

Chapter 8

Conditions Facilitating a “Landscape of Fear from Disease” in African Forest Mammals



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Abstract Alongside the direct cost of predation, predation risk itself can be costly to mammals as it increases prey vigilance, induces avoidance behaviors, and changes movement patterns. Predation attempts can create learned associations between landscape contexts and predation risk, producing landscapes of fear of predation – areas that individuals avoid or show increased vigilance. Evidence suggests that disease could have similar effects, yet this is poorly researched. In this paper, we explore the potential of a “landscape of fear from disease,” which is when individuals show avoidance or increased vigilance of disease threats in specific locations. We present a framework that can identify and link elements responsible for the development of a landscape of fear from disease. We use this framework to pinpoint combinations of pathogen characteristics and host movement behaviors that are likely to facilitate learned associations between landscapes and disease threats. Some of these combinations will occur in the context of African forest mammals and thus could influence their conservation. Given the potential population consequences of a landscape of fear from disease, we discuss the possibility for

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human induced changes to climate and landscapes to alter the development of a landscape of fear from disease.

Keywords Fear of disease · Pathogen transmission · Learning to avoid pathogens · Host movement · Pathogen avoidance behavior

8.1 Introduction

The landscape of fear model is useful to understand the spatial-temporal use of landscapes by prey (Laundré et al., 2010; Gaynor et al., 2019). Under this model, risk of predation is thought to vary across the landscape, and prey are thought to respond by altering movement or time allocation patterns based on the level of fear it has of being injured or killed (Laundré et al., 2010). A major assumption of this model is that animals learn associations between locations, or landscape characteristics, and the risk of predation (Laundré et al., 2010; Gallagher et al., 2017). Predators, in general, have low success rates (e.g., 8–26%: Mech, 1966, Temple, 1987, Longland & Price, 1991). Thus, individuals escaping from a predator can associate landscapes and predation risk through associative learning. This information can then be transmitted to offspring if they range together during a period of extended infant dependency.

The fear of acquiring a disease could similarly help explain spatial-temporal use of the landscape by hosts (Fritzsche & Allan, 2012). For disease risk to influence host movement, however, this assumes that individuals could learn to associate disease risk with certain locations or landscape characteristics. And there is empirical support showing a link between spatial-temporal variation in pathogen risk and movement/behavioral patterns in hosts, suggesting that these associations are possible. For example, Fritzsche and Allan (2012) found that mammals were more likely to abandon food when the risk of infection from the lone star tick (*Amblyomma americanum*) was high. There is also evidence of between individual variations in the avoidance of pathogens. For instance, individual woolly monkeys (*Lagothrix lagotricha*) vary in their level of fecal avoidance (Philippon et al., 2021). Mandrills (*Mandrillus sphinx*) are suggested to distinguish parasitized group members via fecal odors and avoid grooming conspecifics infected with parasites that can be transmitted by contacting feces (Poirotte et al., 2017), and groups move longer distances when group members showed high richness in short-life cycle parasites, like protozoans, a strategy that could allow them to escape contaminated habitats (Brockmeyer et al., 2015). See Hongo this volume (Hongo, 2023) for a greater discussion of the influence of parasites on mandrill movement.

Little theoretical or empirical work has explored the hypothesized mechanisms that would allow a landscape of fear of disease to develop, namely, learning associations between landscape locations or characteristics and disease risk. With a landscape of fear of predation, it is easy to see how predation attempts could create learned associations between landscape contexts and predation risk, as there is an

immediate shock of a predation attempt associated with a location. However, with a landscape of fear of disease, the ability of an animal to learn landscape associations from pathogens is not as straightforward, as there is typically a delay between infection by a pathogen and the negative detectable consequence – illness. This is particularly difficult given (1) the large number of pathogens that can cause the same symptoms (e.g., nausea), (2) the substantial variation in pathogen life cycles (e.g., environmentally or directly transmitted, latency period, sensitivity to microclimates, severity of symptoms), and (3) the large temporal and spatial variation in host movement patterns (e.g., rates of revisiting food and water sources or use of sleeping sites). Similarly, the physical and social environments can play a role in shaping the spatial and temporal distribution of hosts and pathogens and the probability of transmission (Day, 2001; Nunn & Altizer, 2006; MacIntosh et al., 2012). This calls for careful consideration and research to identify the conditions under which a landscape of fear from disease could develop.

