Novel pathogen introduction rapidly alters evolved movement strategies, restructuring animal societies

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Abstract

Animal sociality emerges from individual decisions on how to balance the costs and benefits of being sociable. Movement strategies incorporating social information — the presence and status of neighbours — can modulate spatial associations, helping animals avoid infection while benefiting from social information. When a novel pathogen is introduced into a population, it should increase the costs of sociality, selecting against gregariousness. Yet current thinking about novel pathogen introductions into wildlife neglects hosts' potential evolutionary responses. Using an individual-based model that captures essential features of pathogen transmission among social hosts, we show how introducing a novel pathogen to a population provokes a rapid evolutionary transition to a dynamic social distancing movement strategy. This evolutionary shift triggers a disease-dominated ecological cascade of increased individual movement, decreased resource harvesting, and fewer social encounters. Pathogen-adapted individuals form less clustered social networks than their pathogen-naive ancestors, which reduces the spread of disease. The mix of post-introduction social movement strategies is influenced by the usefulness of social information and disease cost. Our work demonstrates that evolutionary adaptation to pathogen introductions and re-introductions can be very rapid, comparable to ecological timescales. Our general modelling framework shows why evolutionary dynamics should be considered in movement-disease models, and offers initial predictions for the eco-evolutionary consequences of wildlife pathogen spillover scenarios.

Introduction

Animal sociality is an emergent outcome of individual decisions that balance the benefits of associations, such as social information, against the costs, such as pathogen transmission risk (Tanner and Jackson 2012; Gil et al. 2018; Weinstein et al. 2018; Romano et al. 2020; Webber et al. 2022). While such associations yield useful social information about resource availability (Danchin et al. 2004; Dall et al. 2005; Gil et al. 2018), they also provide opportunities for the transmission of infectious pathogens (Weinstein et al. 2018; Romano et al. 2020; Albery et al. 2021; Cantor et al. 2021; Romano et al. 2021). Individuals must therefore balance the costs and benefits of socialising when deciding how to move. Movement strategies that incorporate social information — the presence and status of neighbours — can facilitate or reduce spatial associations, and help animals balance the costs and benefits of sociality (Gil et al. 2018; Webber and Vander Wal 2018; Albery et al. 2021; Webber et al. 2022). Animals' social movements link landscape spatial structure, individual distributions, and the emergent structure of animal societies 2018,webber2022. Together, they influence the dynamics of disease outbreaks in animal populations (White et al. 2018*b*; Romano et al. 2020; 2021), and outbreaks may in turn cause cascading effects on landscape and community ecology (Monk et al. 2022).

Pathogen outbreaks in animal societies often lead to rapid reductions in associations among individuals (Romano et al. 2020), due to a combination of mortality-induced decreases in population density (e.g. Fereidouni et al. 2019) and adaptive behavioural responses that reduce encounter rates (Stroeymeyt et al. 2018; Romano et al. 2020; Stockmaier et al. 2021). When a novel pathogen is first introduced into a population, such as during a spillover event, individuals may have no prior experience of cues that indicate infection, making fine-tuned adaptive individual or social avoidance responses less likely (Weinstein et al. 2018). Fitness reducing pathogens spreading through host-host contacts may select against host social behaviour, and hence against social connectivity itself (Altizer et al. 2003; Cantor et al. 2021; Poulin and Filion 2021; Romano et al. 2021; Ashby and Farine 2022). This selective pressure may be modulated by landscape productivity (Hutchings et al. 2006) and the benefits of grouping (Almberg et al. 2015; Ezenwa et al. 2016), especially if these can offset the cost of infection. Multiple animal taxa — from mammals (Blehert et al. 2009; Fereidouni et al. 2019; Kuchipudi et al. 2022), to birds (Wille and Barr 2022) and amphibians (Scheele et al. 2019) — currently face novel pathogen outbreaks; such scenarios will likely become more common due to climate change (Sanderson and Alexander 2020; Carlson et al. 2022). Wildlife pathogen outbreaks are primarily studied for their immediate ecological (Monk et al. 2022) and potential medical implications (especially for human societies: Kuchipudi et al. 2022; Wille and Barr 2022), with host evolutionary dynamics mostly ignored — presumably because the evolution of pathogen hosts is expected to be slow, and not immediately relevant.

Theory suggests that animal sociality evolves to balance the value of social information against the risk of pathogen transmission (Bonds et al. 2005; Prado et al. 2009; Ashby and Farine 2022). However, analytical models often reduce animal sociality to single parameters (Bonds et al. 2005; Prado et al. 2009; Ashby and Farine 2022), while it actually emerges from individual decisions; social decisions of-

ten also vary among individuals (Tanner and Jackson 2012; Wolf and Weissing 2012; Spiegel et al. 2016). Epidemiological models based on contact networks can incorporate the estimated outcomes of individual variation in social behaviour in the form of their positions in a social network. Yet this approach often cannot capture fine-scale feedbacks between individuals' social and spatial positions — how and where to move in relation to other individuals — making them sensitive to both the network formation process and sampling biases in empirical data collection (White et al. 2017). Mechanistic, individual-based simulation models can incorporate substantial ecological detail, including explicit spatial settings (DeAngelis and Diaz 2019), and detailed disease transmission (White et al. 2018*a*,*b*; Scherer et al. 2020; Lunn et al. 2021). Such models hitherto focus on immediate epidemiological outcomes, such as infection persistence, and do not have an evolutionary component (White et al. 2018*a*; Scherer et al. 2020; Lunn et al. 2021). Incorporating an evolutionary component to movement-disease models could allow predictions on important feedbacks between the ecological outcomes of infectious disease and the consequences for the evolution of host behaviour (Cantor et al. 2021). This could include the emergence of tradeoffs in the costs and benefits of sociability (Gartland et al. 2021), with cascading ecological and social effects (Tanner and Jackson 2012; Spiegel et al. 2017; Monk et al. 2022; Webber et al. 2022). The range of animal taxa at risk from a wide array of pathogens and parasites (Sanderson and Alexander 2020; Carlson et al. 2022) makes it important to conceive of models that can capture the key features of the diversity of host-pathogen interactions, and offer broad conceptual insights (White et al. 2018*a*,*b*).

We built a general model of the essential dynamics of pathogen transmission among animals foraging on patchily distributed resources — a common behavioural context shared by most host taxa (White et al. 2018*a*,*b*). We examined the eco-evolutionary consequences of the introduction of a pathogen into a novel host population (such as during cross-species spillover Blehert et al. 2009; Fereidouni et al. 2019; Scheele et al. 2019; Sanderson and Alexander 2020; Carlson et al. 2022; Kuchipudi et al. 2022; Monk et al. 2022; Wille and Barr 2022). In our evolutionary, spatial, individual-based simulation, we repeatedly introduced an infectious pathogen to populations that had already evolved foraging movement strategies in its absence. We investigated three questions: *(i)* How does the introduction of a novel pathogen affect the evolution of animals' social movement strategies? *(ii)* How do host evolutionary responses to pathogen introduction affect animals' environment, and the emergent structure of animal societies? *(iii)* How are evolutionary responses to pathogen introduction shaped by ecological factors, such as landscape productivity and the cost of infection? We compared how social information was used in movement strategies evolved before and after pathogen introduction, and the ecological outcomes for individual intake, movement, and associations with other foragers. Using network epidemiological models (Bailey 1975; White et al. 2017; Stroeymeyt et al. 2018; Wilber et al. 2022), we examined whether pathogen-adapted populations were more resilient to the spread of infectious disease than their pathogen-naive ancestors. Overall, we provide a theoretical framework broadly applicable to novel host-pathogen introduction scenarios, and demonstrate the importance of including evolutionary dynamics.

