# Sustaining Transmission in Different Host Species: The Emblematic Case of *Sarcoptes scabiei*

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*Some pathogens sustain transmission in multiple different host species, but how this epidemiologically important feat is achieved remains enigmatic.* Sarcoptes scabiei *is among the most host generalist and successful of mammalian parasites. We synthesize pathogen and host traits that mediate sustained transmission and present cases illustrating three transmission mechanisms (direct, indirect, and combined). The pathogen traits that explain the success of* S. scabiei *include immune response modulation, on-host movement capacity, off-host seeking behaviors, and environmental persistence. Sociality and host density appear to be key for hosts in which direct transmission dominates, whereas in solitary hosts, the use of shared environments is important for indirect transmission. In social den-using species, combined direct and indirect transmission appears likely. Empirical research rarely considers the mechanisms enabling* S. scabiei *to become endemic in host species—more often focusing on outbreaks. Our review may illuminate parasites' adaptation strategies to sustain transmission through varied mechanisms across host species.*

*Keywords: sarcoptic mange, scabies, host pathogen traits, disease dynamics, pathogen persistence, endemic transmission*

**P**athogens (parasites and other infectious organisms) are under strong selective pressures to evolve strategies that enable them to persist, infect, and replicate on or in an individual host and to sustain transmission between host individuals (Hudson et al. 2002, Swinton et al. 2002). Pathogens may sustain transmission within a single host species, such as the measles virus in humans and the African swine fever virus in pigs (Gallardo et al. 2015, Furuse and Oshitani 2017, Santibanez et al. 2017). Notably, some pathogens achieve sustained transmission in more than one host species. For example, the canine distemper virus, which affects dozens of species of carnivores; *Batrachochytrium dendrobatidis*, a fungus affecting hundreds of species of amphibians; *Pseudogymnoascus destructans*, which affects at least a dozen bat species; the psittacine beak and feather disease virus, which affects dozens of bird species; and *Sarcoptes scabiei*, a parasitic mite affecting many mammals (Almberg et al. 2010, Kilpatrick et al. 2010, Martinez-Gutierrez and Ruiz-Saenz 2016, Astorga et al. 2018, Raidal and Peters 2018). These pathogens can sustain transmission in many host species that have quite different ecologies. In the present article, we consider sustained transmission to require ongoing maintenance of the pathogen in a host species over an extended duration (years or multiple generations of the host) without

discernible sign of pathogen extinction, and this can include both stable endemic and epidemic dynamics.

The features of pathogens that allow them to sustain transmission in populations of different host species are rarely understood in nature. Although there is a large amount of theory and modeling that explores the transmission dynamics of pathogens (e.g., Anderson and May 1992, Grenfell and Dobson 1995, Artois et al. 1997, Hudson et al. 2002), there are fewer empirical examinations of specific pathogen systems and the host species involved. Identifying the factors that influence the capacity of pathogens to repeatedly exploit different host species for ongoing transmission may present opportunities to improve the understanding of disease emergence and host–parasite coevolution. Using *S. scabiei* (the etiological agent of sarcoptic mange) as an example of pathogens that independently sustain transmission in different host species, we explore the potential mechanisms by which this is achieved. We take a structured approach, first introducing fundamental knowledge about *S. scabiei*. Second, we synthesize how the pathogen can maintain spread via three variable transmission mechanisms (direct transmission, indirect transmission, and combined direct and indirect transmission) and persist in seven well-characterized host species (figure 1). Finally, we propose
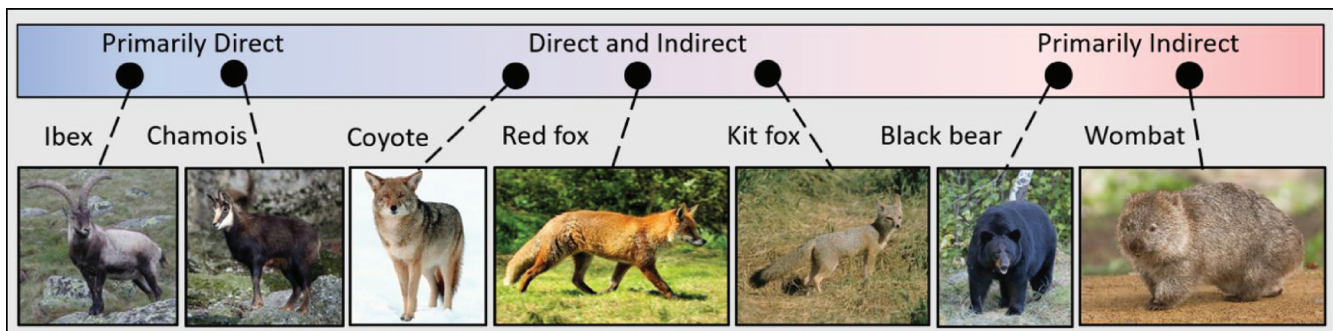
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*Figure 1. Conceptual continuum of host species'* S. scabiei *transmission mechanism, from primarily direct (blue) through to primarily indirect (red) transmission. Direct transmission dominates in species that live in close contact with high levels of sociality (e.g., ibex and chamois species), whereas more solitary species (e.g., black bears and wombats) are likely to have a dominant indirect mechanism of transmission. Species that live in groups and use shared environments may commonly have a combination of both direct and indirect transmission of* S. scabiei *(e.g., coyote and fox species). Photographs: Wikipedia under an open use Creative Commons license.*