Here we first examine the potential costs of disease to hosts and evidence for animals altering their movements or exhibiting spatial-temporal variation in anti-pathogen behavior associated with what could be high disease-risk areas. We then propose a framework, extended from the landscape of fear from predation model, to clearly identify the elements responsible for the development of a landscape of fear from disease. We use this framework to identify conditions where a landscape of fear from disease is likely to occur. We discuss these conditions along two axes: (1) the movement behavior of the host and (2) the characteristics of the pathogen. In particular, we consider how host movement patterns alter the ability of an animal to learn patterns of disease risk in the environment (Lewis et al., 2021). We aim to establish a priori what combinations of landscape-pathogen-host characteristics are likely to lead to a host developing a landscape of fear from disease. Finally, we use these identified conditions to better understand landscapes of fear from disease in forest dwelling African mammals and to consider the possibility for human induced changes to climate and landscapes to alter the development of a landscape of fear from disease.

8.2 Pathogen Characteristics and Effects on Animal Host

Pathogens live temporarily or permanently in or on another organism (host) from which they are physically or physiologically dependent. Pathogens include such organisms as protozoans, nematodes, cestodes, trematodes, and arthropod, such as lice, ticks, and mites (Cheng, 1973). At low levels of infections, pathogens can have minimal effect, but under some conditions, they can significantly affect hosts' fitness by depressing their metabolism, thus suppressing their physiological and immunological responses, increasing their vulnerability to predation and other diseases which may result in death, and this can significantly affect populations. For example, based on more than three decades of observations, researchers have shown that rainforest anthrax caused widespread deaths for a broad range of mammalian

hosts and predicted that it will accelerate the decline and possibly result in the extirpation of local chimpanzee (*Pan troglodytes verus*) populations (Hoffmann et al., 2017). Therefore, understanding their role in wildlife communities is critical for wildlife conservation.

Pathogen transmission can occur directly; thus, the pathogen only requires a single host to complete its life cycle or indirectly involving biological vectors and/or one or more intermediate hosts. Horizontal pathogen transmission occurs through ingesting the infective stage of the pathogen in contaminated food or water (e.g., raw meat (e.g., *Taenia*) or water vegetation (e.g., *Fasciolopsis* flukes), in water (e.g., *Entamoeba*, *Cryptosporidium*, Guinea worm – *Dracunculus medinensis*)), through sexual intercourse (e.g., *Trichomonas vaginalis*), or by direct skin penetration (e.g., *Strongyloides stercoralis*, and biting arthropods: *Trypanosoma* species, *Plasmodium*, *Leishmania*, *Babesia*) (Esch & Fernandez, 2013). Vertical pathogen transmission from the mother to child occurs either through congenital/transplacental (e.g., *Toxoplasma gondii*) or by breast milk (e.g., *S. stercoralis*) route (Cheng, 1973; Esch & Fernandez, 2013) and is not considered here.

Pathogens have far-reaching implications for the conservation of African tropical rainforest faunas. The most pathogenic parasites can confer a combination of pathogenic effects including increased abnormal behaviors like reduced movement and increased inactivity, reduced appetite, inability to avoid predators, and reduction in breeding success. Other pathogenic effects are intestinal ulceration, anemia, tissue damage, delay in puberty, spontaneous abortion, congenital malformation, and mortality (Lilly et al., 2002; Chapman et al., 2005a). Some disease outbreaks severely affect populations. Anthrax is commonly associated with arid ecosystems, particularly African savannahs like the Serengeti (Hampson et al., 2011), but also occurs in forested systems (Leendertz et al., 2006; Gogarten et al., in press). Major outbreaks typically cause high mortality in wild ungulate species and usually exhibit strong seasonal and interannual variation (Hoffmann et al., 2017). For example, in the 1890s, in East and South Africa, rinderpest caused the deaths of approximately 50–90% of wildebeest (*Connochaetes* spp.), buffalo (*Syncerus caffer*), and giraffe (*Giraffa camelopardalis*) (Dobson et al., 2011). Also, die-offs in kudus (*Tragelaphus strepsiceros*) and impalas (*Aepyceros melampus*) occur in the dry season with a 10-year periodicity in Krüger National Park, South Africa (De Vos, 1990). These examples highlight the cost of pathogens on hosts and the potential selection pressures for avoiding infection.

8.3 Evidence That Animals Alter Behavior and Movement in Fear of Pathogens

Animals move to find food, water, shelter, sleeping sites, and suitable mates and avoid predators. During this travel, they will encounter pathogens. Behavioural mechanisms employed by wildlife that appear to function to avoid pathogens have been documented both by opportunistic field observations and quantitative field

experiments. Mechanisms are associated with feeding, elimination, grooming, social, sexual, maternal, and sleeping behaviors.

