



## Assessing the role of dens in the spread, establishment and persistence of sarcoptic mange in an endangered canid

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### ABSTRACT

Sarcoptic mange is a skin disease caused by the mite *Sarcoptes scabiei* that can devastate populations of wild species. *S. scabiei* can survive off-host and remain infective for specific periods. In den-dwelling species, dislodged mites could be protected from the environmental conditions that impair their survival thus supporting pathogen transmission. To assess the potential role of dens in the spread, establishment, and persistence of sarcoptic mange in a population of hosts, we constructed an agent-based model of the endangered San Joaquin kit fox (SJKF; *Vulpes macrotis mutica*) population in Bakersfield, California, that explicitly considered the denning ecology and behavior of this species. We focused on this SJKF urban population because of their vulnerability and because a sarcoptic mange epizootic is currently ongoing. Further, SJKF is a social species that lives in family groups year-round and contact between individuals from different family groups is rare, but they will occupy the same dens intermittently. If mites remain infective in dens, they could support intra-family disease transmission via direct (den sharing) and indirect (contaminated den) contact, but also inter-family transmission if susceptible individuals from different families occupy contaminated dens. Simulations showed that den-associated transmission significantly increases the chances for the mite to spread, to establish and to persist. These findings hold for different within-den *S. scabiei* off-host survival periods assessed. Managers dealing with *S. scabiei* in this species as well as in other den-dwelling species should consider den-associated transmission as they could be targeted as part of the control strategies against this mite.

### 1. Introduction

Sarcoptic mange is a skin disease caused by the mite *Sarcoptes scabiei* that has provoked remarkable population declines in wild canids (e.g., Lindström, 1991; Mörner, 1992; Soulsbury et al., 2007; Uruguchi et al., 2014), including extirpations (e.g., Henriksen et al., 1993; León-Vizcaíno et al., 1999). This disease has caused the collapse of populations of species belonging to other taxa as well (Martin et al., 2017) and could devastate small remnant populations of threatened or endangered species (Pence and Ueckermann, 2002). Dens may be a determinant environmental feature for the dynamics of *S. scabiei* in den-dwelling species such as foxes and wombats (Gerasimov, 1958; Martin et al., 2017; Skerratt et al., 1998). First, dens are regularly used by wild hosts for extended periods; second, they can be shared or used intermittently

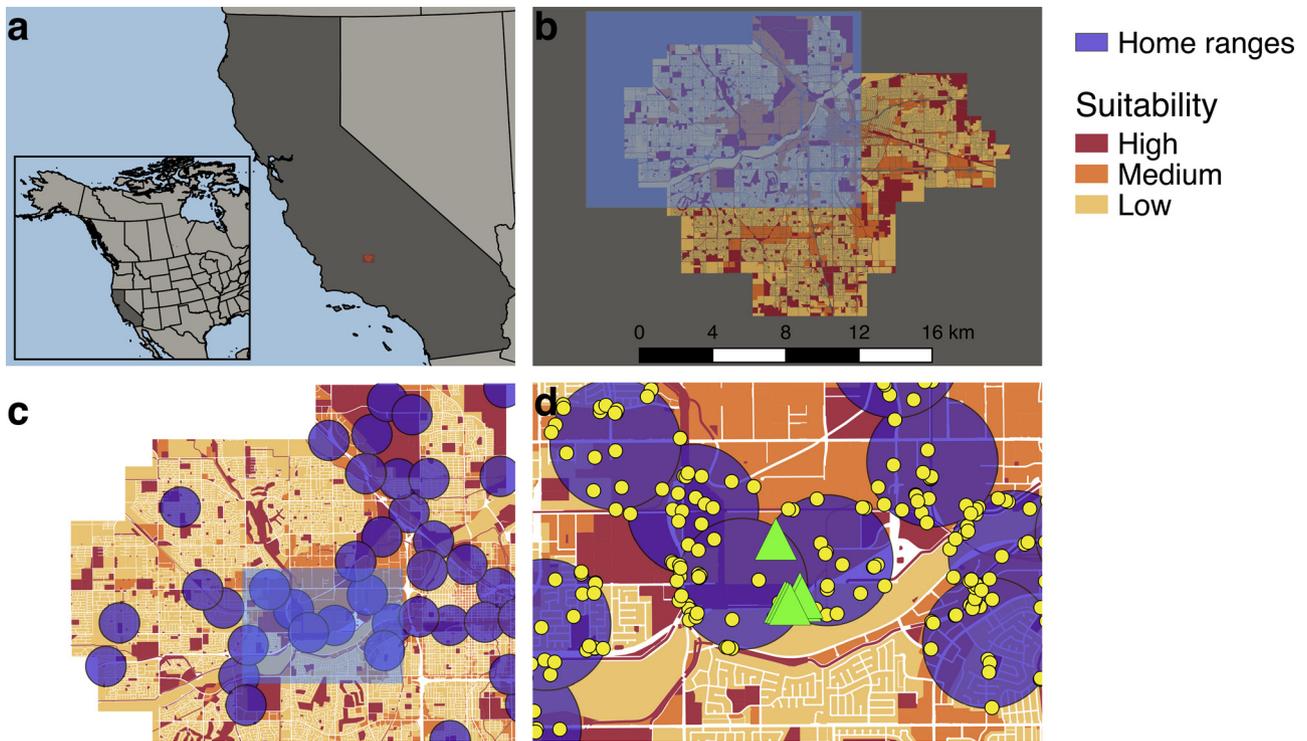
by hosts of a single or several species (e.g., Old et al., 2018); and third, den substrate could become contaminated with mites that dislodge from infested hosts prior to or whilst susceptible hosts occupy these dens. Mites in den substrate would remain protected from environmental conditions that could impair their survival, resulting in extended opportunities for infestation. Although indirect transmission of *S. scabiei* via dens is a supported hypothesis (Gerasimov, 1958; Martin et al., 2017; Skerratt et al., 1998; Soulsbury et al., 2007), this pathway still needs more formal investigation and it is considered a current “critical knowledge gap” (Martin et al., 2017).

