Scaling artificial light at night and disease vector interactions into socio-ecological systems: a conceptual appraisal

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Abstract

There is burgeoning interest in how artificial light at night (ALAN) interacts with disease vectors, particularly mosquitoes. ALAN can alter mosquito behaviour and biting propensity, and so must alter disease transfer rates. However, most studies to date have been laboratory-based, and it remains unclear how ALAN modulates disease vector risk. Here, we identify five priorities to assess how artificial light can influence disease vectors in socio-ecological systems. These are to (i) clarify the mechanistic role of artificial light on mosquitoes, (ii) determine how ALAN interacts with other drivers of global change to influence vector disease dynamics across species, (iii) determine how ALAN interacts with other vector suppression strategies, (iv) measure and quantify the impact of ALAN at scales relevant for vectors, and (v) overcome the political and social barriers in implementing it as a novel vector suppression strategy. These priorities must be addressed to evaluate the costs and benefits of employing appropriate ALAN regimes in complex socio-ecological systems if it is to reduce disease burdens, especially in the developing world.

Keywords: *Aedes*, *Anopheles*, *Culex*, light pollution, malaria, vector-borne diseases

1. Introduction

Artificial light at night (ALAN) is expanding rapidly, changing in spectra and intensity, and has a range of biological impacts [1–5]. Despite calls for its recognition as a global change driver (GCD; [5]), there is still an incomplete understanding of the range of interactions of ALAN with other GCDs, particularly at landscape scales, and in developing nations [6]. In addition, an increase in recent work [6–16], has demonstrated that ALAN may interact with disease vectors, particularly mosquitoes, in a range of surprising ways (for reviews see [6,16]). These include suppression in the biting propensity of nocturnal groups of medical significance (e.g. *Anopheles gambiae*; [14]), increases in biting propensity in diurnal feeders (e.g. *Aedes aegypti*; [13]), and changes across species in their activity and attraction patterns [6,16,17].

Social-ecological systems are complex and interrelated, with multiple feedback loops, resulting in non-predictable, non-linear systems. In these systems the social and ecological aspects need to be explicitly taken into account when future management interventions are considered [18]. The social, financial and ecological dimensions are interdependent and interact in complex ways [19]. This also means that often trade-offs have to be made between the social and ecological aspects when decisions are made (e.g. [20] highlight the trade-offs between various Sustainable Development Goals. Apart from biological impacts, how ALAN is used by humans, in terms of lighting characteristics and the timing thereof, forms another fundamental dimension on how ALAN may be modulating vector disease transfer. In consequence, the influence of ALAN on vector-borne diseases should not only be studied from a biological perspective, as it is inherently a social-ecological problem. Here, we identify five priorities that must be addressed to better assess the mechanisms, cost, and potential impact of operationalizing the correct use of ALAN to help reduce disease transfer from vectors, particularly in the developing world.

2. The mechanistic role of artificial light on mosquitoes

The first priority is an expansion of the current understanding of how the light environment interacts with mosquito biology. For insects in general, there are multiple mechanistic pathways by which ALAN may alter their biology. ALAN can lead to direct population declines [21,22], and alter the interactions between species [23]. This leads to shifts in populations, communities and changes in ecological function [24], all of which are understudied, particularly at the landscape level [25]. There are also differential impacts of different types of light, and across different life cycles of insects [26]. While empirical evidence is scarce, there is an increasing concern that ALAN can alter evolutionary processes, such as behavioural flight responses [24].

For mosquitoes, light is a crucial environmental cue for synchronizing circadian activities [9,27–29]. This synchronization of physiology and behaviour is largely determined by circadian neural circuits and protein cycling within both diurnal and nocturnal mosquito species [8]. Disruption of these innate processes with the introduction of ALAN leads to changes in the timing of key mosquito behaviours such as host-seeking, mating and flight activity with potential population- and subsequent ecological community-level effects [21]. In the context of medically important mosquito vector species, changes particularly to the timing of biting and host seeking activity, and fecundity of females might lead to wide-scale consequences for disease transmission.