Wildlife typically has strategies to avoid eating foods contaminated with fecal material, potentially to avoid fecal-orally transmitted pathogens. For example, with bonobos (*Pan paniscus*) in the forests of the Democratic Republic of Congo, the avoidance of contaminated food correlated negatively with *Balantidium coli* infection, which is a potentially pathogenic protozoan transmitted through the fecal-oral route (Sarabian et al., 2021a). Under experimental conditions, chimpanzees (*Pan troglodytes*) tend to maintain greater distances from contaminants and/or refuse to consume contaminated foods (Sarabian et al., 2017). Similarly, carnivores avoid foraging on other carnivore carcasses and rarely engage in cannibalism, even though these appear to be easily available energy sources (Weinstein et al., 2018). This may limit chances of contracting similar parasites. Wild ungulates avoid eating grass near recently dropped feces even though the grass may be quite luxurious (Ezenwa, 2004a; Ezenwa et al., 2006). Denning canids defecate and urinate away from the den and rest areas. Newborns, however, have no mobility; hence, mothers keep the den clean by consuming the fresh feces and avoid infections themselves as parasite ova take several days to hatch into infective larvae (Sarabian et al., 2018).

In Kibale National Park, Uganda, the gray-cheeked mangabeys (*Lophocebus albigena*) travel further and exhibit less day-to-day overlap in feeding sites during dry weather than during wet days. This may minimize contact with fecal contaminated foliage, because possibly in the dry season rain does not wash fecal material off foliage (Freeland, 1980). Also, in the forests of Kibale, baboons (*Papio anubis*) frequently change sleeping trees which possibly functions to minimize exposure to infectious parasite larvae (Freeland, 1980; Bezjian et al., 2008). Baboons in Amboseli National Park, Kenya, typically use a sleeping site for only two nights and wait about 10 days before returning to the same site (Hausfater & Meade, 1982). During their absence, fecal material is likely to have been washed away or degraded.

Animals also move to avoid ectoparasites (Fritzsche & Allan, 2012). Birds avoid nests infected with ectoparasites (Oppliger et al., 1994), and cervids avoid areas with blood sucking insects (Nelson et al., 1977). To avoid pests and vectors, some animals seek microhabitats where there are fewer insects (Hart, 1990). To avoid intense mosquito bites, antelopes and other ungulates move toward higher altitudes during wet seasons, and arboreal primates move to the tree canopies (Dudley & Milton, 1990; Hart, 1990). Also, windy ridges are advantageous to hosts since they limit mosquito and fly bites.

8.4 Landscapes of Fear from Disease Framework

To better understand how landscapes of fear from disease develop, we modified the mechanistic framework proposed by Gaynor et al. (2019) for landscape of fear from predation to consider the avoidance of pathogens. In our framework, the main elements are the (1) physical/social environment, (2) spatial variation in risk of disease,

(3) perception of risk, and (4) behavioral response of the animal (Fig. 8.1). By taking each element in turn, it is possible to describe how a landscape of fear from disease could develop.

- Starting with the physical/social environment, many physical environmental characteristics (e.g., temperature, moisture, soil type) strongly influence the survival of pathogens. This is especially so for environmentally transmitted pathogens. For example, changes in climate can alter the spatial-temporal distribution of helminths (Bowman, 1999; Bonnell et al., 2010; Chapman et al., 2010a) (Fig. 8.1 i). Similarly, the social environment and group size of the hosts can influence propagation of directly transmitted pathogens (Snaith et al., 2008; Nunn et al., 2011; Nunn et al., 2015; Gogarten et al., *in press*) (Fig. 8.1 ii). For example, for Japanese macaque (*Macaca fuscata*), infections of some pathogens are positively associated with how central a female is within her group, as well as with her dominance (MacIntosh et al., 2012). Similarly, higher ranking male