Model and Analysis

We implemented an individual-based simulation model to represent foraging animals ('foragers') seeking discrete, immobile, depleteable food items (see *SI Appendix Fig. S1 – S2*) (Spiegel et al. 2017; Gupte et al. 2021). Food items are distributed over a two-dimensional, continuous-space resource landscape with wrapped boundaries (a torus). Our model, similar to previous eco-evolutionary individual based models (Getz et al. 2015; Gupte et al. 2021; Netz et al. 2021), has two distinct timescales: (1) an ecological timescale comprising of T timesteps that make up one generation ($T = 100$ by default), and (2) an evolutionary timescale consisting of 5,000 generations (G). At the ecological timescale, individuals sense local counts of food items and competitors, move according to inherited movement strategies, and forage for food. At the same timescale, individuals that carry an infectious, fitness-reducing pathogen, may, when in close proximity with uninfected individuals, pass on the pathogen with a small probability (see *Pathogen Transmission and Disease Cost*). At the evolutionary timescale, individuals reproduce and transmit their movement strategies (see *Starting Location and Inheritance of Movement Rules*) to the their offspring. The number of offspring is linked both to individuals' success in finding and consuming food items, and to the duration that they were infected by the pathogen at the ecological timescale. The model was implemented in R and C++ using Rcpp (Eddelbuettel 2013; R Core Team 2020) and the *Boost.Geometry* library for spatial computations (*www.boost.org*); model code is at *github.com/pratikunterwegs/pathomove*.

Distribution of Food Items

Our landscape of 60×60 units contains 1,800 discrete food items, which are clustered around 60 resource 'kernels', for a resource density of 0.5 items per unit^2 (see *SI Appendix Fig. S1 – S2*). This prevents synchronicity in the availability and regeneration of food items. Each available food item can be sensed and harvested by foraging individuals (see below). Once harvested, another food item is regenerated at the same location after a fixed regeneration time R, which is set at 50 timesteps by default; alternative values of 20 and 100 timesteps represent high and low productivity landscapes respectively. Food item regeneration is delinked from population generations. Thus the actual number of available food items is almost always in flux. In our figures and hereafter, we chose to represent R as the number of times a food item would regenerate within the timesteps in a single generation T (default = 100), resulting in R values of 1, 2, and 5 for regeneration times of 100, 50 (the default), and 20 timesteps. Items that are not harvested remain on the landscape until they are picked up by a forager. Each food item must be processed, or 'handled', by a forager for T_H timesteps (the handling time, default = 5 timesteps) before it can be consumed (Ruxton et al. 1992; Gupte et al. 2021). The handling time dynamic is well known from natural systems in which there is a lag between finding and consuming a food item (Ruxton et al. 1992).

Individual Foraging and Movement

Foraging. Individuals forage in a randomised order, harvesting the first available food item within their movement and sensory range ($d_S = d_M$, a circle with a radius of 1 unit (see *SI Appendix Fig. S1 – S2*). Once harvested, the item is no longer available to other individuals, leading to exploitation competition among nearby foragers. Furthermore, the location of the item also yields no more cues to other foragers that an item will reappear there, reducing direct cues by which foragers can navigate to profitable clusters of food items. As handlers are immobilised at the location where they encountered food, they may be good indirect indicators of the location of a resource cluster 'social information' Danchin et al. 2004; Romano et al. 2020; Gupte et al. 2021. Once individuals finish handling a food item, they return to the non-handling, searching state.

Movement. Our model individuals move in small, discrete steps of fixed size ($d_M = 1$ unit). Each step is chosen based on the individuals' assessment of local environmental cues, and this assessment is made using evolved movement strategies (as in Gupte et al. 2021; Netz et al. 2021). First, individuals scan their current location, and five equally spaced points around their position, at a distance of 1 unit for three cues (d_S, see *SI Appendix Fig. S1 – S2*): the number of food items (F), the number of foragers handling a food item ('handlers': H) and the number of idle foragers not handling a food item ('non-handlers': N). Individuals assign a suitability (see Gupte et al. 2021; Netz et al. 2021) to their current position and each of the five locations, using their inherited preferences for each of the cues: $S = s_F F + s_H H + s_N N + \epsilon$. The preferences s_F, s_F, and s_N for each of the three cues are heritable from parents to offspring, while ϵ is a very small error term drawn for each location, to break ties among locations. The values of each of the cue preferences *relative to each other* determine individuals' movement strategies (Gupte et al. 2021). All individuals move simultaneously to the location to which they have assigned the highest suitability (akin to step-selection; Fortin et al. 2005); this may be their current location, in which case individuals are stationary for that timestep. Since individuals may differ in their inherited preferences for each of the three cues, two individuals at the same location may make quite different movement decisions based on the same local cues. Handlers, however, are considered immobile and do not make any movement decisions.

Pathogen Transmission and Disease Cost

We modelled circumstances that are expected to become increasingly common due to rapid global changes; the population evolves for $3/5^{\text{th}}$ of the simulation (until G = 3,000; of 5,000) in the absence of a pathogen, after which a pathogen is introduced in each generation until the end of the simulation (G = 5,000). Our model captures the essential features of pathogen or parasite transmission among animals (White et al. 2017; Scherer et al. 2020; Lunn et al. 2021): the pathogen may transmit from infected host individuals to their susceptible neighbours with a per-timestep probability p of 0.05. This transmission

is only possible when the two individuals are within a the transmission distance, d_β. For simplicity, we set d_β to be the movement range (1 unit). Once transmitted, the pathogen is assumed to cause a chronic disease which reduces host energy stores by a fixed amount called δE in every following timestep; δE is set to 0.25 by default (alternative values: 0.1, 0.5). Since such infectious contact events can periodically re-occur in natural environments, we set up our model such that the pathogen was introduced to 4% of individuals in each generation (N = 20; 'primary infections'). This is necessary to kick-start the pathogen-movement eco-evolutionary feedback dynamics, and populations may indeed repeatedly acquire novel pathogens (or strains) through external sources, such as infected individuals of other spatially overlapping species (e.g. Kuchipudi et al. 2022; Wille and Barr 2022). For completeness, we also considered scenarios in which novel pathogen introductions only occur sporadically in the generations after the initial event, rather than in every generation (see *SI Appendix*).

Starting Location and Inheritance of Movement Rules

For simplicity, we considered a population of haploid individuals with discrete, non-overlapping generations, and asexual inheritance. At the end of the parental generation, the net lifetime energy of each individual was determined as the difference of the total energy gained through food intake and the energy lost through infection. In the *SI Appendix*, we also consider an alternative implementation in which the pathogen reduces the value of each food item by a certain percentage. The parental population produced an offspring population (of the same size) as follows: to each offspring, a parent was assigned at random by a weighted lottery, with weights proportional to lifetime net energy (Hamblin 2013; Gupte et al. 2021). This way, the expected number of offspring produced by a parent is proportional to the parent's lifetime net energy. The movement decision-making cue preferences s_F, s_H, and s_N are subject to independent random mutations with a probability of 0.001. The mutational step size (either positive or negative) is drawn from a Cauchy distribution with a scale of 0.01 centred on zero. Thus, there can be a small number of very large mutations, while the majority of mutations are small. As in real ecological systems, individuals in the new generation are intialised around the location of their parent (within a standard deviation of 2.0), and thus successful parents give rise to local clusters of offspring (see an alternative implementation in *SI Appendix*).

Model Output

Social Information Use. To understand the evolution of movement strategies, and especially how individuals weighed social information, we recorded the population's evolved cue preferences in every second generation, and interpreted them using the 'behavioural hypervolume' approach (Bastille-Rousseau and Wittemyer 2019). We classified individuals based on how they used social information — the presence and status of competing foragers — into four social movement classes: (1) agent avoiding, if $s_H, s_N < 0$, (2) agent tracking, if both $s_H, s_N > 0$, (3) handler tracking, if $s_H > 0, s_N < 0$, and (4)

non-handler tracking, if $s_H < 0, s_N > 0$. We calculated the relative importance of social cues — H, N — to each individual's movement strategy as $SI_{imp} = (|s_H| + |s_N|)/(|s_H| + |s_N| + |s_F|)$, with higher values indicating a greater importance of social cues.

Proximity-Based Social Network. We created a proximity-based adjacency matrix by counting the number of times each individual was within the sensory and pathogen transmission distance d_β ($= d_S, d_M = 1$ unit) of another individual (Whitehead 2008; Wilber et al. 2022). We transformed this matrix into an undirected social network weighted by the number of pairwise encounters: in a pairwise encounter, both individuals were considered to have associated with each other (White et al. 2017). The strength of the connection between any pair was the number of times the pair were within d_β of each other over their lifetime. We logged encounters and constructed social networks after every 10% of the total generations (i.e., every 500th generation), and at the end of the simulation, and omitted ephemeral pairwise associations with a weight < 5.