Although mosquitoes can feed on humans at any time, the peak biting frequency of the main African malaria vector species, belonging to the *Anopheles* genus, is the period from midnight to 4.00 in the morning, although there is geographical variation (figure 2; [30]). This coincides with the time that most people are asleep. Biting can start as early as 19.00 and continue until the morning, as shown in a recent study in Senegal [31]. The majority of these vectors, however, prefer to be active at night [31,32]. Like malaria vectors, some vectors of arboviruses (*Culex pipiens*) also readily feed on humans between dusk and dawn, while others, like *Ae. aegypti*, are diurnal. *Aedes* have a bimodal biting behaviour: biting increases early in the morning then subsides and resurges again during the afternoon, with little activity at night [13,33–35]. This natural biting pattern of arbovirus vectors can be interrupted by a marked increase in biting rate when mosquitoes receive stimulation with artificial light during the night [13,15].

The clock-modulated light preference behaviour of mosquitoes is distinct per species and sex, with an appreciable influence dependent on spectra [8]. In essence, day-time biters tend to be photophilic, whereas night-time biters are photophobic. *Aedes aegypti*, are aggressive biters with high activity levels, are attracted to light during the day regardless of spectra, as opposed to the malaria vector species, *Anopheles coluzzii*, that specifically avoids UV and blue light spectra during the day and opts to seek out blood-meals from unsuspecting hosts while asleep at night [8]. Since the use of blue light is largely on the rise with the increase in popularity of light emitting diode lights (LEDs; [36]), ALAN could potentially shift the peak activity period of vector species [6], and thus the risk of exposure of humans to disease. Diurnal species may take advantage of the extra hours of light to increase their feeding time, while nocturnal species avoid light and alter their foraging period.

Further to a reduced foraging period and thus less energy intake, there is evidence of exposure to ALAN reducing egg production and egg size in females of the nocturnal urban-adapted mosquito, *Culex pipiens f. molestus*, as well as desynchronizing the overlap of male and female activity through sex-specific expression of clock-genes [28]. Fyie et al. [15] showed that ALAN exposure increased not only the biting rate of *Cx. pipiens* but also led to the aversion of diapause, specifically as an effect of exposure to 'warm-white' light, which increases the potential exposure to disease transmission. ALAN disrupts nutrient accumulation [37], and *Cx. pipiens* is differentially attracted to different spectra of artificial light [17]. Taken together, this means that there are multiple ways in which the introduction of artificial light, and artificial light of different compositions (i.e. spectra, intensity and contrast), can alter various mosquito activity and behaviour patterns and these are species-, sex- and environment-specific [6,16].

3. Assessing the interaction of artificial light at night with other global change drivers

The second priority to further advance work into how ALAN alters mosquito biology, is how it may interact with other GCDs, which have already been demonstrated to influence vector disease dynamics [38–41]. Despite ALANs increasing use and documented impacts [1–3], it has not received as much research attention as other GCDs [5]. ALAN itself is increasingly considered to be a GCD [5], and so must interact with other GCDs. However, because much of the research to date on how ALAN alters mosquito biology is conducted under laboratory conditions, there is little understanding of how ALAN may alter disease vector interactions in real world systems, and how it may interact with other GCDs. In particular, how altered rates of biting propensity will interact with and be modulated by other GCDs, and so change vectorial capacity [42], is not clear, especially in complex socio-ecological systems.

The potential impacts of ALAN on modulating vector disease transfer are superimposed on other GCDs already in progress. Chief among these is land use change, and especially urbanization, where humans are modifying landscapes to better suit mosquitoes, increasing ALAN use, and with increasing human population sizes, increasing the portion of the human population exposed to mosquitoes [41,43,44].

In addition, climate change is already considered to be a major driver increasing disease risk globally [38]. ALAN itself may conceptually interact with these changing drivers, by acting as both a direct driver and a modifier, of factors that could increase or decrease disease transfer (figure 1). As a direct driver, it can alter species biology (e.g. ALAN suppresses biting activity and behaviour in nocturnal groups [14], increases that of diurnal ones [13], can alter community ecology (e.g. benefitting moth feeding in photophilic bats [48], or alter insect community structure in general [23], and potentially does so across spatial, temporal and taxonomic hierarchies. As a modifier, the use of ALAN may alter human behaviour, in particular by extending human activity into darkness, with implications for exposure to both diurnal feeding mosquitoes (by extending their feeding period) and nocturnal feeding mosquitoes (by increased human activity at night) [6]. Both interactions can modulate disease transfer risk. GCDs will alter the impacts of ALAN as a driver or modifier of disease vector interactions. For example, climate change may alter the community structure of mosquito predators [49,50], which in turn may change predation rates. Climate change may increase species fecundity and distribution of mosquitoes and increase human exposure to malaria, and so increase transmission risk to a greater net proportion of people [51]. How ALAN acts synergistically, antagonistically or neutrally with other GCDs thus remains a research frontier, and will probably be very context specific.