future research directions and applications to other pathogen systems. We acknowledge that many of the traits and mechanisms discussed may also be relevant to spillover and interspecies transmission events, but our focus in the present article is on sustained transmission within individual host species.

The ability of a pathogen to sustain transmission in different host species depends on combinations of and the interactions between traits of both the pathogen and the host (Ezenwa et al. 2006), as well as environmental factors. Pathogen traits include the capacity to modulate or evade host immune responses, manipulate host behavior, survive in the environment independent of the host, adapt to different host species, exhibit virulence, ability to exploit vectors, and pathogen fecundity (Kirchner and Roy 2002, Kilpatrick and Altizer 2010, Johnson et al. 2015, Ezenwa et al. 2016). These pathogen traits affect the likelihood of pathogen survival within a host, the mechanism of pathogen transmission, and the chance of further spread between individuals of a host species (Johnson et al. 2015). Social, ecological, and life-history traits of the host can also influence how a pathogen is spread and affect the likelihood and capacity of a pathogen to sustain transmission without pathogen reintroduction. Examples of these traits include group size, social organization, mating system, feeding ecology, habitat use, home range size, and population density (Ezenwa. et al. 2006, Cross et al. 2009, Ezenwa et al. 2016). The life-history strategies of host species can be predictive of individual- and population-level responses to infectious disease (Valenzuela-Sanchez et al. 2021). Our primary aim in this review is to identify host and pathogen traits that have allowed *S. scabiei* to emerge, adapt, and sustain transmission in diverse host species.

## Overview of sarcoptic mange

Sarcoptic mange (or scabies in humans) is caused by the epidermis-burrowing parasitic mite *S. scabiei*. The pathogen

has one of the broadest host ranges of any known mammalian parasite, affecting almost 150 species worldwide, including humans, domestic animals, and wildlife (Mörner 1992, Bornstein et al. 2001, Pence and Ueckermann 2002, Niedringhaus et al. 2019a, Escobar et al. 2021). Scabies is one of the 50 most common infectious diseases of humans (more than 200 million cases per year) and has recently been categorized by the World Health Organization as a neglected tropical disease (Vos et al. 2012, Bernigaud et al. 2019, WHO 2020). In wildlife, sarcoptic mange has been documented to have an expanding host range and is considered an emerging infectious disease in North America and Australia (Tompkins et al. 2015). The parasite is a global animal welfare issue and a priority concern for many species (Tompkins et al. 2015, Escobar et al. 2021).

The severity of sarcoptic mange can vary considerably among different host species. Nevertheless, the general pathology is broadly similar, including in humans (Pence and Ueckermann 2002, Leung et al. 2020). Infection (sometimes also called *infestation*) results in immunopathology characterized by a type I or IV hypersensitivity reaction that leads to skin inflammation and other more severe clinical signs, including alopecia, hyperkeratosis, pruritus, and emaciation (Bornstein et al. 2001, Pence and Ueckermann 2002, Skerratt 2003). Some hosts (such as healthy humans) experience mild skin inflammation as mites are killed by the immune system (type I hypersensitivity). Others (e.g., canids) can display more severe clinical signs and discomfort, but few mites are detectable on the host skin (Peltier et al. 2018, Niedringhaus et al. 2019c). Highly susceptible, as well as immunocompromised hosts (e.g., wombats and immunocompromised humans), experience the most severe form of mange: crusted mange (or scabies), characterized by a cell-mediated immune response (type IV hypersensitivity), emaciation, skin thickening and fissures, secondary infections, and mortality (Pence et al. 1983, Bornstein et al. 2001, Walton 2010, Martin et al. 2018b). Animals may

succumb to starvation, hypothermia, an inability to protect themselves from predation or other threats, and—for some canids, at least—severe protein-losing dermatopathy (Pence and Ueckermann 2002, Martin et al. 2018b, Decandia et al. 2019). The factors that result in marked variation in host susceptibility are unclear in most wildlife species but likely include previous exposure, environmental conditions, and host comorbidities (Arlian 1989).