Model Analysis

We plotted the mix of social information-based movement strategies evolved across generations in each parameter combination. Focusing on our default scenario ($\delta E = 0.25$, $R = 2$), we visualised the mean per-capita distance moved, mean per-capita intake, and mean per-capita encounters with other foragers. We examined how the three main social movement strategies — agent avoidance, agent tracking, and handler tracking — changed in frequency over generations. We also examined differences among strategies in the movement distance, associations with other agents, and frequency of infection, after they had reached an eco-evolutionary equilibrium following pathogen introduction (G > 3,500). We visualised the proximity based social networks of populations in a representative scenario ($\delta E = 0.25$, $R = 2$), focusing on the generations just before and after the pathogen introduction events begin (pre-introduction: G = 3,000; post-introduction: G = 3,500). We compared the time taken for diseases to spread across these social networks by running simple network epidemiological models on the emergent networks (Bailey 1975; White et al. 2017; Stroeymeyt et al. 2018; Wilber et al. 2022) using the *igraph* library (Csardi and Nepusz 2006).

Results

Rapid Evolutionary Shift in Social Movement Strategies Following Pathogen Introduction

In our model, individuals move on a landscape with patchily distributed food items, and select where next to move in their vicinity, based on inherited preferences for environmental cues — food items, and other individuals (see *SI Appendix Fig. S1*). Food items, once consumed, regenerate at a rate R, and

pathogen infection imposes a per-timestep cost δE. We classified individuals' social movement strategies in our model by the sign of their preferences for successful foragers handling a food item ('handlers', preference s_H), and for unsuccessful foragers still searching for food ('non-handlers', preference s_N). In our default scenario, $R = 2$, food regenerates twice per generation, and $\delta E = 0.25$, i.e., consuming 1 food item offsets 4 timesteps of infection. Before the introduction of the pathogen, the populations' social movement strategy was primarily to prefer moving towards both handlers and non-handlers ('agent tracking'; $s_H, s_N > 0$; but see below) (Fig. 1A).

The introduction of the infectious pathogen leads to a remarkably rapid evolutionary shift — within only 25 generations of pathogen introduction — in how social information is incorporated into agents' movement strategies. There is a marked increase in the frequency of individuals that track successful foragers, but avoid non-handlers ('handler tracking'; $s_H > 0$, but $s_N < 0$) (Fig. 1A; $3{,}000 < G < 3{,}025$). Surprisingly, after a brief period (in evolutionary terms) of handler tracking being the most common strategy, a third strategy also becomes more common: avoiding both handlers and non-handlers ('agent avoiding'; $s_H, s_N < 0$). Within 250 generations after pathogen introduction, agent avoiding becomes as common as the handler tracking strategy, and this appears to be a stable equilibrium that is maintained until the end of the simulation (2,000 generations after pathogen introduction; Fig. 1A). The *SI Appendix* shows how modelling choices can alter the nature of the evolutionary shift triggered by pathogen introduction; in brief, such shifts occur even when individuals cannot benefit from local adaptation (Badyaev and Uller 2009), and when the pathogen saps a percentage, rather than an absolute value, from daily intake.

In addition to qualitative changes in social movement strategies, pathogen introduction also leads to social information becoming more important to movement decisions. Prior to pathogen introduction ($G < 3{,}000$), individuals' handler- and non-handler preferences ($|s_H| + |s_N|$; taken together, social information) barely influence their movement strategies (Fig. 1B). These are instead guided primarily by the preference for food items (s_F; see *Model and Analysis*; see also *Supplementary Material Fig. 1*). Social movement decisions are joint outcomes of individual preferences for social cues and the cue value: consequently, in clustered populations (see below), even small positive values of s_H and s_N lead to strong emergent sociality. After pathogen introduction, there is a substantial increase in the average importance of individuals' preferences (or aversions) for the presence of other foragers (Fig. 1B). However, there is significant variation among individuals in the importance of social information to their movement strategies, with distinct evolved polymorphisms that vary substantially between simulation replicates (Fig. 1B).

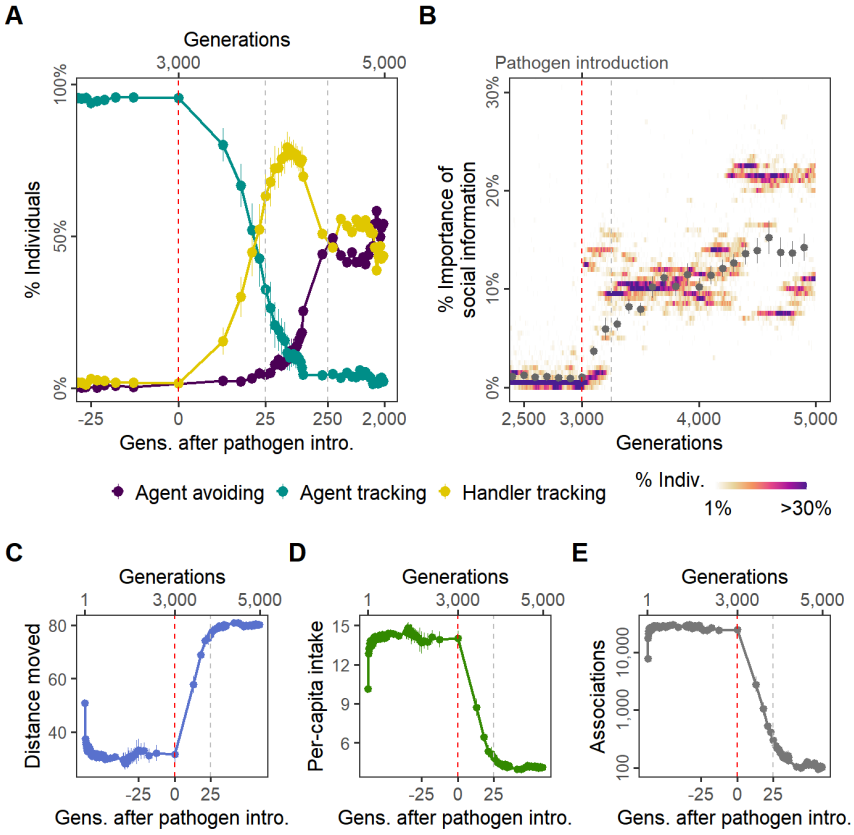

Figure 1: Pathogen introduction leads to rapid evolutionary changes in social information use, with cascading effects on population ecological outcomes. (A) Before pathogen introduction in the default scenario ($R = 2$, $\delta E = 0.25$), populations rapidly evolve a social movement strategy that tracks all other individuals ('agent tracking'; $G \leq 3{,}000$) — however, their overall movement strategy is primarily guided by the presence of food items **(B)**. Pathogen introduction leads to the rapid replacement, within 25 generations, of agent tracking with 'handler tracking' (preference for successful foragers; $3{,}000 < G < 3{,}025$). Within 250 generations, 'agent avoidance' (avoidance of both successful and unsuccessful foragers; $G > 3{,}250$) also becomes common, stably co-existing with the handler tracking strategy in an eco-evolutionary equilibrium. **(B)** After pathogen introduction ($G > 3{,}000$), the importance of social cues (the presence of other individuals; the sum of the absolute, normalised preferences sH, sN) increases substantially on average (grey points). Additionally, there is significant variation in the importance of social cues to individuals (shaded regions), which is not captured by the mean or standard error. At G = 4,500, for example, social information comprises $\approx 10\%$ of some individuals' movement strategies, but some individuals have evolved a stronger weight for social cues ($> 20\%$). The rapid change in social movement strategies following pathogen introduction has cascading effects on ecological outcomes. Individuals, which have evolved strong aversions to at least some kinds of foragers (depending on their strategy), **(C)** move more on average, **(D)** have only 25% of the pre-pathogen average intake, and **(E)** have 100-fold fewer associations with other individuals. All panels show data averaged over 10 replicates, but shaded region in panel B shows only a single replicate for clarity.