In this article, we aimed to improve our understanding of the role of den-associated transmission in *S. scabiei* dynamics by studying this disease in the San Joaquin kit fox (SJKF; *Vulpes macrotis mutica*). The SJKF is an endangered subspecies (Cypher and Cypher, 2010; Knapp,

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**Fig. 1.** Visual representation of the spatial components of the model: a) The location of the study area in California (red square), b) The habitat suitability for the San Joaquin kit fox in Bakersfield, c) home ranges (purple circles), d) the corresponding dens (yellow points), and dens present in areas of home range overlap (green triangles). The squares on top of b and c represent the area zoomed in c and d, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

1978; U.S. Fish and Wildlife Service, 1998) endemic to the San Joaquin Valley and adjacent valleys in central California, presently distributed into 3 main and about a dozen satellite populations (Cypher and Cypher, 2010; Cypher et al., 2013; U.S. Fish and Wildlife Service, 2010). Currently, an epizootic of sarcoptic mange is ongoing in the urban satellite population in the city of Bakersfield (Kern County, California, USA; Cypher et al., 2017), which contained 200–400 individuals before the outbreak (Cypher and Cypher, 2010; Cypher and Frost, 1999). Since March 2013, over 330 cases have been documented. Of these, 58 are known fatalities. Several were captured, treated, and recovered; and the fate of others is unknown (Cypher et al., 2017). All cases whose outcome is known and did not receive medical intervention died and as of 2017, the size of the epizootic continued to increase, threatening the preservation of Bakersfield’s SJKF satellite population (Cypher et al., 2017). There is also a risk to exurban populations if the mite were to spread outside of the city (Cypher et al., 2017). Therefore, it is urgent to understand the processes determining *S. scabiei* dynamics in this population in order to propose and apply efficient management.

This subspecies presents 3 advantages to assess den-associated transmission. First, the SJKF is a social species that lives in family groups (e.g., Frost, 2005; Morrell, 1971) but direct contacts between members of different families are rare (Morrell, 1971; Ralls et al., 2001; White et al., 2000), and therefore, other modes of infestation seem necessary for inter-family transmission of sarcoptic mange and the spread of the disease across the population. Secondly, this fox is a den-obligated species and members of family groups share dens with variable frequency throughout the year (Koopman et al., 1998; Ralls et al., 2001), but dens can also be sequentially used by members of different family groups with overlapping home ranges (Koopman et al., 1998; Ralls et al., 2001). Consequently, dens could support intra-family *S. scabiei* transmission via direct and indirect transmission, but they could also be a key pathway for inter-family infestation via indirect transmission. Finally, the SJKF is a well-studied species for which data on denning behavior is available.