The substantial potential for ALAN to alter disease vector interactions in concert with other GCDs is illustrated by *Anopheles stephensi* invasions in Africa, most likely owing to increases in global transportation. A sharp increase in malaria cases in 2012 in Djibouti was linked to *An. stephensi* invading the Horn of Africa [52]. In the past decade, this species from Asia has now been reported for the first time in Ethiopia, Sudan (2019), Somalia (2019), Nigeria (2020) and Kenya (2022) [53]. The vector competence of *An. stephensi* under African settings thus far seems to be low [53], but could potentially increase under climate change [54]. Wilton & Fay [55] showed that *An. stephensi* responds to photoperiod manipulation. This species, like other anophelines, tends to feed around midnight and is inactive during the daytime (figure 2). In consequence, this species may provide an exemplar of how ALAN might modulate disease transfer in concert with other GCDs. The effect of ALAN in urban and developing rural areas might result in this species, and other anophelines, being inactive for longer and subsequently altering their biting cycle. This implies that mated female anophelines may look for blood meals at different times. In addition, ALAN use indoors might force anophelines to feed outdoors where there are fewer lights and the light is more diffuse and hence change feeding behaviour from indoors to outdoors. Changes or shifts in the timing of biting propensity are readily reported for *Anopheles* species in nature [32,56,57], however, these behavioural changes have not yet been assessed in terms of ALAN in the field.

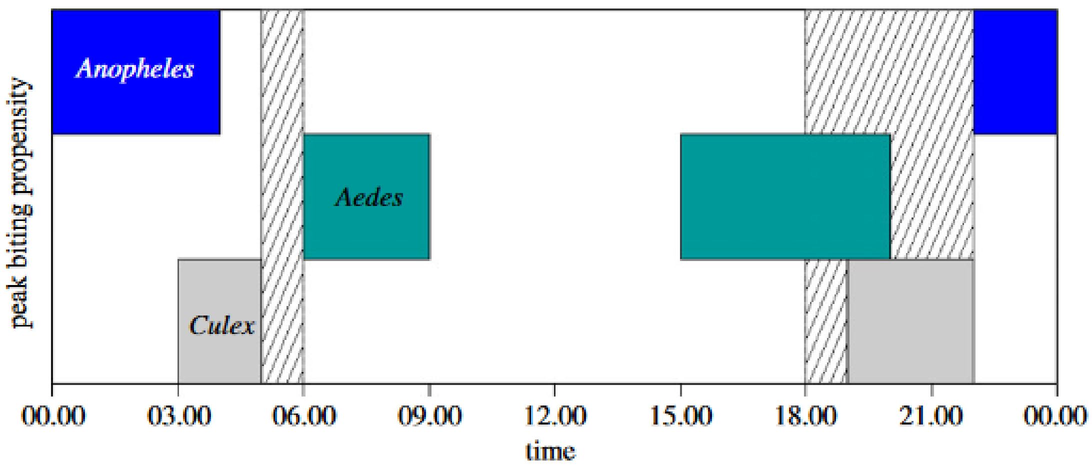

Figure 1. Diel variation for peak biting propensity varies considerably across mosquito species, and different studies report different peak times. Artificial light at night in hatched boxes will hypothetically occur at times that may extend human activity (early mornings and evenings), into more contact with dominant vectors, which in turn may adjust their biting propensity depending on whether they are diurnal (increase) or nocturnal (decrease). Note that for illustrative purposes biting rates are scale free and stacked, and combined across species for *Anopheles* (*An. funestus, An. arabiensis, An. gambiae, An. coluzzii*), *Aedes* (*Ae. aegypti, Ae. albopictus*) and *Culex* (*Cx. univittatus, Cx. quinquefasciatus*). Data adapted from [31,32,45–47].

