly on resting and biting location, need not act uniformly on host choice, complicating any simple prediction that net-driven selection will mechanically increase the zoophagic fraction of a vector population.

Host-choice plasticity is not confined to An. arabiensis, nor is it confined to high-transmission settings. A blood-meal study of malaria vectors in an area of low transmission in Senegal similarly found substantial heterogeneity in host feeding preference across co-occurring Anopheles taxa, reinforcing that the composition of the locally available host community, not the presence or absence of cattle alone, shapes the net direction of host-seeking behaviour in a given setting (Gueye et al., 2023). Taken together with the Kenyan and Ethiopian findings above, this indicates that host-choice data collected in one agro-ecological zone cannot be assumed to generalise to another without local verification, a caution that recurs throughout the methodological appraisal in Section 8.

3.2 The Human Blood Index and Bovine Blood Index as Diversion Metrics

The principal entomological metrics used to quantify host diversion are the human blood index (HBI), the proportion of identified blood meals derived from humans, and its complement for a specific non-human host, most often the bovine blood index (BBI). A systematic review and meta-regression of HBI data for the three major African vectors found substantial and systematic variation in HBI according to sampling location, collection method and the local availability of alternative hosts, cautioning that HBI values reported from a single study site and season should not be extrapolated as fixed species constants (Orsborne et al., 2018). This caution is directly relevant to the zooprophylaxis literature, in which HBI and BBI values are frequently used as the primary or sole outcome measure for judging whether diversion has occurred; because HBI is sensitive to sampling method (indoor resting collections yield systematically different HBI values from outdoor collections, as shown in the Mwea data above) and to the human-to-animal host ratio actually present at a given site and moment, cross-study comparison of HBI values in the absence of matched sampling protocols is prone to conflating true behavioural difference with methodological artefact.

A further limitation, noted across the reviewed literature, is that HBI and BBI describe the origin of completed blood meals and therefore reflect host choice among the successfully fed subset of a mosquito population; they do not directly measure the biting rate on humans, the survival of mosquitoes after feeding, or the malaria transmission risk that results. A reduction in HBI accompanying the introduction of livestock is consistent with, but does not by itself establish, a corresponding reduction in the entomological inoculation rate, since it is possible for the same or a larger absolute number of human bites to occur alongside a larger denominator of non-human bites if the presence of livestock increases overall vector density or survival (Saul, 2003; Sota & Mogi, 1989). This distinction between a proportional and an absolute effect is a recurring source of interpretive divergence in the literature reviewed in Section 4, and it is one that the theoretical modelling literature reviewed in Section 6 addresses explicitly.

4. Passive Zooprophylaxis: Entomological and Epidemiological Evidence

4.1 Foundational and Classic Field Studies

The empirical zooprophylaxis literature is anchored by a small number of well-controlled field studies conducted between the mid-1990s and the early 2010s, several of which reached opposing conclusions under superficially similar conditions, and whose contrasts are instructive precisely because they establish the moderating variables addressed later in this section. In Pakistan, where the principal vectors An. stephensi and An. culicifacies are markedly zoophilic, cattle ownership was nonetheless found to be associated with a significantly higher, not lower, prevalence of malaria, a result the authors interpreted as a failure of passive zooprophylaxis attributable to the close physical proximity in which cattle were typically kept relative to human sleeping areas in the study communities (Bouma & Rowland, 1995). In The Gambia, a paired-cohort study of

204 children matched for the presence or absence of cattle within twenty metres of the sleeping compound found that the human blood index of An. arabiensis was significantly reduced in cattle-owning compounds relative to non-cattle-owning compounds (with HBI in cattle-free compounds reaching 82% for An. arabiensis, against lower and more variable values for the co-occurring An. gambiae sensu stricto and An. melas), yet this entomological shift was not accompanied by any detectable difference in sporozoite rate or in the estimated individual risk of malaria infection between the two groups of children (Bøgh et al., 2001). A companion analysis of the same cohort further noted that any apparent epidemiological benefit associated with cattle ownership was confounded by household wealth, since cattle-owning households were systematically better resourced, complicating any causal attribution of reduced parasitaemia to zooprophylaxis per se (Bøgh et al., 2002).

Ethiopian and East African field experiments have generated a similarly mixed picture under conditions more directly analogous to those addressed by this review. An experimental analysis surrounding a human volunteer with a ring of twenty cattle at ten metres' radius in the Arba Minch district of southern Ethiopia found that the human landing catch of An. arabiensis was reduced by 49% for a volunteer positioned indoors, but showed no statistically significant reduction outdoors, and the corresponding reduction for the secondary vector An. pharoensis was of the order of 44% to 50% both indoors and outdoors (Tirados et al., 2011). The authors concluded explicitly that even a cattle-to-human ratio as favourable as 20:1 did not confer material zooprophylactic protection against An. arabiensis in an area of high endemicity, while acknowledging that the indoor effect, though real, was of a magnitude unlikely to translate into a meaningful reduction in malaria incidence on its own. A subsequent experiment at the same site, examining the effect of calf proximity rather than large cattle herds, found that placing a calf immediately adjacent to or inside a shelter containing a human volunteer increased, rather than decreased, the mosquito landing rate on that volunteer relative to a calf-free control, leading the authors to recommend that cattle be deployed at a substantial distance from human residences rather than allowed to remain close to sleeping quarters (a finding consistent with the zoopotentiation mechanism discussed in Section 4.2).

4.2 Zoopotentiation: When Livestock Increase Risk

The mechanism by which livestock proximity can increase rather than decrease human exposure has been characterised across multiple independent settings, and the realist review by Donnelly et al. (2015) identified spatial proximity between animal shelters and human sleeping quarters, together with vector anthropophily, as the two variables most consistently associated with zoopotentiation across the twenty empirical studies retained in that synthesis. The mechanism operates through two partially distinct pathways. The first is a straightforward increase in local host-seeking mosquito density: livestock kept near a dwelling increase the overall availability of blood meals and carbon dioxide and volatile host cues in the immediate vicinity of the house, attracting a larger absolute number of host-seeking mosquitoes into the airspace around human sleeping quarters even if the proportion of those mosquitoes that ultimately feed on the human occupant is unchanged or reduced. This pathway is consistent with the finding, reported for a calf placed adjacent to a human volunteer in southern Ethiopia, that immediate proximity increased human landing rates relative to a livestock-free control. The second pathway concerns vector survival: because a mosquito that has fed successfully, whether on a human or an animal, is more likely to survive to complete the extrinsic incubation period of the malaria parasite and to seek a further blood meal than a mosquito that has failed to feed, an increase in the overall availability of blood meals near a dwelling can increase the surviving, potentially infectious vector population even where the proportion of human-derived blood meals declines, an outcome anticipated by the modelling work discussed in Section 6 (Saul, 2003; Sota & Mogi, 1989).