Evidence suggests humans may be the original source of *S. scabiei* spillover to other mammals (Roncalli 1987, Currier et al. 2011), with early reports of sarcoptic mange in nonhuman mammals coming from sheep, wolves, and red foxes (Bourguignon 1851, Fürstenberg 1861, Roncalli 1987, Escobar et al. 2021). Broadly, the presence of the disease in ecologically diverse host species is attributed to movements of humans and domesticated animals around the world (Alasaad et al. 2013, Escobar et al. 2021). For example, molecular markers have shown that multiple introduction events from both humans and canids (dogs and foxes) likely facilitated the emergence of *S. scabiei* in Australian marsupials, specifically the bare-nosed wombat (Skerratt et al. 2002, Fraser et al. 2016, Fraser et al. 2019). In North America, multiple introduction events linked to humans and other animal host species are likely the source of *S. scabiei* emergence in bears (Peltier et al. 2017). Comparative studies of *S. scabiei* morphology and microsatellite markers conclude that there is only one, highly variable species of *S. scabiei* (Fain 1978, Walton et al. 2004, Arlian and Morgan 2017), with evidence for a human-specific strain and a strain that infests humans and all other hosts (Fraser et al. 2016, Fraser et al. 2019).

*S. scabiei* can be transmitted both directly and indirectly, and, depending on the host species, these transmission mechanisms likely affect the spread and persistence of mange within a population (Arlian and Morgan 2017, Niedringhaus et al. 2019a, Pence and Ueckermann 2002). Previous empirical and theoretical work suggest that sarcoptic mange can exist in a variety of epidemiological patterns, including outbreaks with the extinction of a host species following parasite invasion, sustained transmission in which the parasite and the host coexist, and parasite extinction when sustained transmission cannot be supported (Beeton et al. 2019). In some communities, multiple host species are involved in endemic or epidemic sarcoptic mange (Astorga et al. 2018). Mange outbreaks and severe wildlife population declines have been reported in species such as Alpine ibex (*Capra ibex*), chamois (*Rupicapra rupicapra*), red foxes (*Vulpes vulpes*), San Joaquin kit foxes (*Vulpes macrotis mutica*), and bare-nosed wombats (*Vombatus ursinus*; Rossi et al. 1995, León-Vizcaíno et al. 1999, Soulsbury et al. 2007, Cypher et al. 2017, Martin et al. 2018a). Endemic mange is also documented within some populations of these species (Gortázar et al. 1998, Martin et al. 1998, Soulsbury et al. 2007, Rossi et al. 2019, Carver et al. 2021). However, empirical evidence of local extinction of *S. scabiei* and sustained transmission through multihost dynamics has been more difficult to demonstrate (Beeton et al. 2019). Furthermore, the underlying

mechanisms driving sustained transmission of *S. scabiei* are poorly understood in most cases, and there is currently a lack of synthesis on how transmission is sustained in so many hosts around the world (Beeton et al. 2019).

## Pathogen traits that support sustained transmission of *S. scabiei*

The capacity of *S. scabiei* to modulate the host's immune system and to survive for short periods in the environment may have a major role in sustaining transmission. In the early stages of infection, mites burrow into the skin of the host and release substances that inhibit some aspects of the immune and inflammatory response (for a detailed review of immune modulation, see Arlian and Morgan 2017). This allows the pathogen to initially evade the host's protective mechanisms and survive. Once mites become established on the host, direct transmission can occur through contact between host individuals. This is because larvae, nymphs, and adult mites inhabit and roam on the surface of the skin of infected individuals and may transfer to an uninfected individual when the two come into direct contact (figure 2; Arlian and Vyszenski-Moher 1988).

*S. scabiei* mites can also survive for short periods off the host (Mellanby et al. 1942, Arlian et al. 1984a). This pathogen trait allows an alternative transmission route, termed *indirect* or *environmental transmission* (figure 2). Laboratory trials have shown that, in humid (97% relative humidity) and relatively cool (10 degrees Celsius) conditions, mites can survive off host for up to 19 days (Arlian et al. 1984a). These conditions sustain mite survival because they reduce desiccation and lower mite metabolic rates (Davis and Moon 1987, Arlian 1989, Arlian and Morgan 2017). Once the mites in the environment contact a new host individual, they recommence epidermal burrowing to feed and reproduce. Mites dislodged for 36 hours in laboratory conditions can reliably penetrate the epidermis of the host once reattached (Arlian et al. 1984a). In optimal conditions, there are also indications that up to two-thirds of mites can survive and remain infective during the 19 day off-host period (Arlian 1989, Arlian and Morgan 2017). In addition, *S. scabiei* mites exhibit host-seeking behaviors that can increase the chances of successful environmental transmission. Mites can sense the temperature and odor of hosts, and they are attracted to these stimuli (Arlian et al. 1984b). Mites can crawl up to 150 millimeters to attach themselves to a new host after being dislodged (Arlian et al. 1984b). The combination of these traits facilitates indirect transmission of *S. scabiei*. Future investigation into how other environmental factors such as substrate type and variation in ultraviolet light influence off-host mite survival may be of value to improve our understanding of pathogen transmission.