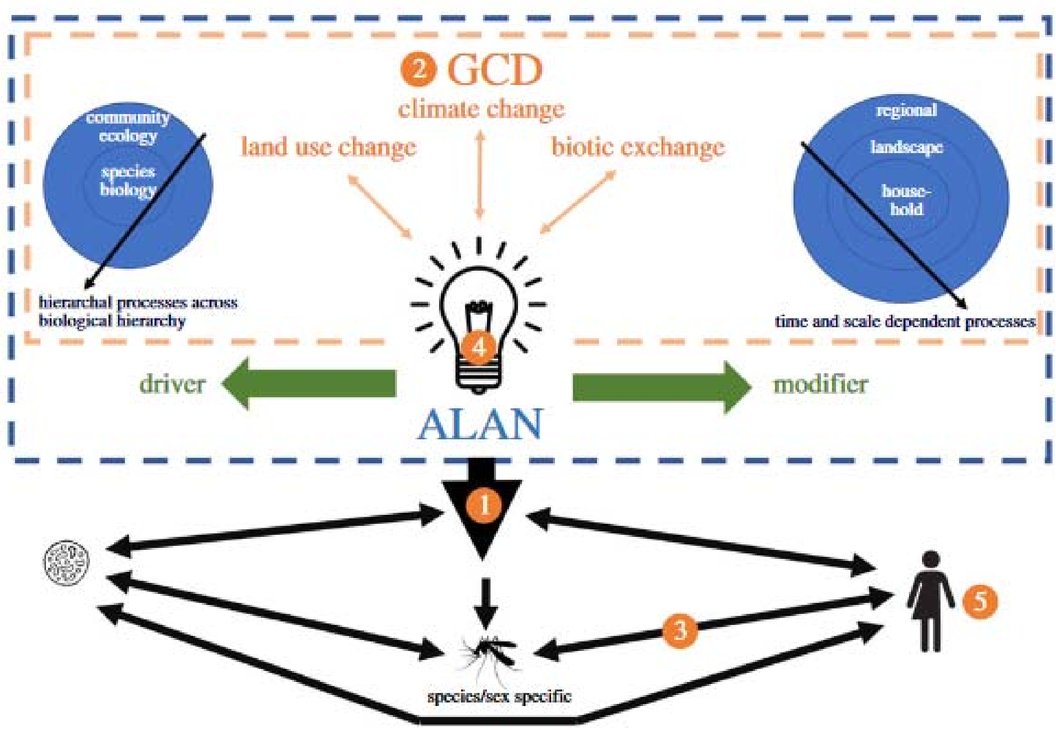

Figure 2. Conceptual framework for visualizing the integration of artificial light at night (ALAN) into complex socio-ecological systems. In essence, the impacts of ALAN are superimposed on other global change drivers (GCDs) already in progress, particularly climate change and land use change, and biotic

exchange. As a direct driver, ALAN can alter species biology across the taxonomic hierarchy. As a modifier, ALAN may change how societies interact with their environment, and are also time and scale dependent. Note that the priorities numbered are discussed in text are in orange: (1) assessing the mechanistic role of artificial light; (2) assessing the interaction of ALAN with other GCDs; (3) determining how ALAN interacts with other vector control strategies; (4) measuring ALAN at scales appropriate for disease vectors; and (5) overcoming socio-political barriers.

4. Artificial light at night interactions with other vector control strategies

Determining how ALAN interacts with existing vector control strategies is the third priority. When it comes to effectively controlling and eliminating mosquito-borne diseases, the most impactful step is to suppress or exterminate the vector. Mosquito vector control and suppression strategies predate the second World War (reviewed by [56]) and have historically depended, and continue to depend, heavily on the use of insecticides. Key control strategies for malaria-vector species include indoor residual spraying of houses and the use of insecticide-treated bed-nets and long-lasting insecticide treated nets and the recently re-introduced larval source management methods (the management of aquatic habitats that are suitable for mosquitoe larvae, which prevents the completion of development of the immature stages). High coverage with any of these interventions, or a combination of all, has generally resulted in large-scale reductions of malaria-related cases and deaths [58]. Integration of similar techniques has also shown successful suppression of arbovirus vectors, particularly *Ae. aegypti* [59].