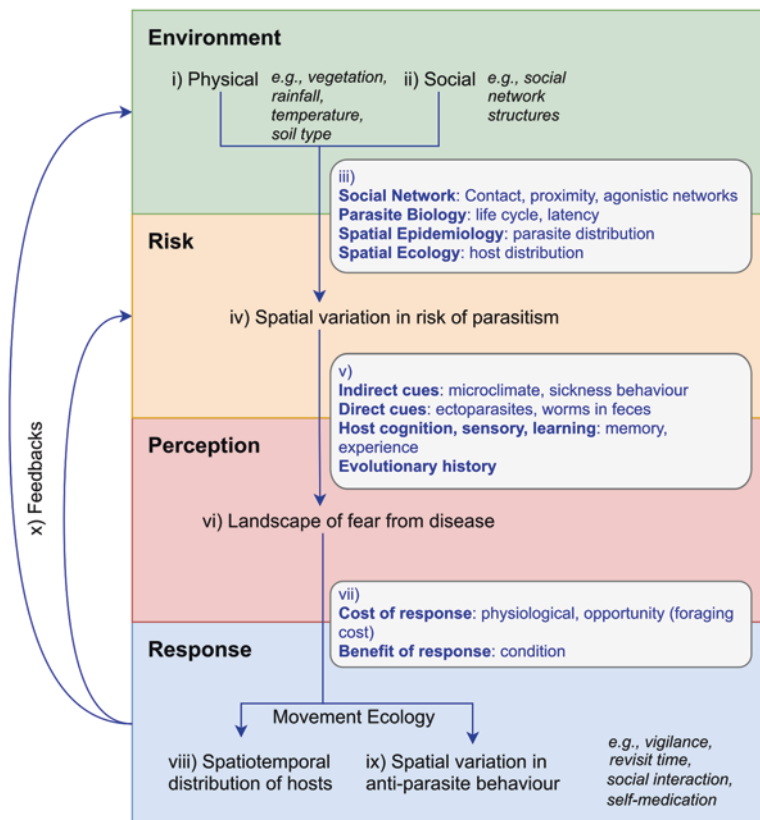


Fig. 8.1 A framework for understanding the development of a landscape of fear from disease. This framework is based on a similar framework developed for the landscape of fear from predation by Gaynor et al. (2019)

chimpanzees have higher testosterone levels and greater helminth burden (Muehlenbein & Watts, 2010). The study of social and physical environment impact on infectious disease is an interdisciplinary field often combining pathogen biology, landscape ecology, climate, and host behavioral ecology (Ostfeld et al., 2005) (Fig. 8.1 iii).

2. The interaction of social and physical environments with pathogens creates spatial-temporal variation in risk across space and time (Fig. 8.1 iv). For example, water sources are foci of animal activity; thus, not surprisingly, the concentration of fecal-oral pathogens in the environment near water holes is up to two orders of magnitude greater than away from them (Titcomb et al., 2021). Correspondingly, forest primates that range in the low valley bottoms that are wet, a condition that allows infective stage pathogens to persist in the environment longer, have elevated indices of pathogen infections compared to those that range in immediately adjacent upland areas (Chapman et al., 2010b).
3. The strength of cues of risk, the spatial-temporal predictability of the risk, and the sensory ability of the animal (Fig. 8.1 v) all determine the extent to which an animal can perceive variation in pathogen risk (Fig. 8.1 vi). Animals clearly have the ability to perceive characteristics of the environment that could be associated with predictably elevated risk of pathogen infection (e.g., they perceive the presence of a water source). They can also detect fecal material that could be contaminated with pathogens and biting arthropods that can transmit diseases (Sarabian et al., 2021b). See also Hongo (2023, this volume).
4. If an animal can perceive variation in risk and the cost of response is low compared to the potential benefits (Fig. 8.1 vii), the spatial-temporal distribution of hosts could be modified by pathogen risk (Fig. 8.1 viii). For example, the animal could avoid dry season water holes in the rainy season when other more temporary water sources area available, or animals can avoid dispersing to social groups with high levels of infection when other groups are available (Baudouin et al., 2019). Additionally, anti-pathogen behavior could similarly vary with pathogen risk (Fig. 8.1 ix). Finally, the resulting changes in host behavior can directly influence both the environment and the risk of pathogens, creating a feedback loop (Fig. 8.1 x). For example, changes in the spatial-temporal distribution of a host in response to perceived pathogen risk can directly alter the subsequent distribution of pathogens, especially in cases where a mobile host sheds pathogens. Similarly, changes in social behavior in response to perceived risk can alter the social environment of the hosts on which transmission of many directly transmitted pathogens relies.

This framework brings clarity to the terms used to describe the landscape of fear from disease. Under this framework, a match between risk maps of pathogen transmission (iv) and behavioral or distributional response of the host in question (viii or ix), along with evidence that the host has the ability to detect the pathogen (directly or indirectly), would be evidence of a landscape of fear from disease (vi).