Quantifying den-associated transmission in order to assess its role in sarcoptic mange dynamics is likely unfeasible in natural systems and modeling approaches appear as a useful alternative. Here, we took advantage of the well-known biology of this species to construct an agent-based model of the satellite population of Bakersfield that explicitly considered the spatial distribution of the foxes, the annual life cycle of these animals, their denning behavior (den sharing among relatives and the movement from one den to another with different frequency across the year), the dens, and the den environment. With this model we simulated the dynamics of the SJKF population during scenarios of epizootic and enzootic *S. scabiei* infestation, considering variable within-den off-host survival of this mite. Specifically, we evaluated whether den-associated transmission, both direct and indirect, is necessary for the spread, establishment, and persistence of sarcoptic mange, or if restricted inter-family direct transmission events, through extra-pair copulations and dominance changes, could drive disease spread, establishment, and persistence alone. Our objective was to support evidence for managers about whether or not targeting dens should be considered as part of the strategies to control sarcoptic mange in den-dwelling species, including the SJKF.

## 2. Methods

The model description follows Grimm et al. (2006, 2010) but was modified when appropriate. The model was constructed in R (R Core Team, 2018) using the packages referenced in Supplementary Material 1 and it is available at [https://github.com/dmontecino/SJKF\\_Model](https://github.com/dmontecino/SJKF_Model).

### 2.1. Entities, state variables, and scales

SJKFs occur in family groups that use dens year round, and within the city of Bakersfield they prefer certain land types (Spiegel and Bradbury, 1992; Frost, 2005; Koopman, 1995; Koopman et al., 1998; Ralls et al., 2001; Spiegel et al., 1996; White and Ralls, 1993; Zoellick

**Table 1**  
 Summary of the entities present in the model, their state variables, and corresponding values. The state variables are the features that characterized the entities, while the state value corresponds to the categories that the state variables could take. The definition explains each possible state value, and the reference column provides the source supporting the inclusion of the state variables and their values.

Entities	State variable	State value	Definition of the state values	Reference
Habitat surface	Suitability	High	Linear, Manicured, Open, and Water catchment basins land types	Frost, 2005, and this study
		Medium	Commercial, Industrial land types	
Home ranges	Land type	Low	Agriculture, Transition, Residential land types	Frost, 2005
		Agriculture	Lands currently used for crop agriculture	
		Commercial	Office buildings, hotels, medical facilities, and their associated parking areas	
		Industrial	Areas of industrial use not generally open to the public, such as manufacturing plants, and shipping yards	
		Linear	Kern River Parkway, canals, roads, railroads, and power line right-of-ways	
		Manicured	Parks, schools, and golf courses	
Dens	Water catchment basins	Open	Vacant lots and fallow agricultural fields	Arljan et al., 1989, 1988, 1984a; Gerasimov, 1958; Kobodziej-Sobocińska et al., 2014; Martin et al., 1998; Skerratt et al., 1998 Spiegel and Bradbury, 1992; Ralls et al., 2001; Reese et al., 1992
		Residential	Apartments and single-family housing developments	
		Transition	Construction is in progress or has recently been completed	
		Water catchment basins	Dug land used to contain urban run-off and rainwater	
		Non-infested	Dens that do not contain alive and infective <i>S. scabiei</i>	
		Dominant	The male and female adults that mate in the corresponding season and can have offspring	
Foxes	Type of fox	Subdominants	Offspring of at least one of the dominants that occupies the home range of its parents	Arljan, 1989; Arlian et al., 1984a; Bornstein et al., 1995; Cypher et al., 2017; Möbner and Christensson, 1984; Newman et al., 2002 and field experience of the authors.
		Dispersers	Subdominants born in the current year that disperse from the parents home range.	
		Pups	The current year offspring of the dominant pair before weaning	
		Susceptible (S)	Not infested foxes that can be infested with <i>S. scabiei</i>	
		Exposed (E)	Newly infested foxes that cannot transmit the mite or contaminate dens. From infestation until 2 weeks later	
		Infectious type I (type I)	Infested foxes that can transmit the mite and contaminate dens but that are in initial steps of the disease and their behavior is not changed. From 2 weeks after initial infestation until 10 weeks after infestation	
Infectious type II (type II)	Infectious type II (type II)	Infested foxes that can transmit the mite and contaminate dens, but the disease is in advanced state (general alopecia, emaciation, hyperkeratosis, etc.). The behavior of these foxes is modified due to disease and the expected outcome is death due to sarcoptic mange. From 10 weeks after infestation until 14 weeks after infestation		

et al., 1987a). Thus, the model considered 3 spatially distributed components: the habitat suitability, family home ranges, and dens (Fig. 1). For a detailed description of the construction of these components see Supplementary Material 2.