## Hosts supporting sustained direct transmission of *S. scabiei*

Direct contact among individuals is generally considered the primary mechanism of *S. scabiei* transmission for many
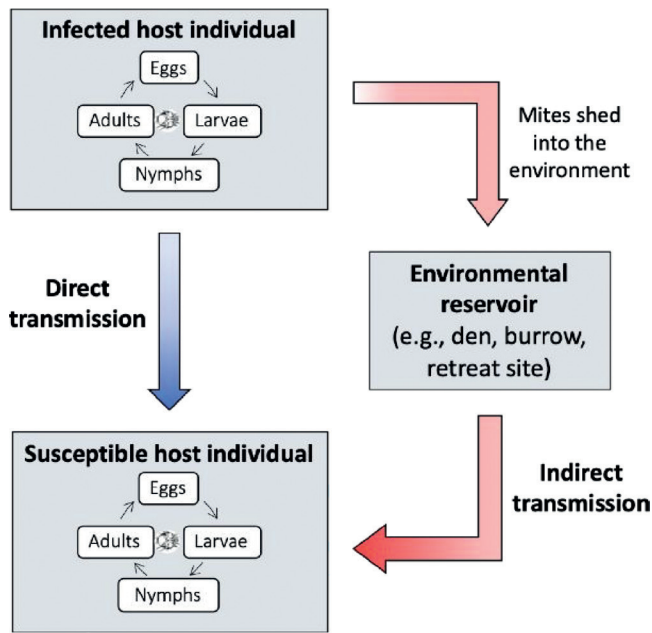
**Figure 2.** *Conceptual diagram of* S. scabiei *transmission. Transmission can occur directly (blue arrow) when an infectious host comes into close contact with a susceptible host. Indirect transmission (red arrows) can also occur when mites are shed from an infectious host into the environment where a susceptible host may encounter them. All life stages of* S. scabiei *(excluding eggs) can survive in the environment for varying amounts of time, depending on the relative humidity and temperature conditions (Arlian et al. 1989). Environments such as dens, burrows, and other retreat sites may be suitable reservoirs for off-host mite survival and subsequent transmission events.*

host species (Walton et al. 2004, Arlian and Morgan 2017), particularly those that are social (living in herds, packs, and family groups) and have frequent interindividual contact (Lunelli 2010, Kołodziej-Sobocińska et al. 2014, Danieli and Sarasa 2015). Whether *S. scabiei* persists endemically, becomes epidemic, or goes locally extinct is likely determined by the rate and nature of contacts among individuals (which can be a function of density) and their susceptibility to clinical disease (Sugiura et al. 2018, Niedringhaus et al. 2019a, Rossi et al. 2019). Both intragroup and intergroup transmission play a role in sustaining the pathogen within a host species. Iberian ibex (*Capra pyrenaica*), Alpine ibex (*Capra ibex*), and both chamois species (*Rupicapra rupicapra* and *Rupicapra pyrenaica*) provide well-known examples in which direct transmission is likely the dominant mechanism of pathogen spread (figure 1; Fernández-Morán et al. 1997, León-Vizcaíno et al. 1999, Lunelli 2010, Rossi et al. 2019). In the present article, we focus on sociality, population density, and herd structure for ibex and chamois, which are widely documented traits of hosts in which direct transmission of *S. scabiei* dominates.

Sarcoptic mange is one of the most important parasitic diseases for ibex, and it can persist in ibex populations with ongoing low prevalence (Yeruham et al. 1996, Pérez et al. 2006, Acevedo and Cassinello 2009, Rossi et al. 2019). Ibex are social species that live in herds in which direct transmission is likely to occur. Sharing of caves and refuges by infected ibexes suggests that indirect transmission of *S. scabiei* through substrate could potentially be involved, but it is not considered the dominant mechanism of transmission (León-Vizcaíno et al. 1999, Castro et al. 2016). Sarcoptic mange typically spreads as a slow-moving front through herds of ibex, with occasional rapid jumps attributed to extensive interactions and physical contact among individuals and, consequently, increased transfer of mites (León-Vizcaíno et al. 1999, Rossi et al. 2019, Pérez et al. 2021). Other factors such as herd demographic structure and the ibex mating system may also affect the likelihood of ongoing transmission. For example, some ibex populations live in mixed groups year-round, whereas others maintain sexual segregation until the mating season (Alados 1985, León-Vizcaíno et al. 1999, Acevedo and Cassinello 2009). The occurrence and timing of the mating season can increase local population density and facilitate direct contact between typically separated individuals (León-Vizcaíno et al. 1999). Individual differences in ibex susceptibility and behavior are related among other factors to sex, and these can influence transmission dynamics and maintenance of *S. scabiei* (Sarasa et al. 2011, Lopez-Olvera et al. 2015). Sarcoptic mange severity is male biased in Iberian ibex. This has been attributed to males living in larger groups, higher rates of contact with other individuals, and a decreased immune response compared with females, which collectively promote further transmission (Lopez-Olvera et al. 2015). Nevertheless, the specific role of ibex population structure in enhancing pathogen transmission, establishment, and persistence has so far been poorly documented (Danieli and Sarasa 2015).