This framework also provides a better understanding of potential mismatches between risk maps (iv) and response maps (viii or ix). For example, if costs of anti-pathogen behavior are low, a “play it safe” behavioral strategy, though not

necessarily a conscious strategy, might result in a host performing anti-pathogen behavior relatively homogeneously across the landscape. Anti-pathogen behavior is just one of many competing factors driving movement and distribution behavior – e.g., finding food, mates, and shelter and avoiding predation. These other factors when imposing a higher cost/benefit could outweigh any anti-pathogen behavior. Similarly, the specific condition of the host likely matters in terms of an individual's response to risk (e.g., a starving animal will lower their response to a landscape of fear from disease or predation). These potential mismatch conditions can help define the case where a landscape of fear from disease is likely to develop: (1) where costs of acquiring the pathogen are high compared to competing factors, (2) the cost of anti-pathogen behavior is not negligible, and (3) the host in question is in a healthy condition.

In cases where a landscape of fear from disease develops, the mechanisms driving the observed anti-pathogen behavior or distribution of host could be innate or learned. Though both cases can be seen as learned responses, one is just being learned within a generation and the other between generation learning. The predominance of one or the other is likely tied to the predictability/stability of the stimuli that the animal is using to detect the risk of pathogen transmission. If the stimuli are constant and predictable, learning an innate response is likely more efficient (e.g., avoiding others who show sickness behavior). Meanwhile, a more subtle and changing stimuli essentially require within generation learning (e.g., learning to avoid regions/conditions where a pathogen is detected through indirect stimuli – such as conspecifics getting sick at a particular water hole).

Learning how an animal perceives its environment and the pathogen risks (vi), as well as the degree to which behavioral responses are learned or innate, will help understand when invasive pathogens or landscape changes might result in ecological traps, where fear response reduces the ability of the animal in question to adapt to changes. When ecological traps are primarily the result of innate behavioral responses, it is likely much harder for populations to adapt. A potentially useful goal, when/if evidence for a landscape of fear from diseases is found, might be to measure how “fix” the behavioral response to perceived risk is. As with forest mammals, the prediction would be that behavioral response would likely show some/high amount of behavioral flexibility, being relatively long-lived mammals living in dynamic environments.

8.5 Learning Associations Between Landscapes and Disease Risk

8.5.1 Pathogen Characteristics

A long delay between the infection of a host and when the host experiences symptoms of illness (i.e., incubation period) will decrease the possibility of associative learning (Mitchell et al., 2009). If the animal becomes ill with perceptible

symptoms soon after experiencing a stimulus associated with infection, the more likely the animal will learn to avoid that stimulus. Possibly, the most easily learned stimuli associated with transmission would involve diseases transmitted by biting insects and ticks, as the animal could easily learn to avoid the pain of the bite. In contrast, it would be difficult to learn that *Trichuris* infections were associated with a sleeping site because after the eggs are shed in the feces of an infected animal, it is only after 15–30 days that the embryonated eggs become infective and another 60–70 days until the female starts to oviposit between 3000 and 20,000 eggs each day (Cheng, 1973). Furthermore, unless the animal is infected by a large number of *Trichuris* adults, it will not become ill with perceptible symptoms (Bowman, 1999; Gillespie et al., 2005).

The presence of stable cues associated with acquiring a pathogen is likely to play an important role in the development of a landscape of fear of disease. In the case of an environmentally transmitted pathogen, if the pathogen is consistently tied to particular landscape characteristics for its survival (e.g., cool, moist, dark soil for helminths), there is an increased chance that an association between illness and landscape characteristics could be learned. Water holes are one particular landscape feature that is associated with increased survival and concentration of the infective stage of pathogens (Chapman et al., 2010b; Ndlovu et al., 2018).

A very consistent cue is the odors, and visual cues associated with feces and many infectious organisms, including bacteria, viruses, parasitic protozoa, and helminths, are found in animal dung. Feces elicit avoidance behavior in a wide range of animals including African ungulates, like the dik-dik (*Madoqua kirkii*), chimpanzees, bonobos, and African elephants (*Loxodonta africana*) (Ezenwa, 2004b; Sarabian et al., 2017; Ndlovu et al., 2018; Sarabian et al., 2021b). Ndlovu et al. (2018) suggested that elephants avoid water holes with high levels of fecal contamination. In the case of directly transmitted pathogens, animals may learn to avoid individuals with particular traits that are associated with elevated risk of infections. Corresponding to this suggestion, mandrills groom heavily parasitized group members less frequently than less parasitized individuals (Poirotte et al., 2017). For social group-living mammals, one would expect that animals avoid unfamiliar individuals as they may harbor novel pathogens not occurring in the group. Sifakas (*Propithecus verreauxi*) follow this expectation and newly encountered individuals are groomed less than long-term residents.