While insecticides have been successful for vector control, the growing threat of resistance has prompted the call for alternative methods to supplement existing interventions [60]. McGraw & O'Niell [61] described four classes of mosquito vector interventions that have shown efficacy in the field; environmental modification (e.g. larval source management [62]), biological control (e.g. larvivorous fishes [63]), chemical treatment (insecticides) and genetic modification (e.g. sterile insect technique [64] and gene drives [61]). Introducing well-managed and coordinated integration of several vector suppression methods, with consistent operational support, is key for effective and sustained vector control and suppression.

Already a challenging research field in itself, the addition and/or interaction of ALAN with existing vector control and suppression strategies adds additional complexity. We are also not aware of any research that has directly tested how ALAN may interact with existing vector control and suppression strategies. Both mosquito and human behaviour changes in the presence of ALAN. Certain vector control strategies, like indoor residual spraying, have seasonal application regimens in some regions. This is usually driven by vector population density changes, determined through mosquito surveillance and monitoring, as well as disease case prevalence. Alterations to mosquito seasonal population density and activity timing owing to ALAN can potentially compromise the effectiveness of these interventions, thus missing a crucial time point for effective control of vector populations. Sterile insect techniques could also be compromised if ALAN alters swarm production and thus affecting exposure of sterile males to wild females.

Access to electricity has tripled in Africa between 2000 and 2019, including in rural areas [65]. Access to electricity allows people to be active (indoors and outdoors) at night for longer periods (working, socializing, etc.) and ALAN could increase the biting frequency of arbovirus vectors during this time (*Aedes* spp.), or increase outdoor disease transmission when people are not protected by bed nets [66]. Rapid urbanization in Africa may increase poverty risk, changes in governance and infrastructure and changes in ALAN regimes [67], and these factors together can increase the risk of vector-borne diseases [68].

5. Measuring artificial light at night at spatial scales appropriate for disease vectors

Priority four is measuring various aspects of biologically relevant artificial light at spatial scales that are relevant to the organisms concerned. We define biologically relevant ALAN as light of the kind and at times where it may significantly alter a range of biological processes. Higher quality and better resolution measurement of light regimes at landscape and smaller scales is a grand challenge for the field of ALAN ecology itself. The physical characteristics of the light environment are inherently multidimensional. In particular, light can be characterized (among other physical attributes), into spectral, intensity, contrast, flicker and polarized components (for definitions see [6,16]). These characteristics work in concert with the host of other parameters like temperature and human behaviour that alter mosquito activity, fecundity and behaviour, and concomitantly, vectorial capacity [6,16].

Historically, many of the kinds of measurements of ALAN have been optimized for human photopic systems, and primarily for engineering and architectural applications. Typically, many artificial light measurements are aimed at determining the ambience of the light [69], which means that much of the biologically relevant components, particularly its spectral and intensity characteristics, may be missed. Even current state of the art techniques with biological applications, like the environmental light field [70], cannot quantify UV light, which is critical for many organisms, especially insects and birds.

To better understand how ALAN may alter disease vector capacity of mosquitoes requires the science to move from the laboratory to the field. ALAN can take on a range of physical characteristics, and often what is tested in the laboratory is usually only one kind of spectra, like LEDs, and often at a constant intensity [13,14,17]. Therefore, it is key to quantify 'real world' light regimes and their biological impacts, especially in those geographical areas at most risk of disease transfer, and how this may alter critical parameters, such as suppressing biting rates. The key requirements are to: (i) conduct ALAN measurements primarily at the household scale, to assess how artificial light is used by people, both its different kinds (especially spectra and intensity) and timing. In addition, how ALAN use alters human behaviour, and potentially increases human activity during peak times of exposure to mosquitoes (i.e. after dusk before bed-net use), remains virtually unknown; (ii) quantify a range of the physical characteristics that make up the ALAN (i.e. spectra, intensity and contrast), and connect it to changes in mosquito biology. While the influence of contrast has been shown to alter the attractiveness of humans to *Ae. aegypti* [7], its role at household and landscape scales is unknown. Polarized light may be a key aspect used by female nocturnal mosquitoes to find water to lay eggs, as it is in other groups [71]; (iii) while it is untested in the literature, because they mainly use olfactory attraction cues at larger spatial scales, it is unlikely that ALAN can attract mosquitoes over large distances (greater than 100 m). Nonetheless, better measurement of ALAN at larger/landscape and ecologically relevant spatial scales will elucidate how landcover alters ALAN, how different measurement methods may be integrated and complement each other, and how point source and skyglow pollution may alter ecological patterns, which will build a more holistic view of ALAN impacts; (iv) once such conditions are measured in the field, they could be used to parametrize contemporary vector capacity models, to understand how different light regimes alter the proportion of infections, and what the costs and impact of such a potential disease vector ALAN interaction may be, in a spatially explicit manner [72–74]; and ultimately, (v) the above will allow the creation of well executed field trials, and test how ALAN changes disease transfer and possibly, how adaptation of ALAN regimes can be used to decrease (or at least not increase) disease transmission risk.