Epidemiological evidence for zoopotentiation extends beyond the classic Pakistan and Gambia studies. Contemporary multi-country analyses of urban malaria risk in sub-Saharan Africa have reported a substantially elevated pooled odds of malaria infection among households keeping livestock, on the order of a fourfold increase across pooled estimates from several urban settings, albeit with wide confidence intervals and appreciable heterogeneity between the constituent studies, a pattern the reviewing authors attributed in part to close cohabitation between people and animals characteristic of unplanned urban and peri-urban settlement. Conversely, a large cohort study in south-central Ethiopia found that livestock ownership was associated with a reduced, not increased, incidence of malaria over a multi-year follow-up period, with the protective association strengthening as the livestock-to-human ratio increased, a result the authors related explicitly to the exophilic, pre-bedtime biting behaviour of the locally dominant An. arabiensis population and to a high bovine blood index recorded among outdoor-collected vectors in the same area. These apparently contradictory findings, elevated risk in some urban cohorts and reduced risk in some rural Ethiopian cohorts, are not necessarily inconsistent once vector ecology and housing arrangement are taken into account: the moderating variables identified by Donnelly et al. (2015), namely vector anthropophily and the spatial separation of animals from sleeping quarters, differ systematically between densely settled urban compounds, where livestock are typically kept in immediate proximity to living space, and rural agro-pastoral settings, where corralling at a distance from the house is more feasible and more commonly practised.

4.3 Spatial Placement of Livestock as a Determinant

Across the studies reviewed in Sections 4.1 and 4.2, the single variable most consistently identified as determining the sign of the livestock effect is distance between animal housing and human sleeping quarters. A study of household-level cattle presence and corralling distance in Chikwawa district, southern Malawi, found that the presence of cattle near a house was associated with a significant reduction in the abundance of indoor-resting An. funestus sensu lato, and that this protective association was strongest where cattle were corralled overnight at fifteen metres or less from the house, whereas the abundance of An. arabiensis, the more strongly zoophilic species at the same site, showed no significant association with cattle presence at any distance examined (Mburu et al., 2021). This species-specific divergence, in which cattle proximity appeared protective for one vector but neutral for the more zoophilic vector at the same site, illustrates that even within a single study population the zooprophylaxis-zoopotentiation balance cannot be generalised across co-occurring Anopheles taxa, and that findings framed simply as "cattle reduce (or increase) vector abundance" without species disaggregation risk averaging over opposing effects.

Housing condition more broadly has also been examined as a determinant of indoor vector density independent of livestock placement specifically; a study in a highland area of central Ethiopia found that housing characteristics were significantly associated with indoor-biting and indoor-resting An. arabiensis density, a finding relevant to the present review because household wealth, housing quality and livestock ownership are frequently correlated in the same populations, reinforcing the concern, already raised in relation to the Gambia cohort, that epidemiological associations between livestock ownership and malaria risk can reflect socioeconomic confounding as readily as a genuine entomological mechanism (Animut et al., 2013). Collectively, the spatial-placement literature supports a qualified conclusion: where zoophilic vector species predominate, where livestock are corralled at a meaningful distance from sleeping quarters, typically on the order of tens of metres rather than a few metres, and where the alternative host population is not so large as to increase overall vector density and survival disproportionately, passive zooprophylaxis can produce a measurable, if generally modest, reduction in human-vector contact; where any of these conditions is violated, the same intervention can plausibly increase risk. Table 2 summarises the representative entomological and epidemiological studies discussed in this section, organised by the direction of effect each reported.

Table 2. Representative entomological and epidemiological evidence on livestock presence, placement and malaria risk, organised by direction of effect

Study (location, design)	Vector species	Key finding	Direction of effect reported	Supporting references
Pakistan, cross-sectional cohort	An. stephensi, An. culicifacies	Cattle ownership associated with higher malaria prevalence; attributed to close proximity of animals to housing	Zoopotentiation	Bouma & Rowland, 1995
The Gambia, paired-cohort (204 children)	An. arabiensis, An. gambiae s.s., An. melas	Reduced HBI for An. arabiensis with cattle present, but no difference in sporozoite rate or malaria risk; wealth confounding noted	Entomological diversion without epidemiological benefit	Bøgh et al., 2001; Bøgh et al., 2002

Study (location, design)	Vector species	Key finding	Direction of effect reported	Supporting references
Arba Minch, Ethiopia, experimental cattle ring (20:1 ratio)	An. arabiensis, An. pharoensis	Indoor human landing catch reduced 49% with cattle ring; no significant outdoor reduction for An. arabiensis	Partial, location-dependent zooprophylaxis	Tirados et al., 2011
Arba Minch, Ethiopia, calf-proximity experiment	An. arabiensis	Calf placed adjacent to or inside human shelter increased mosquito landing rate relative to calf-free control	Zoopotentiation	Tirados et al., 2011
Chikwawa, Malawi, distance-stratified household survey	An. funestus s.l., An. arabiensis	Cattle within 15 m associated with reduced indoor-resting An. funestus; An. arabiensis unaffected by cattle presence at any distance	Species-specific zooprophylaxis	Mburu et al., 2021
Lake Victoria, Kenya, cross-sectional entomological survey (high ITN coverage)	An. arabiensis, An. gambiae s.s., An. funestus s.s.	Cattle associated with reduced human feeding specifically by An. arabiensis, jointly with ITN coverage; no effect on other species	ITN-associated, species-specific zooprophylaxis	Iwashita et al., 2014
Central Ethiopia, housing-condition survey	An. arabiensis	Housing quality significantly associated with indoor vector density, independent of livestock placement	Confounding factor rather than direct livestock effect	Animut et al., 2013

Note. ITN = insecticide-treated net; LLIN = long-lasting insecticidal net; ITL = insecticide-treated livestock; HBI = human blood index; BBI = bovine blood index; IRS = indoor residual spraying; MDA = mass drug administration