Finally, the virulence of the pathogen is likely to increase selection pressures for behaviors or learning mechanisms that lead to lower infections, but only up to a point. Pathogens with extreme virulence (i.e., almost always fatal) would end any selection pressure on behaviors. A disease with extreme virulence is Ebola. Census data following an Ebola outbreak in Minkebe Forest in Gabon indicate catastrophic declines in the chimpanzee and gorilla (*Gorilla gorilla*) populations of greater than 90% (Huijberghs & Wachter, 2003). This suggests that mid-virulent pathogens would facilitate associative learning the most. However, in species with social learning, it is possible that individuals learn from the examples of conspecifics who become infected and avoid behaviors which might become associated with becoming infected.

Thus, we suggest these pathogen characteristics (P) can be viewed as three axes in a landscape of fear of disease:

- (Axis P1) How tied to landscape characteristics is the pathogen?
- (Axis P2) What is the delay between infection and illness?
- (Axis P3) How virulent is the pathogen?

8.5.2 *Movement Characteristics*

Host movement patterns also influences the chance of learning associations that could reduce the risk of disease. The frequency that the host revisits areas is key to both learning and pathogen transmission. Repeated exposure to similar conditions is required for associative learning to take place, allowing selection to act on variation in behavior in those conditions (Mitchell et al., 2009). In many species, such as species with high home range fidelity, the animal occupies a home range and can have varying degrees of predictability in use, e.g., specific route used at predictable times throughout the day (Di Fiore & Suarez, 2007). Predictability is particularly high in species that repeatedly use fixed sleeping sites, such as emergent trees or cliffs (Anderson, 1984; Chapman, 1989; Mekonnen et al., 2021), and is a pattern often found in baboons that use open habitats (Hamilton, 1982; Abie et al., 2017). Similarly, predictability in movement can be high for species that return to the same feeding sites (e.g., fig trees (Shanahan et al., 2001)) or watering holes (Shannon et al., 2009). For example, the most heavily used travel routes of elephants in Tembe Elephant Park, South Africa, were associated with water holes (Shannon et al., 2009). Similarly, baboons (*Papio ursinus*) travel along highly repetitive routes among their favorite fig trees (Noser & Byrne, 2006; Noser & Byrne, 2009).

The frequency of revisits is also key to pathogen transmission as an infection can only occur if the animal visits a site when the pathogen is infective. For example, *Oesophagostomum bifurcum* is a gastrointestinal parasite occurring in ungulates, including the giant forest hog (*Hylochoerus meinertzhageni*) and bush pigs (*Potamochoerus porcus*), and primates of Kibale National Park, Uganda (Reyna-Hurtado et al., 2023, this volume). It causes intestinal obstruction, abdominal pain, and fever (Chapman et al., 2005b, Chapman unpublished data). It only takes 3 days for a larva to be infective after defecation (<https://www.cdc.gov/dpdx/oesophagostomiasis/index.html>). In contrast, *Trichuris* sp. that is found in the same species and can, when acute, cause severe abdominal pain and severe anemia takes between 15 and 30 days to become infective (Ghai et al., 2014; Ochieng et al., 2021). This difference in parasite life cycle could impact the ability of an animal to learn to avoid infected areas. For example, learning to avoid repeatedly returning to a fruiting tree that typically bears ripe fruit for only a couple of weeks, e.g., many figs (Janzen, 1979), would be more likely in the case of *Oesophagostomum* compared to *Trichuris* infections. Thus, the possibility of becoming reinfected by revisiting a site

will be a function of both how frequently the animal returns to a specific location and the parasite life cycle.

Some species show little home range fidelity and encounter many different conditions, but rarely the same conditions repeatedly, such as the herds of ungulates on the Serengeti (Sinclair et al., 2007). If the host movements cover a wide range of conditions, where the host experiences a heterogeneous landscape, there is more of a chance that variation in the landscape can be associated with variation in risk. That is, if the host home range is homogenous, it becomes more difficult to develop an association between a specific location and risk of parasitism. These two movement characteristics of the host (M) might then be thought of as two axes:

- (Axis M1) How repeatable are movement patterns of the host (revisit rates)?
- (Axis M2) How heterogenous is the landscape within the host home range?