Disease-dominated Ecological Cascade Due to Evolutionary Shift in Movement Strategies

The evolutionary shift in social movement strategies causes a drastic change in ecological outcomes (Fig. 1C – E; see *SI Appendix Fig. S3* for other scenarios). There is a sharp increase in mean distance moved by individuals; while pre-introduction individuals moved 35% of their lifetimes on average (i.e., 35 timesteps; handling for the remainder), post-introduction, individuals move for 80% of their lifetimes (i.e., 80 timesteps; Fig. 1C). The handler tracking and agent avoiding strategies lead individuals to move away from groups of individuals ('dynamic social distancing'; Pusceddu et al. 2021). Individuals being most likely to be found near resource clusters, this leads to movement away from productive areas of the landscape. Consequently, there is a rapid, four-fold drop in mean per-capita intake after pathogen introduction (Fig. 1D). The concurrent, near 100-fold drop in encounters between individuals after pathogen introduction (Fig. 1E) suggests that most encounters were likely taking place on or near resource clusters. The reductions in intake observed are equivalent to those expected from halving landscape productivity (*SI Appendix Fig. S3*). Our model shows how even a non-fatal pathogen, by influencing the evolution of movement strategies, can have substantial indirect ecological effects — a disease dominated ecological cascade (Monk et al. 2022).

Co-existence of Social Movement Strategies

At eco-evolutionary equilibrium (G > 3,500) the relationship between movement and avoiding associations (and further, infection) is mediated by individual differences in how exactly social information is incorporated into movement strategies. Individuals using the agent avoiding strategy move more than handler tracking ones (Fig. 2A), about 85% of their lifetime (default scenario: $R = 2$; $\delta E = 0.25$). At this limit, every step moved allows them to avoid approximately 2 encounters with other individuals. Handler tracking individuals move much less ($\sim$ 60% – 80%), but are able to avoid approximately 20 encounters with other individuals with every extra step. These differences may explain why agent avoiding and handler tracking individuals have similar mean infection rates, at $\sim$ 25% and $\sim$ 33% respectively (Fig. 2B). All other strategies, especially the agent tracking strategy common in pre-introduction populations, are barely able to translate increased movement into fewer associations (Fig. 2A). These strategies have a wide range of infection rates (Fig. 2B), potentially because they are very rare — these likely represent mutants that do not give rise to persistent lineages.

Reorganisation of Spatial-social Structure

Following pathogen introduction, the mixture of individual-level movement strategies elicits a substantial re-organisation of emergent spatial and social structure at the population level. Pre-introduction populations are strongly clustered in space (Fig. 3A), due to movement strategies that favour follow-

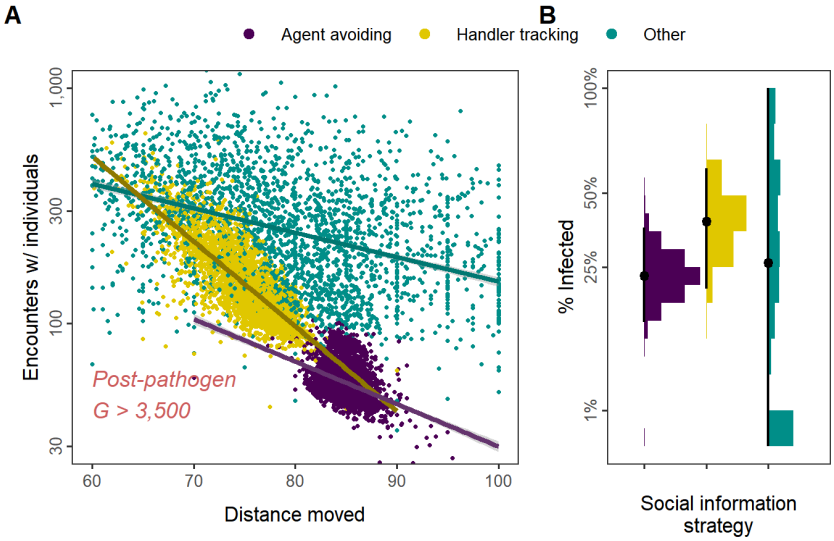

Figure 2: Social movement strategies trade movement for associations through dynamic social distancing, leading to differences in infection rates. In post-introduction populations at eco-evolutionary equilibrium (G > 3,500), **(A)** both agent avoiding and handler tracking individuals can reduce encounters with other individuals by moving to avoid other foragers (dynamic social distancing). Handler tracking individuals have many more encounters than agent avoiding individuals, but surprisingly, are better able to reduce encounters through increased movement. Individuals using other strategies (mostly agent tracking) have a wider range of movement distances, but cannot efficiently avoid other foragers by moving more. **(B)** Avoiding all other foragers leads to marginally lower infection rates than tracking successful foragers (and avoiding unsuccessful ones; handler tracking). Surprisingly, rare pre-introduction strategies such as following any nearby individuals (agent tracking) may also have low infection rates, potentially due to their rarity. Panel A shows linear model fits with a log scale Y-axis; panel B shows infection rates; all data represent generation- and replicate-specific means ($3{,}000 < G < 3{,}500$; $R = 2$, $\delta E = 0.25$).

ing most other foragers. This spatial proximity means that most individuals encounter each other at least once, leading to numerous unique partners (the 'degree') for each forager (Fig. 3 inset 1: *blue*). In contrast, Spread-out networks in pathogen-adapted populations suggest that most foragers move substantially from their initial locations over their lifetime, associating only ephemerally with foragers from all over the landscape (Fig. 3B). This reflects movement strategies which lead to near-perpetual movement to avoid associations; a sort of dynamic social distancing seen in real animal societies under risk of pathogen spread (Stroeymeyt et al. 2018; Weinstein et al. 2018; Pusceddu et al. 2021; Stockmaier et al. 2021). This dispersed population structure means that most foragers encounter fewer than 10% of the population over their lifetime (Fig. 3 inset 1: *red*).