5. Interaction between ITNs and Livestock-Mediated Host Diversion: The Push-Pull Hypothesis

5.1 Direct Entomological Evidence

The specific hypothesis that ITN deployment amplifies livestock-mediated diversion, framed explicitly as a "push-pull" mechanism in which nets push mosquitoes away from protected humans and livestock pull them toward an alternative host, was tested directly in a study conducted across three villages of high ITN coverage (over 80%) along the Kenyan shore of Lake Victoria (Iwashita et al., 2014). Combining a full livestock census with georeferenced overnight tethering points, mosquito collection across 295 household spray catches yielding 8,123 mosquitoes of which 1,664 were Anopheles vectors, and blood-meal and sporozoite analysis, the study found that vector household abundance was jointly predicted by the number of household occupants, the number of goats and sheep tethered nearby, and ITN presence, with ITNs approximately halving overall mosquito abundance. Critically for the push-pull hypothesis, the presence of cattle was associated with a significant reduction in human feeding specifically for An. arabiensis, while feeding rates on humans by the co-occurring An. gambiae sensu stricto and An. funestus sensu stricto were unaffected by cattle presence, and vector density itself did not increase with livestock abundance for these latter two species as it did for An. arabiensis. The authors interpreted this pattern as evidence that ITNs and cattle jointly reduced human-vector contact through a mechanism specific to the opportunistic feeder An. arabiensis, describing ITNs as having "pushed" a decline in indoor mosquito abundance historically, with cattle then further "pulling" surviving host-seeking An. arabiensis away from human hosts (Iwashita et al., 2014).

This study remains the clearest direct entomological test of the ITN-livestock interaction identified in the present review, and its findings merit careful qualification rather than uncritical adoption as evidence of a robust, generalisable push-pull effect. First, the effect was specific to cattle and to An. arabiensis; goats and sheep, despite being associated with higher overall mosquito abundance, were not associated with a corresponding reduction in human feeding, indicating that the diversion effect is not a generic property of "livestock" but depends on the specific host species and its attractiveness relative to humans. Second, the study design was cross-sectional and observational with respect to both ITN use and livestock placement; because both were pre-existing community practices rather than randomised or experimentally manipulated conditions, the analysis could statistically associate ITN coverage, livestock presence and reduced human feeding, but could not establish an interaction term demonstrating that the marginal effect of cattle on human feeding was different in the presence versus the absence of high ITN coverage, since ITN coverage was uniformly high (over 80%) across all three study villages and therefore did not vary sufficiently within the dataset to support such a test. The study, in other words, demonstrates that cattle and ITNs are jointly associated with reduced An. arabiensis feeding on humans in a high-ITN-coverage setting; it does not, on its own design, demonstrate that ITNs caused an amplification of the cattle effect relative to a lower-coverage counterfactual.

No subsequent study identified in this review has replicated the Lake Victoria design with an explicit low-coverage comparison arm or a before-and-after design spanning an ITN scale-up campaign in a livestock-keeping community, leaving the causal, ITN-dependent version of the push-pull hypothesis as biologically plausible and consistent with the one directly relevant field study available, but empirically under-tested relative to the strength with which the mechanism has subsequently been invoked in review and policy-proposal literature (Otolorin et al., 2026; Ruiz-Castillo et al., 2022). This livestock-mediated push-pull mechanism should be distinguished from a separate, synthetic push-pull strategy tested in western Kenya, in which repellent and attractant chemical blends rather than live animals were deployed around houses to reduce mosquito entry (Menger et al., 2014). The two approaches share a common conceptual structure but differ fundamentally in their deployment logistics, cost and dependence on local livestock-keeping practice, and the synthetic approach does not carry the zoopotentiation risk documented in Section 4.2 for live animal hosts kept in close proximity to dwellings.

5.2 Behavioural and Species Shifts as a Confounding and Reinforcing Process

A related and better-replicated body of evidence documents that ITN scale-up itself alters vector species composition and behaviour in ways that are mechanistically connected to, but conceptually distinct from, livestock-mediated diversion, and that must be disentangled from it when interpreting temporal trends in HBI or BBI. Paired experimental hut trials conducted in two ecologically distinct sites in northeastern Tanzania found that mortality induced by ITNs and LLINs was consistently lower for An. arabiensis than for An. gambiae sensu stricto and An. funestus across six insecticide products tested, a differential susceptibility to nets that the authors proposed as an explanation for the species shifts toward An. arabiensis dominance observed following ITN and LLIN scale-up in areas where the two species previously co-occurred (Kitau et al., 2012). A four-year longitudinal study following a mass LLIN distribution in Tanzania found that An. funestus sensu lato density declined significantly over the study period while both An. arabiensis and the residual An. funestus population showed an increasing tendency to rest outdoors rather than indoors, a behavioural shift consistent with selection pressure from indoor-targeted nets acting on resting location even in the absence of a parallel shift in host choice (Kreppel et al., 2020). More recent bionomic surveillance in south-eastern Tanzania under conditions of high, sustained ITN coverage has confirmed the persistence of substantial An. arabiensis and An. funestus activity inside houses despite net coverage, indicating that species replacement and behavioural avoidance have not eliminated indoor human-vector contact even where they have altered its composition (Limwagu et al., 2024).

The implication for the zooprophylaxis literature is that any observed decline in HBI or increase in BBI following ITN scale-up in a mixed-species vector population may reflect a shift in the relative abundance of species with differing baseline host preferences (a compositional effect operating at the population level) rather than, or in addition to, a behavioural change in host choice within a given species induced by net-driven exclusion from human hosts (a genuine push-pull effect operating at the individual or species level). Distinguishing these two mechanisms requires species-disaggregated data collected consistently before and after net scale-up, a requirement that few of the epidemiological zooprophylaxis studies reviewed in Section 4 were designed to meet, since many predate the routine molecular species identification and blood-meal genotyping methods that became standard only in the past fifteen years.