Chamois also typically live in social groups. Sarcoptic mange is one of their most severe diseases and has been persistent in some chamois populations for centuries (e.g., in the Austrian Alps; Salvadori et al. 2016, Rossi et al. 2019). Chamois populations do not show complex group structuring, as ibex do, and transmission appears to follow a density-dependent relationship with direct transfer of mites and no evidence of indirect transmission (Rossi et al. 2007, Lunelli 2010). Therefore, high population density and local population size appear to be key factors for transmission in this system (Rossi et al. 1995). In comparison with ibex, the spread of infection in chamois populations occurs at a relatively low rate (Rossi et al. 2019). Chamois are described as more distant animals (i.e., they often occur together but contact each other infrequently), which likely results in fewer chances for direct transmission of mites (Rossi et al. 1995). Because of the difficulty of observing interactions between infectious and susceptible chamois, the contact rate between individuals is typically described or estimated rather than quantified in the literature (Lunelli 2010).

Collectively, studies on ibex and chamois suggest that host density and intraspecific contact are important traits driving the sustained and dominant direct intraspecific transmission of *S. scabiei*. Although the rates of contact within each species are poorly understood, their differing ecology suggests that *S. scabiei* can persist across a range of host contact frequencies.

## Hosts supporting sustained indirect transmission of *S. scabiei*

The ability of a pathogen to survive in the environment allows for the potential for indirect transmission between hosts. Indirect transmission could reduce the chance of pathogen fadeout and could, consequently, promote persistence, particularly when hosts are solitary or at a low density (i.e., where there are few opportunities for direct contact; Hoyt et al. 2015, 2020). The ability of *S. scabiei* mites to survive when dislodged from the host is a key factor for pathogen establishment and sustained transmission in some species (Beeton et al. 2019, Montecino-Latorre et al. 2019). However, there has been little quantification of the environmental component of *S. scabiei* transmission and how this affects pathogen persistence in affected host species (Arlian and Morgan 2017, Beeton et al. 2019). In the present article, we focus on two host species, American black bears (*Ursus americanus*) and bare-nosed wombats (*Vombatus ursinus*), for which indirect transmission is considered the dominant transmission mode (figure 1).

The American black bear is emblematic of the expanding host range of *S. scabiei*, with the pathogen emerging and establishing endemically in this species since the 1980s (Bornstein et al. 2001, Niedringhaus et al. 2019b). Because of the solitary behavior of bears, contact between individuals is rare, suggesting the importance of indirect transmission of mites (Niedringhaus et al. 2019b, 2019c). The few exceptions include cases of transmission during cub rearing and during contexts that bring the animals into closer proximity, such as the breeding season (Schmitt et al. 1987). Bears exhibit denning behavior, with repeated use of den locations by the same and different individuals (Alt and Gruttadauria 1984, Waller et al. 2012, Sommerer 2014). Bears with lesions consistent with sarcoptic mange have been observed within dens (Costello et al. 2006). Leaf litter, straw in bear traps, and other denning material are thought to contain mites shed from infected individuals. In addition, trees used by infected bears as territorial markers, artificial feeding sites, culvert traps used to catch individuals, or scratching posts could be a source of mites to uninfected individuals (Sommerer 2014). Although dens have the potential to facilitate indirect transmission, the colder climates that bears inhabit likely limits their suitability as a prolonged reservoir, and some mites may need to overwinter on infected bears to sustain transmission across years (Niedringhaus et al. 2019c). In addition, bears often visit dens during the colder months and less frequently visit them during warmer seasons (Garshelis and Pelton 1980). Consequently, the role that dens play in the sustained transmission of mites between individual bears is likely to be different from mammals that use their dens regularly throughout the year, and there is still much to be learned (Sommerer 2014, Astorga et al. 2018, Niedringhaus et al. 2019b).