More generally, movement behavior influenced by the landscape of fear from disease can be considered as an element of the relatively new paradigm in ecology, movement ecology (Nathan et al., 2008), which deals with causes and consequences of animal movement. This chapter attempts to highlight the importance of pathogens within this paradigm.

8.6 African Forest Mammals

Given the proposed framework, we can apply the identified axes to understand when a landscape of fear from disease might develop in African forest mammals and the consequences of landscape modification and climate changes. As more empirical and theoretical work would be needed to fully validate and understand the implications of a landscape of fear from disease, the application of this framework remains speculative.

Parasite characteristics that increase the chance of associative learning (Axis P1–P3) suggest that mid-virulent parasites that are heavily tied to landscape features and take little time to develop the infective stage are more likely to facilitate associative learning. This suggests that in the African mammal context, *Schistosoma mansoni*, *Ascaris lumbricoides*, *Necator americanus*, *Enterobius vermicularis*, and *Strongyloides* species among other parasites are likely candidates. Hosts with high site fidelity that are reliant on clumped resources (e.g., fruiting trees, water holes) and species that cover heterogeneous terrain (forest edges, water holes, fragmented landscapes) are most likely to develop associations between risk of parasitism and landscape characteristics (Axis M1–M2). Similarly, species which do not have fixed home ranges, or who have large home ranges, but return to specific locations repeatedly (e.g., forest elephants returning to water holes) are also likely candidates for developing a landscape of fear from disease (Axis M1) (Fig. 8.2).

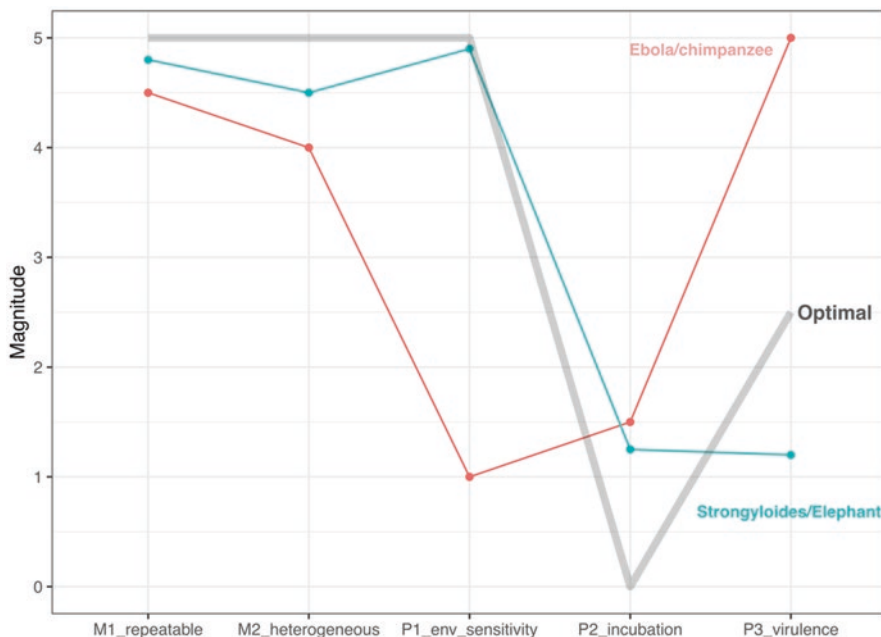


Fig. 8.2 Display of the proposed five axes that are likely to influence the development of a landscape of fear from disease. An optimal line is drawn, alongside two examples of host-pathogen combinations. M1) How repeatable are movement patterns of the host (revisit rates)? M2) How heterogenous is the landscape within the host home range? P1) How tied to landscape characteristics is the pathogen? P2) What is the delay between infection and illness? P3) How virulent is the pathogen?

8.7 Applying the Landscape of Fear from Disease to African Conservation

Humanity faces unprecedented environmental challenges, and nowhere are these challenges greater than in Africa, the poorest and second most populous continent in the world (UN, 2015). Already, 20% of the continent's land surface (6.6 million km²) is degraded, an area twice the size of India (Archer et al., 2018), and Africa's population is predicted to quadruple by 2100 (UN, 2015). Climate model predict that the effects of climate change will be severe in Africa (Niang et al., 2014); thus, environmental conflict is projected to rise sharply (Laurance et al., 2014). These changes will severely impact biodiversity, and it is predicted that by 2100, more than half of Africa's bird and mammal species could be lost (Archer et al., 2018).