5.3 Residual and Outdoor Transmission as the Broader Context

The push-pull hypothesis and the insecticide-treated-livestock literature reviewed in Section 7 both sit within the broader residual-transmission problem quantified by Sherrard-Smith et al. (2019) and reviewed comprehensively elsewhere as a distinct threat to the effectiveness of indoor-targeted vector control (Sougoufara et al., 2020). This broader literature is directly relevant to the present review for two reasons. First, it establishes the scale of the problem that livestock-based diversion, whether passive or insecticide-augmented, would need to address to be programmatically meaningful: an intervention that reduces human-vector contact only marginally, of the kind reported by Tirados et al. (2011) for outdoor exposure, is unlikely to make an appreciable dent in a residual-transmission burden estimated in the tens of millions of cases annually across the continent. Second, it clarifies that outdoor and early-evening biting, the behavioural niche in which livestock-based diversion is most plausible, is itself heterogeneous across settings and years, with entomological surveillance in Burkina Faso finding no significant longitudinal shift in outdoor-biting or outdoor-resting behaviour over a multi-year period despite rapidly rising physiological insecticide resistance in the same vector population, indicating that behavioural and physiological resistance mechanisms do not necessarily co-evolve in lockstep and that livestock-based approaches cannot be assumed to generalise uniformly across settings simply because outdoor biting has been documented somewhere in the region.

6. Theoretical and Mathematical Modelling of Zooprophylaxis

6.1 The Foundational Two-Host Framework

Formal mathematical treatment of zooprophylaxis substantially predates the recent entomological literature and has consistently identified the same structural tension that the empirical studies reviewed in Section 4 illustrate in practice. An early two-bloodmeal-host extension of the Ross-Macdonald malaria transmission framework, combining a density-dependent larval-stage model with an adult blood-feeding-success model incorporating both human and animal hosts, found that introducing domestic animals that are readily fed upon by mosquitoes tends to increase overall mosquito density and, under a range of parameter combinations, to increase rather than decrease the frequency of human bites and the resulting malaria endemicity, because improved blood-meal availability increases mosquito survival and reproductive success; the model predicted that malaria elimination through zooprophylaxis alone would require an implausibly large ratio of easily accessible animals to humans (Sota & Mogi, 1989).

This structural result was substantially generalised in a widely cited simulation study that modelled zooprophylaxis and its converse, zoopotentiation, as outcomes of a single underlying parameter set rather than as distinct phenomena requiring separate models (Saul, 2003). The central finding of this analysis is that the sign and magnitude of the net effect of introducing animal hosts depends critically on the mortality rate experienced by mosquitoes while host-seeking, a parameter that is difficult to measure directly in the field and is consequently rarely reported alongside the entomological outcomes, such as HBI and vector density, that most empirical zooprophylaxis studies do report. Where host-seeking mortality is high, meaning that a mosquito faces substantial risk of dying before locating and completing a blood meal, the introduction of additional, easily accessible animal hosts can reduce this mortality risk sufficiently to increase overall vector survival and, counter-intuitively, increase transmission even as the proportion of bites falling on humans declines; where host-seeking mortality is low, the diversion effect can dominate and reduce transmission. Because field studies of zooprophylaxis have, with rare exceptions, reported blood-meal-based outcomes (HBI, BBI) or density-based outcomes (mosquito abundance) without concurrently estimating host-seeking mortality, the modelling literature and the empirical literature have developed along largely parallel tracks, and reconciling a given field finding with the theoretical prediction of protection versus harm is frequently not possible from the reported data alone.

6.2 Extensions Incorporating Insecticide-Treated Nets and Livestock Mortality

Subsequent modelling work has extended this two-host framework to incorporate ITNs and insecticide-treated livestock explicitly, moving the theoretical literature closer to the specific question addressed by this review. A deterministic model of mosquito host-seeking behaviour and mortality that jointly incorporated bed nets, cattle, insecticides and excito-repellency effects found that the presence of cattle could substantially alter the predicted impact of ITN coverage on human biting rate, with the direction and magnitude of the effect again sensitive to the relative mortality mosquitoes experience when contacting treated nets versus feeding on untreated versus treated animals (Killeen & Thomas, 2007). An ecological model explicitly combining endectocide-treated livestock with insecticidal bed nets found that the two interventions could act complementarily, since ITNs primarily affect indoor-biting, endophilic behaviour while livestock-targeted endectocides act on the outdoor, zoophagic component of the same vector population that ITNs do not reach, but the projected combined impact depended strongly on assumptions about the proportion of the vector population exhibiting zoophagic behaviour and on the coverage and turnover rate achievable for livestock treatment in a real programmatic setting (Yakob et al., 2017). A related difference-equation model incorporating a heterogeneous host population reached a broadly consistent conclusion, namely that ITN coverage and host-seeking mortality parameters derived from field studies of livestock and net use jointly determine whether the sporozoite rate and entomological inoculation rate decline monotonically with increasing ITN coverage or instead exhibit non-monotonic behaviour at intermediate coverage levels, depending on how strongly mosquitoes are diverted to non-human hosts as human availability declines.

Two conclusions follow from this modelling literature that bear directly on the interpretation of the empirical evidence reviewed in Sections 4 and 5. First, the theoretical prediction that ITN deployment could amplify livestock-mediated diversion, the mechanistic premise underlying the Iwashita et al. (2014) push-pull finding, is consistent with the mathematical structure of these models under plausible parameter ranges, lending biological plausibility to the empirical finding rather than treating it as an isolated anomaly. Second, the same models demonstrate with equal force that the same structural change, reduced human availability owing to high ITN coverage, could instead increase overall vector survival and, if host-seeking mortality is low and livestock density is high, increase rather than decrease transmission risk for unprotected household members or in years or seasons of lower net use, a possibility not directly tested by the available field studies and worth explicit consideration in any programme messaging that encourages livestock-keeping as a malaria-control adjunct to net distribution.

7. From Passive Diversion to Lethal Diversion: Insecticide-Treated Livestock and Endectocide-Based Approaches

7.1 Rationale and Early Efficacy Studies

Because passive zooprophylaxis diverts mosquitoes without killing them, and because the modelling literature reviewed in Section 6 demonstrates that diversion without mortality can increase rather than decrease vectorial capacity under plausible conditions, a substantial body of more recent research has pursued the alternative strategy of treating livestock with insecticides or endectocides so that a mosquito feeding on the animal is killed or has its reproductive capacity impaired, converting an epidemiologically ambiguous diversion event into an unambiguous reduction in the surviving vector population (Ruiz-Castillo et al., 2022). This approach, generally termed insecticide-treated livestock (ITL) when topical or systemic insecticides are used and endectocide-based vector control when veterinary antiparasitic drugs such as ivermectin, eprinomectin or moxidectin are administered to livestock for their mosquitocidal side effect, has been tested through a progression of laboratory, semi-field and field study designs over the past two decades.