The bare-nosed wombat is particularly affected by sarcoptic mange, which is widespread across their geographic range (Martin et al. 1998, Skerratt 2005), persisting endemically with periodic epizootics causing localized population decline and extirpation events (Gray 1937, Martin et al. 1998, Skerratt 2005, Martin et al. 2018a). Owing to their solitary behavior, indirect transmission through environmental exposure appears to be the dominant transmission mode (Martin et al. 2018a). Wombats rarely come into direct contact in the field except for mating (Triggs 2009). They are nonterritorial and use a small number of core burrows (for rest, thermoregulation, and avoidance of predators), which they switch every 4–10 days (Evans 2008, Martin et al. 2019b). Individual wombats often overlap in their use of core burrows, so when one wombat departs a core burrow another may begin using it; this is called *asynchronous burrow sharing* (Skerratt et al. 2004, Martin et al. 2019a). Bedding chambers in burrows are widely considered to be the site responsible for most *S. scabiei* transmission events (Old et al. 2017, Martin et al. 2018a). This is supported by evidence suggesting that the microclimate within burrows may approximate those needed to maximize mite survival off host (high humidity and cool temperatures; Brown 1984, Shimmin et al. 2002, Arlian and Morgan 2017, Browne et al. 2021). Furthermore, mathematical modeling and observations of disease spread in nature support transmission in burrows as the mechanism of *S. scabiei* transmission and persistence in wombats (Beeton et al. 2019, Martin et al. 2019b). Owing to the challenge of accessing and sampling within wombat burrows, research within these environments has been limited and is an area for further study (Browne et al. 2021, Ross et al. 2021).

Research on wombats and black bears suggests that *S. scabiei* can sustain transmission predominantly through indirect mechanisms for solitary host species. The key traits that appear to facilitate the indirect transmission of mites between host individuals are sharing of potentially infected areas by different individuals, the use of retreat sites (wombats more so than bears), and the suitability of environmental conditions for off-host mite survival. An improved understanding of these traits could have management implications, such as potential treatment of dens to prevent pathogen transmission. However, these traits and their influence on *S. scabiei* transmission remain understudied.

## Hosts supporting sustained direct and indirect transmission of *S. scabiei*

Evidence suggests that direct and indirect transmission are not mutually exclusive mechanisms associated with the persistence of *S. scabiei* in some host species, and the relative

dominance of one mode of transmission over the other can be difficult to distinguish (Montecino-Latorre et al. 2019). For example, in populations of some carnivore species, both direct and indirect transmission can occur, because individuals live in groups with high levels of sociality and use dens (Kołodziej-Sobocińska et al. 2014, Herrera and Nunn 2019). Group living and the use of dens potentially increase the transmission and prevalence of sarcoptic mange in some carnivore populations (Kołodziej-Sobocińska et al. 2014, Montecino-Latorre et al. 2019). When multiple individuals come into close contact within a contaminated space, both modes of transmission may occur simultaneously. Two species of fox (*V. vulpes* and *V. macrotis mutica*) and the coyote (*Canis latrans*) appear to experience both direct and indirect transmission of *S. scabiei* (figure 1). Previous studies have rarely been able to quantify the relative importance of direct and indirect transmission for pathogen persistence in these systems, and this can limit the development of targeted management strategies.

The geographic range of red foxes (*V. vulpes*) is among the widest of any living carnivore, and endemic sarcoptic mange occurs widely across this range, often where foxes live in high densities (Soulsbury et al. 2007, Saunders et al. 2010, Kołodziej-Sobocińska et al. 2014, Uraguchi et al. 2014). Population dynamics, social behavior, and other aspects of red fox spatial ecology (e.g., dispersal, migration, and changes in home ranges) contribute to the close contact between individuals and influence ongoing direct transmission (Pisano et al. 2019). Mange is also able to persist at low fox densities when reduced inter- and intragroup encounters may limit opportunities for infectious contact (Gortázar et al. 1998, Devenish-Nelson et al. 2014). Pathogen persistence when direct contact may be reduced suggests the potential importance of indirect transmission. Because foxes are a den-dwelling species, mite survival within den substrates and the sharing of these potentially infested areas are likely to be important for influencing pathogen persistence (Montecino-Latorre et al. 2019). Although indirect transmission is generally accepted, the understanding of the role of this mechanism in red fox populations is limited (Soulsbury et al. 2007, Kołodziej-Sobocińska et al. 2014).