6. Socio-political barriers

Priority five is overcoming the substantial socio-ecological barriers to operationalizing ALAN as a potential disease vector suppression strategy in nocturnal groups. ALAN, by its very nature, is embedded within a particular social-ecological context, and any potential application of ALAN towards disease vector suppression or transmission risk reduction should take a systems, rather than issue-based, approach. For example, if a specific ALAN regime shows potential for repulsion of mosquito vectors, this intervention should be considered within a broader ecological, financial and social cost-benefit framework. If not, then the solution proposed for a singular problem (e.g. vector control and suppression), can result in a slew of other, sometimes unexpected and unrelated, costs or problems. A classic example in the ALAN context is the rising popularity for the use of LED lighting for both new lighting installations and retrofitting of pre-existing ones owing to its lighting and energy efficiency. This is widely seen as a technological revolution for lighting, but in recent years it has also become increasingly evident that these efficiency benefits need to be weighed against their unintended biological impacts, and impacts of the loss of darkness. The LED lights that are commonly used for outdoor lighting have significant emissions in the blue wavelengths to which biological responses are particularly sensitive [4], leading to unintended impacts on human health, such as disruptions of sleep patterns and potentially even cancer risk [75].

As such, even though these lights are considered environmentally friendly by many owing to their energy efficiency, they have costs that are less well-appreciated. The increased energy efficiency of LEDs therefore needs to be considered against the backdrop of s costs, such as impacts on environmental and human health [6], or new mitigating solutions need to be sought, like spectral-mixing LEDs [16]. Similarly, potential ALAN solutions to vector suppression or disease transmission risk reduction will have to be critically assessed against criteria broader than just vector control and suppression efficiency, such as the critical need to preserve dark skies and spaces for humanity and biodiversity. There is also substantial risk in the misuse of newer ALAN technologies. Just as bed-nets may be used for fishing instead of vector control, a simple strategy to implement lighting regimes, even if correctly applied and intended, may fail if it does not consider local socio-economic conditions [76]. There are also political barriers to consider. The World Health Organization does not yet consider ALAN use as a potential vector suppression strategy [77], probably owing to a lack of field-based testing and application. There may also be socio-political hesitation to adopt other vector control strategies until it is recognized by the World Health Organization.

An adaptive management framework, i.e. a learning by doing approach [78], may provide a useful framework for taking results from the evidence-based reductionist and experimental laboratory-based studies, and testing ALAN regimes that show promise for vector suppression or disease risk reduction in a real-world context [79]. Adaptive management uses best available knowledge as a starting point, and with strong feedbacks between the planning, implementation, monitoring and evaluation phases, enables iterative learning. This provides for a responsive approach towards implementation, learning and adaptation in the face of inherent uncertainty when intervening in social-ecological systems.

7. Conclusion

Altered mosquito biology by ALAN, especially in biting propensity and attraction, can now be demonstrated across several species in laboratory settings. Nonetheless, much work could be usefully directed into the five priorities we high-lighted above. The end-goal lies in practical application. Because the global vector disease burden remains high, and with the looming threat of vector resistance and expansion, it is critical that research be directed at alternative vector control and suppression strategies. ALAN alters mosquito biology across groups, and since its expansion and adoption is inevitable, accelerated research must clarify its role in vector-borne disease transfer. The problem is far from trivial, especially given the range of responses across different species, how ALAN alters human behaviour, understanding the complexities, interrelatedness and trade-offs in real-world contexts. Only once the research community can successfully address these priorities, the potential of ALAN as an additional vector suppression strategy, or understanding where it may increase vector diseases, be truly assessed and realised.

Data accessibility. This article has no additional data.

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