Semi-field and field efficacy trials in western Kenya evaluated ivermectin, eprinomectin and fipronil administered orally or topically to Zebu cattle and found that all three compounds significantly reduced the survival time of An. arabiensis fed on treated animals, with eprinomectin and fipronil providing the longest-lasting effect, remaining significantly effective at twenty-one days post-treatment at higher doses (Poché et al., 2015). A field-scale pilot of topical eprinomectin applied weekly to cattle in the Samia District of western

Kenya produced measurable, though time-limited, entomological effects on local An. arabiensis populations (Lozano-Fuentes et al., 2016), and a corresponding pilot of oral fipronil at the same site found a suggestive but not statistically robust reduction in indoor-resting vector density, with An. gambiae sensu stricto density unaffected between treatment and control plots, consistent with the species-specificity of the underlying diversion mechanism already established in the passive zooprophylaxis literature (Poché et al., 2017). Semi-field trials of ivermectin-treated cattle in south-eastern Tanzania similarly demonstrated reduced blood digestion, reduced egg production and reduced survivorship among a free-living An. arabiensis population feeding on treated animals (Lyimo et al., 2017).

A slow-release ivermectin implant formulation, designed to overcome the short effective duration of standard injectable or oral dosing, produced a marked reduction in An. arabiensis survival that was sustained for over six months in a controlled cattle trial, representing a substantial advance in the practical durability of the intervention relative to earlier formulations that required repeated dosing at intervals as short as one to three weeks (Chaccour et al., 2018). Complementary work in Burkina Faso demonstrated that mass administration of ivermectin to peridomestic cattle, alongside human mass drug administration, could target the vector reservoir sustained by zoophagic feeding, addressing directly the concern that human-only ivermectin administration leaves zoophagic vectors, and the transmission they sustain, untouched (Pooda et al., 2015).

7.2 Cluster-Randomised and Field-Scale Evidence

The evidentiary standard for ITL and endectocide-based approaches has progressed, though unevenly, toward cluster-randomised and village-randomised field designs capable of supporting stronger causal inference than the semi-field efficacy trials described above. The clearest existing example of a livestock-based intervention achieving a directly measured epidemiological, rather than purely entomological, endpoint remains a community-randomised trial in Pakistan in which deltamethrin was applied by sponging to the great majority, roughly 93%, of the local cattle, sheep and goat population; this intervention was associated with a 56% reduction in Plasmodium falciparum incidence and a 54% reduction in prevalence relative to control communities, with efficacy reported as comparable to conventional indoor residual spraying but at substantially lower cost, as synthesised in the One Health review of livestock-based malaria interventions by Franco et al. (2014). This trial remains, more than two decades after its conduct, the principal piece of evidence that insecticide-treated livestock can achieve a clinical malaria endpoint at the community level, and its heavy citation across the subsequent literature reflects the continued absence of a comparable replication.

More recent village-randomised trials have tested endectocide-treated cattle with entomological rather than clinical endpoints. A cluster-randomised trial of ivermectin-treated cattle across six villages in Central Vietnam, using cattle-baited traps to sample anopheline populations before and after a two-day ivermectin administration period in treatment villages, found a substantial decline in total anopheline catches in both treatment and control villages over the study period, complicating interpretation of the specific treatment effect, and the authors attributed this limitation to unexpectedly high spatiotemporal variability in trapping rates and possible spillover of treatment effects between neighbouring villages, illustrating a recurring methodological challenge for field-scale evaluation of livestock-based vector control in settings with high anopheline diversity and mobile vector populations (Cramer et al., 2024). A small-scale pilot trial of fipronil and ivermectin applied to cattle in northern Belize found that both compounds significantly reduced survivorship and ovarian development in field-collected An. albimanus for up to seven days post-treatment, with efficacy declining by fourteen days, demonstrating that the transient duration of standard endectocide dosing observed in African trial settings generalises to a Central American zoophagic vector system as well (Dreyer et al., 2019). Table 3 draws together the principal field and semi-field evaluations of insecticide-treated livestock and endectocide-based approaches discussed in this section.

7.3 Toward Integrated Deployment and Its Evidentiary Requirements

The logical convergence of the passive zooprophylaxis and ITL literatures is an integrated deployment in which ITNs address indoor, anthropophilic, endophilic transmission while insecticide-treated or endectocide-treated livestock addresses the outdoor, zoophagic residual component that ITNs structurally cannot reach, a proposal advanced explicitly in recent conceptual literature (Otolorin et al., 2026; Ruiz-Castillo et al., 2022) and supported in principle by the modelling work of Yakob et al. (2017) and Killeen and Thomas (2007). A phase III cluster-randomised trial explicitly designed to evaluate ivermectin and alternative endectocides administered to both cattle and humans as a combined malaria-vector-control strategy has been registered and is described in a published trial protocol, representing to date the most methodologically rigorous test of the integrated approach to have reached the stage of field implementation (Chaccour et al., 2023).

Table 3. Field and semi-field evaluations of insecticide-treated livestock and endectocide-based approaches

Compound/formulation	Delivery route	Target vector (setting)	Principal entomological or epidemiological outcome	Supporting references
Deltamethrin, sponge-on	Topical, community-wide (93% coverage)	An. stephensi, An. culicifacies (Pakistan)	56% reduction in P. falciparum incidence; 54% reduction in prevalence; comparable efficacy to IRS at lower cost	Franco et al., 2014
Ivermectin, eprinomectin, fipronil (comparative dosing)	Oral and topical	An. arabiensis (western Kenya, semi-field)	All three compounds significantly reduced survival time; eprinomectin and fipronil effective to 21 days post-treatment	Poché et al., 2015
Eprinomectin, topical	Weekly topical application	An. arabiensis (Samia District, western Kenya, field pilot)	Measurable but time-limited reduction in vector density	Lozano-Fuentes et al., 2016
Fipronil, oral	Single oral dose	An. arabiensis (Samia District, western Kenya, field pilot)	Suggestive but not statistically robust reduction in indoor-resting density; no effect on An. gambiae s.s.	Poché et al., 2017
Ivermectin, injectable	Semi-field exposure	An. arabiensis (south-eastern Tanzania)	Reduced blood digestion, egg production and survivorship in free-living population	Lyimo et al., 2017
Ivermectin, slow-release implant	Subcutaneous implant	An. arabiensis (controlled cattle trial)	Marked reduction in survival sustained for over six months	Chaccour et al., 2018
Ivermectin, injectable, mass administration	Peridomestic cattle plus human MDA	Anopheles spp. (Burkina Faso)	Proposed and piloted as a combined human-livestock approach to target zoophagic vector reservoir	Pooda et al., 2015