The San Joaquin kit fox (*V. macrotis mutica*) is an endangered subspecies of kit fox, and sarcoptic mange persists in their populations (Cypher et al. 2017). Like with red foxes, high-density populations, family group contact, mating interactions, and shared use of dens are all traits that appear to have allowed the pathogen to invade kit fox populations and may facilitate the observed ongoing transmission of mites among individuals (Cypher et al. 2017, Montecino-Latorre et al. 2019). San Joaquin kit foxes are a den-obligate species that uses the underground retreat sites for raising pups, avoiding predators, and sheltering from extreme temperatures (Cypher 2010, Montecino-Latorre et al. 2019, Loredo et al. 2020). Family groups often switch dens, with individuals using an average of eleven different dens per year (Koopman et al. 1998). Monitoring of environmental conditions within these dens revealed that they can support off-host survival of mites for approximately 5 days, sufficient time for serial switching to occur (Loredo et al. 2020). Therefore, although the primary transmission mode is still unknown, environmental transmission is plausible and may contribute to sarcoptic mange persistence in this system (Loredo et al. 2020). Mathematical modeling also supports both den-associated transmission and out-of-den transmission through social contact as key parameters for pathogen persistence in kit foxes (Montecino-Latorre et al. 2019). Because the microclimates of the dens of other wild canine species are likely comparable with San Joaquin kit fox dens, the importance of indirect transmission in other host species may therefore be underrepresented in the literature.

Coyotes provide a further example of a canid species in which both indirect and direct transmission appear to play a role in the persistence of the disease (Pence et al. 1983). The species often lives in pairs or small packs in which high densities and social behavior can enhance direct transmission of *S. scabiei* (Pence et al. 1983, Pence and Windberg 1994). However, the social organization of packs, such as the spacing between groups and the degree of territoriality coyote packs exhibit can moderate the likelihood of direct transmission (Pence and Windberg 1994, Leung and Grenfell 2003). The proportion of transient coyotes also influences ongoing transmission of *S. scabiei*. Roaming coyotes provide an opportunity for contact with other packs and subpopulations that may be susceptible (Leung and Grenfell 2003). The scavenging behavior of coyotes can also lead to aggregations of individuals around a kill, enabling further opportunity for direct transfer of mites (Murray and St. Clair 2017). Infected coyotes suffering from sarcoptic mange appear to be more reliant on anthropogenic sources of food and shelter. This increases the risk of both susceptible and infected foragers coming into close proximity around these anthropogenic resources (Murray and St. Clair 2017). As a result of these host traits and behaviors, direct transmission is attributed as the primary mode of mite transfer. However, their denning behavior and den sharing by multiple individuals also suggests that indirect transmission may contribute to sustaining transmission of *S. scabiei*, but the literature is limited (Murray and St. Clair 2017).

The above case studies suggest that host sociality and den use (retreat sites) may be key factors facilitating *S. scabiei* transmission in canids. The relative contribution of direct and indirect mechanisms affecting the transmission of *S. scabiei* have been rarely investigated and warrant further research. Furthermore, direct and indirect transmission may vary in dominance for intragroup versus intergroup transmission and this relation is seldom acknowledged or explored.

## Synthesis, future research, and conclusions

In the present article, we highlighted a knowledge gap by focusing on sarcoptic mange—a system emblematic of

**Table 1. Summary of studies investigating transmission of sarcoptic mange in wildlife.**

| Dominant transmission mechanism | Study species | Study type | Identified factors affecting transmission | Source |
|---|---|---|---|---|
| Direct | Grey wolves | Observational | Sociality | Almberg et al. (2015) |
| | Pigs | Experimental | Rate of contact between hosts | Elbers et al. (2000) |
| | Rabbits | Experimental | Host flexibility | Fazal et al. (2016) |
| | Grey wolves | Observational | Sociality | Fuchs et al. (2016) |
| | Red deer, Iberian ibex | Observational | High host density | Iacopelli et al. (2020) |
| | Desert sheep | Experimental | Host flexibility | Ibrahim and Abusamra (1987) |
| | Pigs | Experimental, modelling | Rate of contact between hosts | Stegeman et al. (2000) |
| | Chamois, ibex[a] | Observational | Sociality, intra/interspecies contact | Rossi et al. (2019) |
| | Red foxes[a] | Observational | High host density | Scott et al. (2020) |
| Indirect | San Joaquin kit foxes[a] | Observational, modelling | Shared use of dens, off-host mite survival | Loredo et al. (2020) |
| | Bare-nosed wombats[a] | Observational | Shared use of core burrows | Martin et al. (2019a) |
| | Bare-nosed wombats[a] | Modelling | Frequency of burrow switching | Martin et al. (2019b) |
| | Black bears[a] | Experimental | Off-host mite survival | Niedringhaus et al. (2019c) |
| | Pigs | Experimental | Exposure time in infected environment | Smith (1986) |
| Direct and indirect | N/A | Review | Off-host mite survival, infectivity | Arlian and Morgan (2017) |
| | Iberian ibex[a] | Observational | Exposure to infected environment | Castro et al. (2016) |
| | Red foxes,[a] badgers, wolves, racoon dogs, stone martens, lynx | Observational | Sociality, high density, and den use | Kołodziej-Sobocińska et al. (2014) |
| | Dogs, racoon dogs, racoons, Japanese martens, wild boar, Japanese serows | Observational | Sociality, shared habitat use, predator–prey dynamics | Matsuyama et al. (2019) |
| | San Joaquin kit foxes[a] | Modelling | Sociality, shared use of dens | Montecino-Latorre et al. (2019) |