Grappling with these challenges requires mobilizing as much information as possible and strengthening Africa's research capacity (Atickem et al., 2019; Mekonnen et al., 2022). Considering how climate and landscape changes in Africa

may impact the development of a landscape of fear from disease may prove useful in the development of informed management plans for some species.

According to predictions (Masson-Delmotte et al., 2021), all of Africa will get warmer, but changes in rainfall patterns will vary across the continent. Some areas are projected to become wetter, such as much of Uganda, while others will experience drying effects, including much of southern Africa (Kalbitzer & Chapman, 2018; Ahmadalipour et al., 2019). However, generally the climate will become more variable (Ahmadalipour et al., 2019). This increased variability in climate is likely to impact an animals’ ability to develop associations between landscape characteristics and parasitism risk. In particular, an animal’s ability to assess spatial risk of parasitism could be reduced if climate variability leads to high spatial-temporal variation in where environmentally transmitted parasites are found (Axis P1) or increased variability in host movement (Axis M1). Alternatively, if climate variability leads to increased landscape heterogeneity (Axis M2), an increased distinction between landscape patches might facilitate an animal learning to associate certain landscape patches with high/low disease risk.

With respect to climate change induced variation in resource availability, there are few records of sufficient duration to be helpful to understand what the future will bring for the conservation of African mammals. However, 32 years of tree phenology data from Lope National Park, Gabon, reveal an 81% decline in fruiting that corresponded to an 11% decline in body condition of fruit-dependent forest elephants in the last decade (Bush et al., 2020). In Kibale National Park, Uganda, a 40-year climate and phenological record reveals that the proportion of the tree community fruiting predictably declined with ENSO and Indian Ocean Dipole events, and both of these climatic phenomena are increasing in frequency and duration (Kalbitzer and Chapman unpublished data). However, individual species respond differently to climate variables, thus making clear predictions of how individual host species will respond will be challenging. If these patterns play out, and landscapes of fear of disease do not form, disease levels will increase further endangering Africa’s wildlife. It is possible that with climate change there will be a convergence on rare resources and food shortages. This would facilitate associative learning. However, under such a scenario, animals likely have no option but to converge on these rare resources, so learning could likely not be put to use.

Globally, forests are being reduced in size and fragmented into smaller and smaller blocks. In fact, areas of continuous tracts of forest larger than 500 km² suitable for large animals (possibly including naturally treeless areas, with no remotely detected signs of human activity) comprise only 20% of remaining tropical forests, and these forests are disappearing at a rate of 7.2% each year (Potapov et al., 2017). Unfortunately, only 12% of these areas are protected (Potapov et al., 2017). Furthermore, it is predicted that with 50 years the number of fragments will increase 33-fold and the mean size of fragments will decline to between 0.25 and 17 ha (Taubert et al., 2018). Increased habitat fragmentation is likely to facilitate the association between landscape characteristics and risk of parasitism.

8.8 Conclusion

The landscape of fear from disease model has the potential to be an important ecological theory integrating the fields of ecology, parasitology, behavior, movement ecology, and population biology. Given that developing a landscape of fear from disease can reduce pathogenic infections, any anthropogenic change that causes a reduction of the ability of animals to form associations between landscape characteristics and parasite risk has the potential to increase parasite burdens within populations and cause population declines. Thus, refining the concept of the landscape of fear of disease will have useful implications for the conservation of endangered species. Within the wider paradigm of movement ecology, the incorporation of landscapes of fear from disease also offers another important driver for understanding animal movement patterns. We suggest that parasite avoidance is far more prevalent than is currently appreciated (Buck et al., 2018). However, this area of research is in its infancy; thus, we encourage more research to identify the conditions that promote the landscape of fear from disease to develop. Only with a firm understanding of these conditions will it be possible to understand the consequences of humans reshaping landscapes of fear through habitat modification, climate change, and resource extraction.

Acknowledgments We would like to thank Rafael Reyna-Hurtado and Mario Melletti for inviting us to contribute to this chapter and overseeing the review process. We thank Claire Hemingway and Dipto Sarkar for helpful ideas and comments on this project. The funding that helped us develop some of these ideas is the IDRC grant “Climate Change and Increasing Human-Wildlife Conflict.” CAC was supported by the Wilson Center while writing this paper.

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