Compound/formulation	Delivery route	Target vector (setting)	Principal entomological or epidemiological outcome	Supporting references
Ivermectin, injectable	Village-randomised administration	Anopheline complex (Central Vietnam)	No robust treatment-specific effect isolated; high spatiotemporal variability and possible spillover	Cramer et al., 2024
Fipronil and ivermectin, topical and injectable	Pilot field trial	An. albimanus (northern Belize)	Both compounds reduced survivorship and ovarian development for up to 7 days; efficacy declined by 14 days	Dreyer et al., 2019
Ivermectin and alternative endectocides	Combined cattle and human administration	Multiple Anopheles vectors (multi-country, phase III protocol)	Registered cluster-randomised trial protocol; results pending	Chaccour et al., 2023

Note. ITN = insecticide-treated net; LLIN = long-lasting insecticidal net; ITL = insecticide-treated livestock; HBI = human blood index; BBI = bovine blood index; IRS = indoor residual spraying; MDA = mass drug administration

Notwithstanding this methodological progress, the evidentiary base for integrated ITN-ITL deployment remains substantially weaker than the evidentiary base for ITNs alone, for three specific reasons that recur across the trials reviewed in this section. First, with the partial exception of the Pakistan deltamethrin trial, the great majority of ITL and endectocide field studies to date have measured entomological endpoints, principally mosquito survival, fecundity or trap catch, rather than clinical malaria incidence or prevalence, leaving the translation from entomological efficacy to epidemiological impact largely inferential. Second, the duration of mosquitocidal effect achievable with currently approved dosing regimens for ivermectin and related endectocides is transient, typically one to three weeks even for the more persistent compounds and formulations, necessitating either frequent re-treatment, a substantial logistical and cost burden in resource-limited settings, or further development of long-acting formulations such as the six-month implant tested by Chaccour et al. (2018), which has not yet been evaluated at village scale. Third, because the underlying diversion mechanism is species-specific, effective almost exclusively against zoophagic vectors such as An. arabiensis and largely ineffective against the more strictly anthropophilic An. gambiae sensu stricto and An. funestus sensu stricto populations that continue to dominate transmission in much of West and Central Africa, the geographic and entomological settings in which ITL could plausibly contribute a meaningful marginal reduction in transmission are narrower than the settings in which ITNs are deployed, and programme planning would need to incorporate local vector bionomic surveillance, of the kind reviewed in Section 3, as a precondition for rational targeting rather than assuming uniform applicability.

8. Methodological Quality and Sources of Heterogeneity across the Evidence Base

Assessment of the literature synthesised in Sections 4 through 7 identifies several recurring methodological features that constrain the strength of conclusions that can be drawn about the ITN-livestock interaction specifically, as distinct from livestock effects or ITN effects considered separately. The first and most consequential is confounding by household wealth and housing quality. Livestock ownership, particularly cattle ownership, is correlated with household socioeconomic status across nearly every setting examined in this review, and better-resourced households are also more likely to possess improved housing, an established independent protective factor against indoor vector density and malaria risk. The Gambia cohort study explicitly identified this confound as complicating interpretation of an observed epidemiological difference between cattle-owning and non-cattle-owning households (Bøgh et al., 2002), and it applies with equal or greater force to the urban and rural livestock-ownership cohort studies discussed in Section 4.2, few of which employed the kind of matched-cohort or statistical adjustment design used in the Gambia study.

The second recurring limitation is a mismatch between the outcome measured and the outcome of ultimate interest. As discussed in Section 3.2, HBI and BBI measure the composition of completed blood meals and are informative about host choice but not directly about human biting rate, vector density or transmission risk; many of the entomological studies reviewed report HBI or BBI shifts without a paired measure of absolute vector abundance or survival, precluding assessment of whether an observed proportional diversion corresponds to an absolute reduction in human exposure, the distinction the modelling literature identifies as determinative of whether zooprophylaxis or zoopotentiation results (Saul, 2003).

The third limitation concerns sampling method heterogeneity. Human landing catches, pyrethrum spray catches, exit traps, cattle-baited traps and resting collections each sample a different, only partially overlapping, component of a mosquito population's behavioural repertoire, and the Mwea Kenya data reviewed in Section 3.1 demonstrate that BBI and HBI values for the same species at the same site can differ substantially between indoor and outdoor collections (Muriu et al., 2008). Cross-study comparison of zooprophylaxis effect sizes without attention to sampling method risks attributing to biological difference what may in substantial part be a methodological artefact of differential sampling.

The fourth limitation, specific to the ITN-livestock interaction that is the central concern of this review, is the near-absence of study designs capable of statistically isolating an interaction effect. As discussed in Section 5.1, the principal directly relevant field study (Iwashita et al., 2014) was conducted at uniformly high ITN coverage and could not, by design, compare the livestock effect under high versus low coverage. Most epidemiological studies of livestock and malaria risk either do not report ITN use as a covariate at all or include it only as an independent term in a regression model rather than as an interaction term with livestock ownership, meaning that even where both livestock ownership and ITN use are measured, the specific quantity of interest for this review, namely whether the marginal effect of livestock on human exposure differs by level of ITN coverage, is frequently not estimable from the reported analysis.

Finally, the ITL and endectocide intervention trials reviewed in Section 7 exhibit a consistent progression in methodological rigour, from uncontrolled laboratory and semi-field efficacy studies toward cluster- and village-randomised designs, but even the most rigorous recent trials have encountered substantial practical obstacles to causal inference, including high spatiotemporal variability in vector trapping rates and probable spillover between geographically proximate treatment and control villages (Cramer et al., 2024), obstacles that are likely to recur in any future trial attempting to isolate an ITN-ITL interaction effect at village or community scale. These recurring limitations, together with the specific studies in which they are most evident, are summarised in Table 4.