*Note:* A Web of Science literature (May 2020) search using the terms *"Sarcoptes scabiei"* and "transmission" produced 89 results. 46 of these were excluded as they were not relevant to transmission or were specific to human public health. A further 24 referred to transmission but did not investigate or describe transmission dynamics, mechanisms or other related host or pathogen factors influencing transmission. This resulted in 19 studies (summarized in the table) that were characterized as "transmission studies." [a]Case study species used in this review.

repeated pathogen persistence in host species with differing ecologies. The ability of *S. scabiei* to be transmitted directly, indirectly, and by both mechanisms appears a key factor to sustaining pathogen transmission. Collectively, research suggests that direct and indirect transmission have varying importance in different mange affected host species, reflecting the adaptability of the pathogen to accommodate variable host physiological and behavioral traits. In social species (e.g., chamois and ibex), the dominant mechanism of transmission is direct contact, whereas solitary species (e.g., bears and wombats) primarily transfer mites indirectly, and in social, den-using species (i.e., foxes and coyotes), a combination of both direct and indirect transmission can occur (Kołodziej-Sobocińska et al. 2014, Martin et al. 2019a). Multiple host traits drive these patterns in the different host species; however, it is broadly clear that the level of sociality and the use of shared environments (e.g., burrows or dens) suitable for pathogen survival are

key (Kołodziej-Sobocińska et al. 2014, Montecino-Latorre et al. 2019).

Research on the occurrence and impact of sarcoptic mange has largely been focused on epidemic outbreaks, with less focus on the epidemiological dynamics that support sustained transmission (e.g., Pence and Windberg 1994, Cypher et al. 2017, Martin et al. 2018a). Therefore, the underlying factors that influence how *S. scabiei* independently sustains transmission in multiple host species is an area for future scientific investigation. In this article, we found a range of research on the mode of *S. scabiei* transmission (table 1), but relative to the scale and global impact of sarcoptic mange, the extent of this literature is limited. Indeed, the mode of transmission is typically assumed but rarely investigated. The limited studies concentrated on *S. scabiei* transmission (table 1) have identified traits that can facilitate direct transfer of *S. scabiei* mites—for example, density and sociality, which promote close contact between susceptible

and infected individuals (Kołodziej-Sobocińska et al. 2014, Danieli and Sarasa 2015). Nevertheless, there is a lack of understanding of how specific traits, such as the structure of populations or groups, may enhance host compatibility for sustained transmission of *S. scabiei*.

There has been increasing recognition of the role of indirect transmission for mange-affected species. However, there is considerably less empirical research relative to direct transmission of *S. scabiei* (Beeton et al. 2019). Similar to other priority diseases of wildlife (e.g., chytridiomycosis, bat white-nose syndrome and chronic wasting disease), the environmental component of transmission is likely key for ongoing transmission and persistence of disease (Kolby et al. 2015, Escobar et al. 2020, Hoyt et al. 2020). Reviewed studies of mange-affected species show that for *S. scabiei* to persist predominately by indirect transmission, a refuge with appropriate environmental conditions that is shared by conspecifics may be crucial (Arlian et al. 1984a, Montecino-Latorre et al. 2019, Loredo et al. 2020). However, when there is a combination of different modes of transmission (i.e., direct and indirect), we expect that the pathogen may be less reliant on suitable conditions for off-host survival. Therefore, although sharing of infected areas is important for transmission within canid species (e.g., the endangered San Joaquin kit fox), they may be particularly crucial for disease management and control of mange in solitary species such as bears and wombats (Martin et al. 2019b, Montecino-Latorre et al. 2019). Furthermore, investigation into the potential for off-host mite survival in the environment would be valuable to support the existing modeling and laboratory data (Browne et al. 2021).

Other factors, such as host resistance, pathogen virulence, and environmental variability, that were outside of the scope of this review, may also play a role in sustaining endemic transmission of *S. scabiei* and other similar pathogens (Liu et al. 2016, Swinton et al. 2002, Kilpatrick and Altizer 2010). The importance of understanding empirical mechanisms shaping sustained transmission is not limited to *S. scabiei* and extends more broadly to other pathogens of wildlife that can also independently sustain transmission between host individuals—for example, the feline foamy virus (endemic in wild and domestic felids), chytrid fungus, the psittacine beak and feather disease virus, and the canine distemper virus (Winkler et al. 1999, Briggs et al. 2010, Martinez-Gutierrez and Ruiz-Saenz 2016, Raidal and Peters 2018). Although different pathogens may be reliant on other mechanisms of transmission, the examination of host and pathogen traits represents a unifying framework to examine and compare differing disease systems.

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