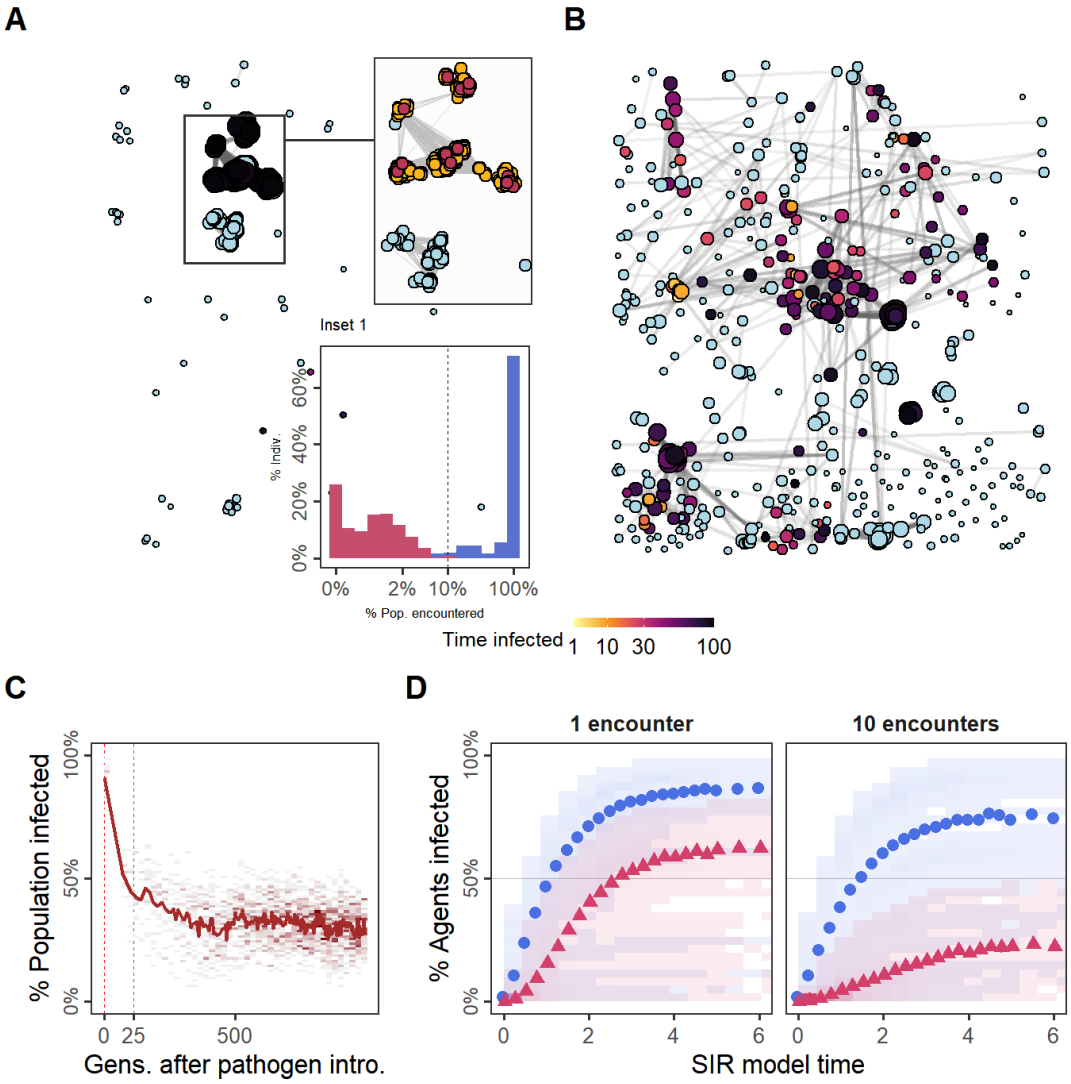

Figure 3: Reduced spatial-social clustering and disease transmission in populations adapted to the presence of an infectious pathogen. Pathogen-naive populations (**A**; G = 3,000) are much more spatially clustered than pathogen-adapted populations (**B**; G = 3,500), and are thus rapidly infected (red: primary infections; yellow: secondary infections; blue: never infected). Pre-introduction individuals encounter many more unique neighbours (**inset 1**, blue) than pathogen-adapted individuals (**inset 1**; red). Dashed grey line represents 10% of individuals encountered (N = 50). Main panels show social networks from a single replicate of the default scenario ($R = 2$, $\delta E = 0.25$), insets show 10 replicates. Nodes represent individuals positioned at their final location. Connections represent pairwise encounters, and node size represents encounters (larger = more encounters). Darker node colours indicate longer infection (light blue = no infection). **(C)** In the first generations following pathogen introduction, nearly every single individual in the population is infected. However, within 25 generations, tracking the evolutionary shift towards movement strategies that avoid some or all other individuals, only about 50% of individuals are ever infected; this drops to a stable 30% within 500 generations after pathogen introduction. **(D)** The progression of two hypothetical diseases, requiring a single encounter, or 10 encounters for a potential transmission, on emergent social networks. The transmission of both diseases is reduced in populations with disease-adapted movement strategies (pre-introduction: G = 3,000, blue circles; post-introduction: G = 3,500, red triangles). Subfigures in panel D show means of 25 SIR model replicates (transmission rate $\beta = 5.0$, recovery rate $\gamma = 1.0$), run on emergent social network; both panels represent 10 simulation replicates the default scenario.

Pathogen-adapted Movement Strategies Make Animal Societies More Resilient to the Spread of Disease

Nearly every individual in the generations just after pathogen introduction was infected. However, tracking the evolutionary change in movement strategies, the number of infected individuals fell to just about 50% within 25 generations (Fig. 3C). To examine potential pathogen spread in pre-introduction populations, we ran a simple epidemiological model on the social networks emerging from individuals' movements before and after pathogen introduction (pre-introduction: $G = 3{,}000$; post-introduction: $G = 3{,}500$). We modelled two diseases, *(i)* first, a disease requiring one encounter,and *(ii)* second, a disease requiring ten encounters between individuals for a potential transmission event (transmission rate $\beta = 5.0$, recovery rate $\gamma = 1.0$). Both the single encounter and multiple encounter diseases would infect 75% – 80% of individuals when spreading through the networks of pre-introduction populations (Fig. 3D) Pathogen-adapted populations' social networks are more resilient to both the single encounter and multiple encounter disease, compared to their pre-introduction, pathogen-naive ancestors (Fig. 3D), as these social networks are sparser and individuals are more weakly connected (Fig. 3D; see Fig. 3D). Less than 60% of post-introduction populations were finally infected by the single encounter disease, compared with > 75% of pre-introduction, pathogen-naive ancestors; in pathogen-adapted populations, the spread of the multiple encounter disease was even slower (ever infected: $\approx 20\%$).

Usefulness of Social Information and Infection Cost Influence Evolution of Social Movement Strategies

We further explored the effect of two ecological parameters, landscape productivity ($R \in 1, 2, 5$) and infection cost per timestep ($\delta E \in 0.1, 0.25, 0.5$) on simulation outcomes. Before pathogen introduction, landscape productivity alone determines the value of social information, and thus which social movement strategies evolve (Fig. 4). On low-productivity landscapes ($R = 1$), social information is valuable as direct resource cues are scarce; here, the handler-tracking strategy persists. On high-productivity landscapes ($R \in 2, 5$), social information is less valuable as individuals can directly detect food items more often; here, the agent tracking strategy is most common. Across parameter combinations, the introduction of the infectious pathogen leads to a rapid evolutionary shift in social movement strategies. The benefits of social information, and infection cost jointly determine how pathogen introduction alters the mix of social movement strategies, but populations generally shift away from indiscriminate agent tracking, as that strategy is associated with higher infection risk.

When the benefit of social information is equivalent to the cost of infection, the handler tracking strategy is common ($R = 1$, $\delta E = 0.1$; $R = 5$, $\delta E = 0.25$). When apparent social information benefits are lower than infection costs (e.g. $\delta E = 0.5$), the agent avoiding strategy is common. The effect of landscape productivity in obviating a sensitivity to social information cues (especially, conspecific