Table 4. Methodological limitations recurring across the zooprophylaxis and insecticide-treated-livestock literature

Limitation	Explanation	Illustrative studies affected	Supporting references
Confounding by household wealth and housing quality	Livestock ownership correlates with socioeconomic status and housing quality, both independently protective against malaria, complicating causal attribution of risk differences to zooprophylaxis	The Gambia paired-cohort study explicitly identified this confound; comparable adjustment is largely absent from urban and rural cohort studies of livestock ownership	Bøgh et al., 2002; Animut et al., 2013
Outcome mismatch between blood-meal indices and transmission risk	HBI and BBI describe completed host choice, not biting rate, vector density or survival, so	Studies reporting HBI or BBI shifts without paired density or survival measures	Saul, 2003; Orsborne et al., 2018

Limitation	Explanation	Illustrative studies affected	Supporting references
	proportional diversion cannot be equated with absolute exposure reduction		
Sampling-method heterogeneity	Human landing catches, resting collections, exit traps and cattle-baited traps sample different, only partially overlapping components of vector behaviour, and yield different HBI/BBI values for the same population	Indoor versus outdoor blood-index divergence documented in the Mwea rice-scheme dataset	Muriu et al., 2008
Absence of an explicit ITN-livestock interaction term	Most studies measure livestock effects and ITN effects independently rather than testing whether the marginal livestock effect differs by ITN coverage level	The principal directly relevant field study was conducted at uniformly high coverage, precluding a coverage-gradient comparison	Iwashita et al., 2014
Reliance on entomological rather than clinical endpoints in ITL trials	Most insecticide-treated-livestock and endectocide trials report mosquito survival or fecundity rather than malaria incidence or prevalence	The Pakistan deltamethrin trial remains the principal exception with a directly measured clinical endpoint	Franco et al., 2014; Poché et al., 2015
Transient intervention efficacy and re-treatment burden	Standard endectocide dosing regimens retain mosquitocidal efficacy for only one to three weeks, necessitating frequent re-treatment for sustained impact	Efficacy decline documented across Kenyan, Tanzanian and Belizean field and semi-field trials	Poché et al., 2015; Dreyer et al., 2019
Spatiotemporal variability and spillover in village-randomised designs	High natural variability in vector trapping rates and movement of vectors between neighbouring treatment and control villages can obscure a true treatment effect	Explicitly identified as a limiting factor in the Vietnam cluster-randomised trial	Cramer et al., 2024

Note. ITN = insecticide-treated net; LLIN = long-lasting insecticidal net; ITL = insecticide-treated livestock; HBI = human blood index; BBI = bovine blood index; IRS = indoor residual spraying; MDA = mass drug administration

9. Future Directions

Four research priorities follow directly from the gaps identified in Sections 5 and 8, ordered here from the most immediately actionable to the most resource-intensive and summarised, alongside their rationale and proposed study designs, in Table 5.

The most immediate priority is the conduct of entomological studies explicitly designed with an ITN coverage gradient or a before-and-after ITN scale-up comparison in livestock-keeping communities, so that the interaction term between net use and livestock-mediated diversion can be statistically estimated rather than inferred from studies conducted at uniform coverage. Such studies should employ species-disaggregated blood-meal analysis using molecular methods, given the demonstrated divergence in host choice and net susceptibility between An. arabiensis and its sibling species (Kitau et al., 2012; Main et al., 2016), and should report paired measures of blood-meal composition (HBI, BBI) and absolute vector abundance or survival, so that proportional diversion can be distinguished from absolute exposure reduction, addressing the interpretive gap identified in Section 8. A stepped-wedge or cluster-randomised design introducing ITNs sequentially across villages with pre-existing, mapped livestock husbandry practices, with entomological sampling before and after each step, would represent a feasible near-term study design capable of generating the interaction estimate the current literature lacks.

Table 5. Research gaps and proposed priorities for future investigation

Gap	Rationale	Proposed study design	Supporting references
No study has isolated an ITN-coverage-by-livestock interaction term	The principal directly relevant field study was conducted at uniformly high ITN coverage, precluding a coverage-gradient comparison	Stepped-wedge or cluster-randomised ITN introduction across villages with mapped, pre-existing livestock husbandry, with species-disaggregated entomological sampling before and after each step	Iwashita et al., 2014
Host-seeking mortality is rarely measured in field zooprophylaxis studies	Theoretical modelling identifies this parameter as determinative of whether diversion protects or endangers a population, yet it is largely absent from field datasets	Mark-release-recapture and survival analysis of host-seeking mosquitoes conducted alongside standard blood-meal and density sampling	Saul, 2003; Sota & Mogi, 1989
Insecticide-treated-livestock evidence rests on entomological rather than clinical endpoints	Only one trial, now methodologically dated, has demonstrated a clinical malaria endpoint from livestock-based insecticide treatment	Adequately powered cluster-randomised trials with malaria incidence or prevalence as the primary endpoint	Chaccour et al., 2023; Franco et al., 2014
Endectocide efficacy is transient under currently approved dosing	Standard formulations retain mosquitocidal activity for only one to three weeks, limiting programmatic feasibility	Field-scale evaluation of long-acting and slow-release formulations at village or district scale	Chaccour et al., 2018
No validated criteria exist for targeting livestock-based interventions geographically	Effectiveness is mechanistically restricted to settings where zoophagic, opportunistic vectors predominate	Development and field validation of rapid, molecular vector-bionomic surveillance protocols to guide programmatic targeting	Kitau et al., 2012; Main et al., 2016

Note. ITN = insecticide-treated net; LLIN = long-lasting insecticidal net; ITL = insecticide-treated livestock; HBI = human blood index; BBI = bovine blood index; IRS = indoor residual spraying; MDA = mass drug administration

A second, closely related priority is the routine field measurement of host-seeking mortality, the parameter identified by theoretical modelling as determinative of whether livestock-mediated diversion protects or endangers a human population (Saul, 2003; Sota & Mogi, 1989). Mark-release-recapture methods and survival analysis of mosquitoes tracked from emergence through host-seeking and feeding, though logistically demanding, would allow direct empirical estimation of this parameter in the specific ecological settings where zooprophylaxis field trials are conducted, enabling reconciliation of empirical findings with theoretical prediction in a way that is currently not possible from the data reported in most field studies reviewed in Section 4.

A third priority, applicable to the insecticide-treated-livestock literature specifically, is the conduct of adequately powered cluster-randomised trials with clinical malaria incidence or prevalence as the primary endpoint, extending beyond the entomological survival and fecundity endpoints that dominate the current evidence base. The registered BOHEMIA trial protocol represents a step toward this standard (Chaccour et al., 2023), and its results, together with those of comparable future trials, should be prioritised for synthesis as they become available; in parallel, further development and field-scale testing of long-acting endectocide formulations, extending the six-month efficacy window demonstrated for a slow-release ivermectin implant under controlled conditions (Chaccour et al., 2018) to a programmatically deployable product, would address the transient-efficacy limitation identified as a recurring constraint in Section 7.3.

A fourth and longer-term priority concerns the geographic and entomological targeting of livestock-based interventions. Because the underlying mechanism is effective specifically against zoophagic, opportunistic vectors and is of limited relevance where strictly anthropophilic, endophilic species dominate transmission, future research should develop and validate practical, field-deployable criteria, potentially incorporating routine molecular species identification and blood-meal analysis, for identifying the settings in which livestock-based diversion or insecticide-treated livestock could plausibly contribute meaningfully to transmission reduction, so that programmatic resources are not directed toward settings, such as those dominated by An. gambiae sensu stricto or An. funestus sensu stricto, where the available evidence indicates the intervention is unlikely to be effective.

10. Conclusions

This review set out to examine whether, and under what conditions, insecticide-treated nets alter the magnitude or direction of livestock-mediated diversion of malaria vectors from humans. The synthesised evidence supports several defensible conclusions. Host diversion toward livestock is a real and well-documented phenomenon for opportunistic vectors, principally Anopheles arabiensis, but it is not a fixed or generalisable property of livestock keeping; its sign and magnitude depend on vector species composition, the spatial distance between animal housing and human sleeping quarters, the ratio of animals to humans, and, on the theoretical evidence, on a host-seeking mortality parameter that is rarely measured in field studies. Passive zooprophylaxis, in the absence of insecticide treatment of the animals concerned, has produced inconsistent epidemiological results across well-controlled studies conducted in comparable settings, with some populations showing reduced malaria risk associated with livestock ownership and others showing increased risk, a divergence that the literature attributes convincingly to the spatial and ecological moderators identified above rather than to any single, universally applicable mechanism. The specific hypothesis that ITN deployment amplifies livestock-mediated diversion through a push-pull dynamic is biologically plausible, is consistent with formal mathematical modelling of mosquito host-seeking behaviour, and is supported by one directly relevant field study demonstrating a species-specific reduction in human feeding by An. arabiensis associated jointly with high ITN coverage and cattle presence; it has not, however, been tested with a study design capable of isolating a genuine interaction effect, and it should accordingly be regarded as an evidence-consistent hypothesis rather than an established finding. Converting passive diversion into a lethal event through insecticide-treated livestock or endectocide administration addresses the principal theoretical objection to passive zooprophylaxis, namely that diversion without mortality can increase rather than decrease overall vector survival, and this approach has produced consistent entomological efficacy across a progression of laboratory, semi-field and field studies; its epidemiological impact at community scale, however, rests on a single, methodologically dated trial from Pakistan, and contemporary cluster-randomised evidence with clinical endpoints remains awaited. Taken together, the evidence supports cautious, context-specific consideration of livestock-based diversion and insecticide-treated livestock as adjuncts to, rather than substitutes for, insecticide-treated nets in settings where zoophagic vector species contribute substantially to residual transmission, while cautioning strongly against generic promotion of livestock-keeping near human dwellings as a malaria-control measure, given the demonstrated potential for such practices to increase, rather than reduce, human exposure under common husbandry conditions.

11. Limitations

As with any narrative review, the principal limitation is the potential for selection and interpretive bias in the choice and weighting of studies, notwithstanding the transparent search strategy and stated appraisal criteria set out in Section 2; a different reviewing team applying the same search strategy might reasonably weight certain contested findings, particularly the Iwashita et al. (2014) push-pull study and its interpretive limits, somewhat differently. The review was restricted to English-language, full-text-accessible sources, which may have excluded relevant evidence published in French, Portuguese or Spanish from West African, Lusophone or Latin American research programmes on zoophagic vectors, and this language restriction should be regarded as a genuine gap in coverage rather than an assumption that no relevant non-English literature exists. Access to subscription-only bibliographic databases and journal archives was not complete, and while backward and forward citation searching was used to mitigate this limitation, some relevant primary studies, particularly older regional entomological surveys not indexed with full open-access metadata, may not have been identified or could not be verified with sufficient bibliographic confidence for inclusion.

The underlying evidence base itself is heterogeneous in study design, vector species examined, geographic setting, outcome measurement and sampling method, precluding formal quantitative synthesis and limiting the review to a qualitative, thematic appraisal; readers should treat the magnitude estimates reported from individual studies, such as the specific percentage reductions in human landing catch or malaria incidence cited in Sections 4 and 7, as findings from single studies conducted under specific local conditions rather than as pooled or generalisable effect sizes. The evidence on the central question of this review, the interaction between ITN coverage and livestock-mediated diversion, is particularly sparse, resting substantially on a single directly relevant field study, and conclusions regarding this interaction should be understood as provisional pending the kind of interaction-focused study designs recommended in the Future Directions section. Reliance on observational and cross-sectional epidemiological evidence for much of the livestock-malaria-risk literature, as opposed to randomised designs, leaves residual confounding, particularly by household wealth and housing quality, as an unresolved threat to causal interpretation across a substantial portion of the reviewed studies. Finally, the field addressed by this review is under active development, with cluster-randomised trials of insecticide-treated livestock currently in progress; the synthesis presented here reflects the evidence available as of the stated search date and should be updated as results from ongoing trials become available.

Declaration of AI Use

This manuscript was prepared through the combined contributions of all author(s), including contributions to the study design, data, content development, results, interpretation, and related scholarly work. The author(s) acknowledge the use of Grammarly and ChatGPT to assist with grammar checking, language refinement, reference formatting. These AI-assisted tools were not used as authors and did not replace the intellectual contributions or scholarly judgment of the author(s). All AI-assisted outputs, including content, references, and interpretations, were carefully reviewed, revised, verified, and approved by the author(s). The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Author has declared that no competing interests exist.

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