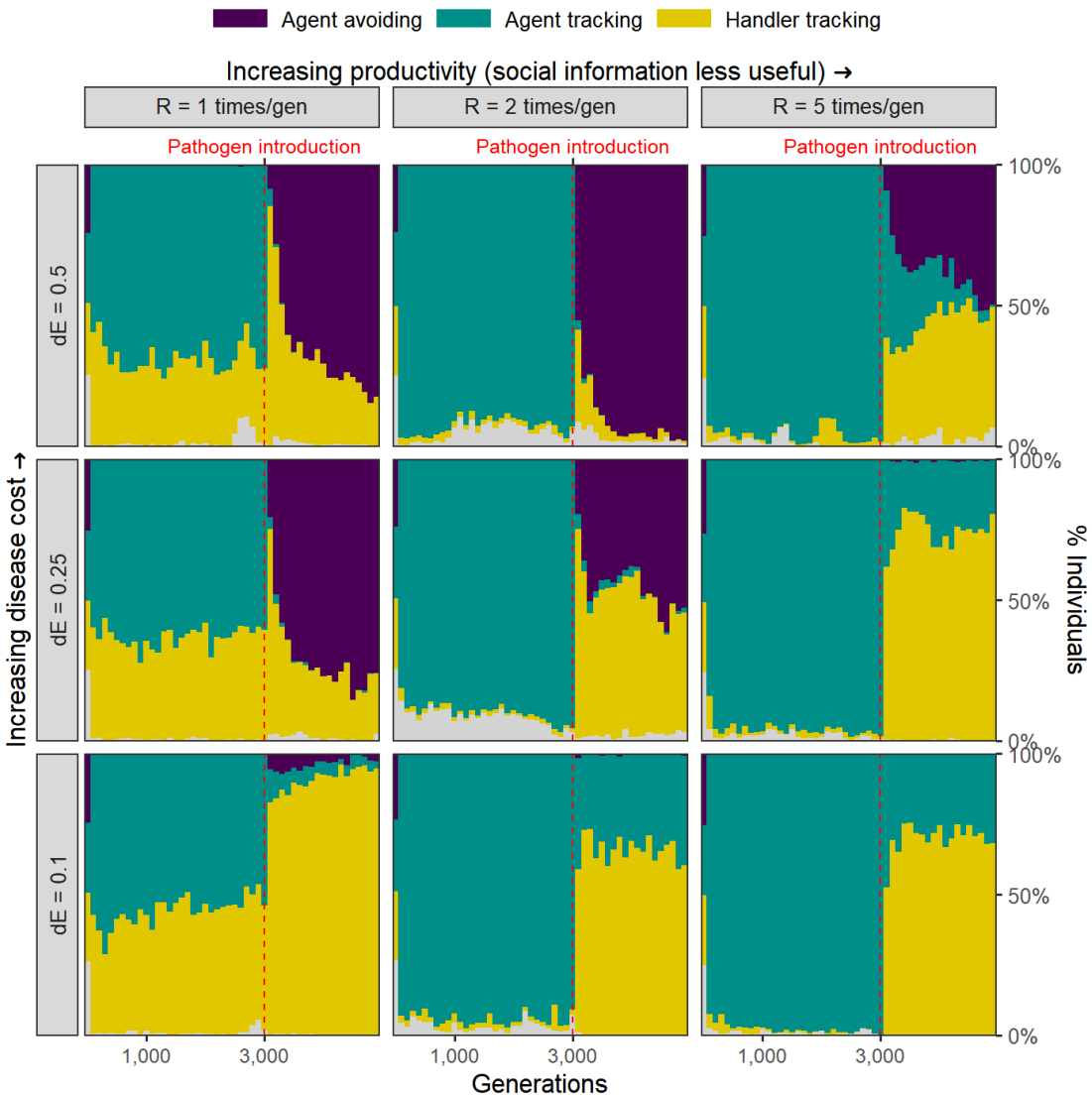

Figure 4: The balance of infection cost and the usefulness of social information together shape the rapid evolutionary change in movement strategies triggered by pathogen introduction. Pre-introduction (G = 3,000; dashed line) populations contain a mix of individuals that either track all foragers (agent tracking), or only successful foragers (handler tracking). Handler tracking is more common on low-productivity landscapes ($R = 1$), where social information is more useful to find patchily distributed resources. After pathogen introduction, handler tracking rapidly becomes the most common strategy when the apparent usefulness of social information is greater than the cost of infection. This occurs both when productivity is low ($R = 1$) and infection costs are low ($\delta E = 0.1$), but also when productivity is high ($R = 5$) with intermediate infection costs ($\delta E = 0.25$). When the cost of infection outweighs the apparent usefulness of social information, the agent avoidance (avoiding both successful and unsuccessful foragers) emerges and rapidly becomes a common strategy ($\delta E = 0.5$; $\delta E = 0.25$, R = 1). In scenarios of high landscape productivity combined with low infection costs (e.g. $R = 5$, $\delta E = 0.1$), the agent tracking strategy persists in a large proportion after pathogen introduction, as these individuals can balance disease costs with intake alone. All panels show mean frequencies over 10 replicate simulations in 100 generation bins; frequencies are stacked. Grey areas show the relatively uncommon 'non-handler' tracking strategy.

status) is also eroded by pathogen introduction. On high-productivity landscapes where individuals were indiscriminately social, ($R \in 2, 5$, $\delta E = 0.1$), the handler tracking strategy becomes common, as individuals prioritise higher-quality social information (handlers, which indicate a resource cluster). However, high landscape productivity can also compensate for the cost of infection, as evidenced by the agent tracking strategy remaining prevalent: this is only possible if these individuals can consume sufficient resources to overcome disease costs.

Discussion

Our general model captures important features of the infectious pathogen transmission among host animals in a context that is applicable across multiple taxa, and the resulting eco-evolutionary dynamics. We demonstrate the tension inherent to sociality under the risk of an infectious pathogen, in an explicitly spatial context. We show how populations, initially evolved to find patchily distributed food using social information, rapidly evolve to eschew social encounters when an infectious pathogen is introduced. Our work shows how qualitatively and quantitatively different social movement strategies — each making a different trade-off between social information and infection risk — can co-exist in a single population (Wolf and Weissing 2012; Webber and Vander Wal 2018; Gartland et al. 2021; Webber et al. 2022).

Prior to pathogen introduction, the value of social information influenced which social movement strategies were evolved. When individuals are initialised ('born') near their parent's final location, they may benefit from 'ecological inheritance' of their parent's favourable position near resource clusters (see *SI Appendix Fig. S2, S4*) (Badyaev and Uller 2009). In this case, avoiding potential competitors (and kin) correlates with avoiding profitable areas. This leads to the persistence of the indiscriminately social agent tracking strategy, despite the evident costs of exploitation competition (see *SI Appendix* for an alternative implementation). Following pathogen introduction, the evolutionary shift in social movement strategies is much more rapid than the timescales usually associated with the evolution of complex traits such as sociality.

Avoiding potentially infectious individuals is a key component of navigating the 'landscape of disgust' (Weinstein et al. 2018). To navigate this landscape effectively, animals must first be sensitive, or become more sensitive, to cues of high transmission risk. Our results show that such sensitivity can rapidly evolve following the introduction of a novel pathogen, leading to strong qualitative changes in movement strategies within 100 generations. The average increase in individuals' sensitivity to social cues is combined with substantial between-individual variation in the importance of social cues overall. A mix of individuals with different sensitivities to social cues, relative to resource cues, is key to the evolution of large-scale collective behaviours, such as migration (Guttal and Couzin 2010). Our work suggests how by leading to the necessary diversity in social movement strategies, a novel pathogen may actually lay the groundwork for the evolution of more complex collective behaviour. The emergence of individual variation in social movement strategies, and especially the trade-off between movement,

associations, and infection risk also suggests a clear mechanism by which sociality could evolve as a personality trait (Gartland et al. 2021). Pathogens themselves typically have shorter generation times than their hosts, and may also evolve rapidly in response to changes in host sociality (Ashby and Farine 2022). Though not examined here, a mixture of social strategies could allow for the evolution of a corresponding diversity in pathogen strategies as well (Prado et al. 2009; Ashby and Farine 2022).

In our model, landscape productivity (R), serves as a proxy for the usefulness of social information, and sociality overall. Social information benefits in a disease models often have no mechanistic relationship with the subject of the information (e.g. food, predators) (Ashby and Farine 2022). In contrast, social information benefits in our model are emergent outcomes of animal movement and foraging mechanisms. Our model's predictions may help explain intra- and inter-specific diversity in social systems across different contexts of infection risk and the usefulness of social information (Altizer et al. 2003; Sah et al. 2018). At the population level, this suggests one pathway by which gregarious, clustered species, which are expected to be more at risk from transmissible pathogens (Sah et al. 2018), could transition to a more solitary social organisation over evolutionary timescales. More positively, our results suggest that animals may be able to adapt relatively quickly to the spillover and eventual persistence of infectious pathogens, even when they cannot specifically detect and avoid infected individuals (Altizer et al. 2003; Stroeymeyt et al. 2018; Pusceddu et al. 2021; Stockmaier et al. 2021; Kuchipudi et al. 2022).

Ecological models expect even isolated pathogen outbreaks, such as that of swine fever in wild boar, to last over a decade due to interacting effects of host movement and landscape structure (Scherer et al. 2020). These outbreaks are expected to have substantial cascading effects for landscape and community ecology (Monk et al. 2022). Our model shows that rapid, disease-dominated ecological cascades — individuals have less intake, exerting less top-down pressure on their resource — can occur even without mortality effects, due to evolutionary shifts in movement alone. Furthermore, our results suggest that selection against sociality (usually held constant in ecological models) could bring infection outbreaks under control more swiftly than predicted, as the population shifts from gregarious to solitary. Our predictions are contingent upon sustained introduction of the pathogen to host populations; more sporadic introductions (once every few generations) apparently do not cause evolutionary shifts in social movement (*SI Appendix*). Yet many long-lived species are likely to experience multiple pathogen introduction events during the average individual's lifetime (e.g. of avian influenza into sea- and waterbirds; Wille and Barr 2022); this suggests that our once-per-generation introductions are not rare in wildlife populations. Nonetheless, the altered ecological state (here, less resource consumption, as in Monk et al. 2022) may be maintained long after — and indeed because — a population has adapted to be less social in the presence of a pathogen. Our work suggests that decreased sociality resulting from adaptation to a novel pathogen could slow the transmission of future novel pathogens. While decreased sociality could also reduce the prevalence of previously endemic pathogens adapted to a more social host (Sah et al. 2018), it may also degrade 'social immunity' through reduced sharing of beneficial commensal

microbes, or of low, immunising doses of pathogens (Ezenwa et al. 2016).

In order to be widely applicable to diverse novel host-pathogen introduction scenarios, our model is necessarily quite general, including only essential processes. Overall, our novel approach shows how evolution can be easily incorporated into mechanistic movement-disease models, and how this approach extends current understanding of animal spatial and social ecology (Webber and Vander Wal 2018; Romano et al. 2020; Albery et al. 2021; Romano et al. 2021; Webber et al. 2022). Presently, most movement-disease models are non-evolutionary (White et al. 2017; 2018*a*; Scherer et al. 2020; Lunn et al. 2021), presumably because evolution is expected to be too slow to impact epidemiological-ecological outcomes (Monk et al. 2022). Yet we find that evolution can be very rapid: evolutionary transitions in sociality occur over fewer generations than required for the development of key aspects of animal ecology, such as migration routes (Jesmer et al. 2018; Cantor et al. 2021). Current and expected cross-species transmissions of novel pathogens (Sanderson and Alexander 2020; Carlson et al. 2022; Kuchipudi et al. 2022; Monk et al. 2022) should thus prompt concern that the evolutionary consequences of pathogen introduction could slow the transmission of, and erode, animal culture (Cantor et al. 2021). Our infectious pathogen is easily transmitted through proximity, and causes a chronic yet non-fatal disease; though realistic, these assumptions cannot capture the full diversity of pathogens and their dynamics (White et al. 2017; 2018*a*; Scherer et al. 2020; Lunn et al. 2021). Yet, our framework can be expanded and specifically tailored to real-world situations in which populations are repeatedly exposed to novel pathogens (or strains), such as swine fever in wild boar (Scherer et al. 2020), avian influenza in Arctic birds (Wille and Barr 2022), or the introduction of SARS-CoV 2 to deer (Kuchipudi et al. 2022). Such detailed paramterisation could account for the differential effects of proximity and social contacts on transmission. It is challenging to study whether sharp, temporally restricted outbreaks of fatal epizootics exert substantial evolutionary pressure against sociality (Blehert et al. 2009; Fereidouni et al. 2019; Scheele et al. 2019; Wille and Barr 2022). Future work would ideally combine wildlife monitoring to detect novel cross-species spillovers (Kuchipudi et al. 2022), with recent advances in animal tracking, to examine joint movement-disease dynamics and strategies (White et al. 2017; Bastille-Rousseau and Wittemyer 2019; Monk et al. 2022; Wilber et al. 2022). Our model shows why it may be key to consider evolutionary responses in movement-disease studies, and provides a general framework to further the integration of evolutionary approaches in wildlife spatial epidemiology.

Data and Code Availability

The *Pathomove* simulation model code is available on Zenodo at https://zenodo.org/record/6782640, and on Github at github.com/pratikunterwegs/pathomove. Code to run the simulations and analyse the output is on Zenodo at https://zenodo.org/record/6782665, and on Github at: github.com/pratikunterwegs/pathomove-evol.

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References

Albery, G. F., Kirkpatrick, L., Firth, J. A., and Bansal, S. (2021), "Unifying spatial and social network analysis in disease ecology", *Journal of Animal Ecology*, 90/1: 45–61.

Almberg, E. S., Cross, P. C., Dobson, A. P., Smith, D. W., Metz, M. C., Stahler, D. R., and Hudson, P. J. (2015), "Social living mitigates the costs of a chronic illness in a cooperative carnivore", *Ecology Letters*, 18/7: 660–7.

Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Dobson, A. P., Ezenwa, V., Jones, K. E., Pedersen, A. B., Poss, M., and Pulliam, J. R. (2003), "Social organization and parasite risk in mammals: Integrating theory and empirical studies", *Annual Review of Ecology, Evolution, and Systematics*, 34/1: 517–47.

Ashby, B. and Farine, D. R. (2022), "Social information use shapes the coevolution of sociality and virulence", *bioRxiv : the preprint server for biology*.

Badyaev, A. V. and Uller, T. (2009), "Parental effects in ecology and evolution: Mechanisms, processes and implications", *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364/1520: 1169–77.

Bailey, N. T. J. (1975), *The Mathematical Theory of Infectious Diseases and Its Applications* (2nd ed., London: Griffin).

Bastille-Rousseau, G. and Wittemyer, G. (2019), "Leveraging multidimensional heterogeneity in resource selection to define movement tactics of animals", *Ecology Letters*, 22/9: 1417–27.

Blehert, D. S., Hicks, A. C., Behr, M., Meteyer, C. U., Berlowski-Zier, B. M., Buckles, E. L., Coleman, J. T. H., Darling, S. R., Gargas, A., Niver, R., Okoniewski, J. C., Rudd, R. J., and Stone, W. B. (2009), "Bat white-nose syndrome: An emerging fungal pathogen?", *Science (New York, N.Y.)*, 323/5911: 227.

Bonds, M. H., Keenan, D. D., Leidner, A. J., and Rohani, P. (2005), "Higher disease prevalence can induce greater sociality: A game theoretic coevolutionary model", *Evolution*, 59/9: 1859–66.

Cantor, M., Maldonado-Chaparro, A. A., Beck, K. B., Brandl, H. B., Carter, G. G., He, P., Hillemann, F., Klarevas-Irby, J. A., Ogino, M., Papageorgiou, D., Prox, L., and Farine, D. R. (2021), "The importance of individual-to-society feedbacks in animal ecology and evolution", *Journal of Animal Ecology*, 90/1: 27–44.

Carlson, C. J., Albery, G. F., Merow, C., Trisos, C. H., Zipfel, C. M., Eskew, E. A., Olival, K. J., Ross, N., and Bansal, S. (2022), "Climate change increases cross-species viral transmission risk", *Nature*: 1–1.

Csardi, G. and Nepusz, T. (2006), "The *igraph* software package for complex network research", *InterJournal*, Complex Systems: 1695.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., and Stephens, D. W. (2005), "Information and its use by animals in evolutionary ecology", *Trends in Ecology & Evolution*, 20/4: 187–93.

Danchin, É., Giraldeau, L.-A., Valone, T. J., and Wagner, R. H. (2004), "Public information: From nosy neighbors to cultural evolution", *Science*, 305/5683: 487–91.

DeAngelis, D. L. and Diaz, S. G. (2019), "Decision-making in agent-based modeling: A current review and future prospectus", *Frontiers in Ecology and Evolution*, 6.

Eddelbuettel, D. (2013), *Seamless R and C++ Integration with Rcpp* (Use R!; New York: Springer-Verlag).

Ezenwa, V. O., Ghai, R. R., McKay, A. F., and Williams, A. E. (2016), "Group living and pathogen infection revisited", *Current Opinion in Behavioral Sciences*, Behavioral Ecology, 12: 66–72.

Fereidouni, S., Freimanis, G. L., Orynbayev, M., Ribeca, P., Flannery, J., King, D. P., Zuther, S., Beer, M., Höper, D., Kydyrmanov, A., Karamendin, K., and Kock, R. (2019), "Mass die-off of Saiga antelopes, Kazakhstan, 2015", *Emerging Infectious Diseases*, 25/6: 1169–76.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., and Mao, J. S. (2005), "Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park", *Ecology*, 86/5: 1320–30.

Gartland, L. A., Firth, J. A., Laskowski, K. L., Jeanson, R., and Ioannou, C. C. (2021), "Sociability as a personality trait in animals: Methods, causes and consequences", *Biological Reviews*, n/a/n/a.

Getz, W. M., Salter, R., Lyons, A. J., and Sippl-Swezey, N. (2015), "Panmictic and clonal evolution on a single patchy resource produces polymorphic foraging guilds", *PLOS ONE* 10/8: e0133732–e0133732.

Gil, M. A., Hein, A. M., Spiegel, O., Baskett, M. L., and Sih, A. (2018), "Social information links individual behavior to population and community dynamics", *Trends in Ecology & Evolution*, 33/7: 535–48.

Gupte, P. R., Netz, C. F. G., and Weissing, F. J. (2021), "The joint evolution of animal movement and competition strategies", *bioRxiv*.

Guttal, V. and Couzin, I. D. (2010), "Social interactions, information use, and the evolution of collective migration", *Proceedings of the National Academy of Sciences*, 107/37: 16172.

Hamblin, S. (2013), "On the practical usage of genetic algorithms in ecology and evolution", *Methods in Ecology and Evolution*, 4/2: 184–94.

Hutchings, M. R., Judge, J., Gordon, I. J., Athanasiadou, S., and Kyriazakis, I. (2006), "Use of trade-off theory to advance understanding of herbivore–parasite interactions", *Mammal Review*, 36/1: 1–16.

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., McWhirter, D. E., Miyasaki, H. M., Monteith, K. L., and Kauffman, M. J. (2018), "Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals", *Science*, 361/6406: 1023–5.

Kuchipudi, S. V., Surendran-Nair, M., Ruden, R. M., Yon, M., Nissly, R. H., Vandegrift, K. J., Nelli, R. K., Li, L., Jayarao, B. M., Maranas, C. D., Levine, N., Willgert, K., Conlan, A. J. K., Olsen, R. J., Davis, J. J., Musser, J. M., Hudson, P. J., and Kapur, V. (2022), "Multiple spillovers from humans and onward transmission of SARS-CoV-2 in white-tailed deer", *Proceedings of the National Academy of Sciences*, 119/6.

Lunn, T. J., Peel, A. J., McCallum, H., Eby, P., Kessler, M. K., Plowright, R. K., and Restif, O. (2021), "Spatial dynamics of pathogen transmission in communally roosting species: Impacts of changing habitats on bat-virus dynamics", *Journal of Animal Ecology*, n/a/n/a.

Monk, J. D., Smith, J. A., Donadío, E., Perrig, P. L., Crego, R. D., Fileni, M., Bidder, O., Lambertucci, S. A., Pauli, J. N., Schmitz, O. J., and Middleton, A. D. (2022), "Cascading effects of a disease outbreak in a remote protected area", *Ecology Letters*, n/a/n/a.

Netz, C. F. G., Hildenbrandt, H., and Weissing, F. J. (2021), "Complex eco-evolutionary dynamics induced by the coevolution of predator–prey movement strategies", *Evolutionary Ecology*.

Poulin, R. and Filion, A. (2021), "Evolution of social behaviour in an infectious world: Comparative analysis of social network structure versus parasite richness", *Behavioral Ecology and Sociobiology*, 75/7: 105.

Prado, F., Sheih, A., West, J. D., and Kerr, B. (2009), "Coevolutionary cycling of host sociality and pathogen virulence in contact networks", *Journal of Theoretical Biology*, 261/4: 561–9.

Pusceddu, M., Cini, A., Alberti, S., Salaris, E., Theodorou, P., Floris, I., and Satta, A. (2021), "Honey bees increase social distancing when facing the ectoparasite varroa destructor", *Science Advances*, 7/44: eabj1398.

R Core Team (2020), *R: A Language and Environment for Statistical Computing* (manual; Vienna, Austria: R Foundation for Statistical Computing).

Romano, V., MacIntosh, A. J. J., and Sueur, C. (2020), "Stemming the flow: Information, infection, and social evolution", *Trends in Ecology & Evolution*, 35/10: 849–53.

Romano, V., Sueur, C., and MacIntosh, A. J. J. (2021), "The tradeoff between information and pathogen transmission in animal societies", *Oikos*, n/a/n/a.

Ruxton, G. D., Gurney, W. S. C., and de Roos, A. M. (1992), "Interference and generation cycles", *Theoretical Population Biology*, 42/3: 235–53.

Sah, P., Mann, J., and Bansal, S. (2018), "Disease implications of animal social network structure: A synthesis across social systems", *Journal of Animal Ecology*, 87/3: 546–58.

Sanderson, C. E. and Alexander, K. A. (2020), "Unchartered waters: Climate change likely to intensify infectious disease outbreaks causing mass mortality events in marine mammals", *Global Change Biology*, 26/8: 4284–301.

Scheele, B. C., Pasmans, F., Skerratt, L. F., Berger, L., Martel, A., Beukema, W., Acevedo, A. A., Burrowes, P. A., Carvalho, T., Catenazzi, A., De la Riva, I., Fisher, M. C., Flechas, S. V., Foster, C. N., Frías-Álvarez, P., Garner, T. W. J., Gratwicke, B., Guayasamin, J. M., Hirschfeld, M., Kolby, J. E., Kosch, T. A., La Marca, E., Lindenmayer, D. B., Lips, K. R., Longo, A. V., Maneyro, R., McDonald, C. A., Mendelson, J., Palacios-Rodriguez, P., Parra-Olea, G., Richards-Zawacki, C. L., Rödel, M.-O., Rovito, S. M., Soto-Azat, C., Toledo, L. F., Voyles, J., Weldon, C., Whitfield, S. M., Wilkinson, M., Zamudio, K. R., and Canessa, S. (2019), "Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity", *Science (New York, N.Y.)*, 363/6434: 1459–63.

Scherer, C., Radchuk, V., Franz, M., Thulke, H.-H., Lange, M., Grimm, V., and Kramer-Schadt, S. (2020), "Moving infections: Individual movement decisions drive disease persistence in spatially structured landscapes", *Oikos*, 129/5: 651–67.

Spiegel, O., Leu, S. T., Bull, C. M., and Sih, A. (2017), "What's your move? Movement as a link between personality and spatial dynamics in animal populations", *Ecology Letters*, 20/1: 3–18.

Spiegel, O., Leu, S. T., Sih, A., and Bull, C. M. (2016), "Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints", *Methods in Ecology and Evolution*, 7/8: 971–9.

Stockmaier, S., Stroeymeyt, N., Shattuck, E. C., Hawley, D. M., Meyers, L. A., and Bolnick, D. I. (2021), "Infectious diseases and social distancing in nature", *Science*, 371/6533: eabc8881.

Stroeymeyt, N., Grasse, A. V., Crespi, A., Mersch, D. P., Cremer, S., and Keller, L. (2018), "Social network plasticity decreases disease transmission in a eusocial insect", *Science (New York, N.Y.)*, 362/6417: 941–5.

Tanner, C. J. and Jackson, A. L. (2012), "Social structure emerges via the interaction between local ecology and individual behaviour", *Journal of Animal Ecology*, 81/1: 260–7.

Webber, Q. M. R., Albery, G., Farine, D. R., Pinter-Wollman, N., Sharma, N., Spiegel, O., Wal, E. V., and Manlove, K. (2022), "Behavioural ecology at the spatial-social interface", *EcoEvoRxiv*.

Webber, Q. M. R. and Vander Wal, E. (2018), "An evolutionary framework outlining the integration of individual social and spatial ecology", *Journal of Animal Ecology*, 87/1: 113–27.

Weinstein, S. B., Buck, J. C., and Young, H. S. (2018), "A landscape of disgust", *Science*, 359/6381: 1213–4.

White, L. A., Forester, J. D., and Craft, M. E. (2017), "Using contact networks to explore mechanisms of parasite transmission in wildlife", *Biological Reviews*, 92/1: 389–409.

—— (2018*a*), "Disease outbreak thresholds emerge from interactions between movement behavior, landscape structure, and epidemiology", *Proceedings of the National Academy of Sciences*, 115/28: 7374–9.

—— (2018*b*), "Dynamic, spatial models of parasite transmission in wildlife: Their structure, applications and remaining challenges", *Journal of Animal Ecology*, 87/3: 559–80.

Whitehead, H. (2008), *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis* (University of Chicago Press).

Wilber, M. Q., Yang, A., Boughton, R., Manlove, K. R., Miller, R. S., Pepin, K. M., and Wittemyer, G. (2022), "A model for leveraging animal movement to understand spatio-temporal disease dynamics", *Ecology Letters*, n/a/n/a.

Wille, M. and Barr, I. G. (2022), "Resurgence of avian influenza virus", *Science*, 376/6592: 459–60.

Wolf, M. and Weissing, F. J. (2012), "Animal personalities: Consequences for ecology and evolution", *Trends in Ecology & Evolution*, 27/8: 452–61.