### 2.1.1. Habitat suitability in Bakersfield

The city of Bakersfield is located in Kern County, California, USA (35.3733°N, 119.0187°W). We focused on the urban zone of this city, an area of ~294 km<sup>2</sup>, and following (Frost, 2005), we re-classified its land types as ‘High’, ‘Medium’, and ‘Low’ suitability for SJKFs (Table 1). The area covered by each suitability type was ~68, ~55 and ~171 km<sup>2</sup>, respectively, and based on the authors’ experience, the suitability was ground-truthed (Fig. 1a–b).

### 2.1.2. Family home ranges

Each home range is circular (Spiegel and Bradbury, 1992; Koopman, 1995; Koopman et al., 2000; Zoellick et al., 1987b), with an area of 1.72 km<sup>2</sup>, and used by an entire family because home ranges of relatives overlap by 80% (Frost, 2005). There were 59 home ranges: 34, 19, and 6 in ‘High’, ‘Medium’, and ‘Low’ suitability areas, respectively (Table 1; Supplementary Material 2). Their location was informed by the habitat suitability and by other home ranges, such that there is a 1 km minimum distance between their centroids (Fig. 1c). This distance caused an expected home range-overlap of 18% (Frost, 2005). Family home ranges contained a dominant pair, and usually between 3–4 subdominants (Supplementary Material 5 and 7). These families had a higher number of total adult individuals compared to non-urban SJKF populations, and more females as expected in Bakersfield (Cypher and Cypher, 2010).

### 2.1.3. Dens

Dens were located in the home ranges based on SJKF land type preference (Frost, 2005). The number of dens per family was randomly chosen between 15–20. Due to overlap among home ranges, this range of dens yielded a total number of 18–25 dens within a family home range, matching previous reports (Koopman et al., 1998; Reese et al., 1992). Dens were characterized by the land type upon which they were built and *S. scabiei* status (Table 1).

### 2.1.4. Foxes

SJKFs were classified by: i) sex; ii) type of fox; iii) parents; iv) family; v) den currently occupied; and vi) sarcoptic mange status: susceptible (S), exposed (E), infectious type I (type I) and infectious type II (type II) following previous research on sarcoptic mange in foxes (Table 1).

In the absence of disease, the simulated population ranged between ~250 and ~370 individuals matching previous reports (Cypher and Cypher, 2010; Cypher and Frost, 1999; Supplementary Material 7).

## 2.2. Process overview and scheduling

Time was discrete with steps representing 1 week. During the simulations, seasonal events corresponded with the timing for this species based on the literature. Fox events included reproduction (mating, birthing, and nursing), mortality due to sarcoptic mange and other causes, denning behavior (sharing and changing dens), dispersal, *S. scabiei* transmission among foxes, disease progression, den infestation with *S. scabiei*, *S. scabiei* transmission from infested dens to susceptible individuals, and clearance of *S. scabiei* from infested dens (Fig. 2).

## 2.3. Sub models of weekly and seasonal events

All events were randomly defined by suitable probability distributions parameterized using previous literature and/or field experience. The summary of model parameterization is provided in Table 2.

Below we describe *S. scabiei* transmission-associated events. For a

detailed description of SJKF reproduction, dispersal, survival without disease, and competition for dominance, refer to Supplementary Material 3.

### 2.3.1. Out-of-den sarcoptic mange transmission

Sarcoptic mange could be transmitted during social contact due to allogrooming and other social behaviors (Murdoch et al., 2008; Ralls et al., 2001), mating (*Mating*), and nursing (*Nurse*). These activities allowed out-of-den fox-to-fox transmission based on Bernoulli trials. We assumed that each trial added all the adequate contacts and corresponding transmission probabilities per fox per event per week. Therefore, each relative type I or type II fox present in a family resulted in one transmission trial for each S fox in that family.

For *Social*, foxes were assumed to have social contacts with each living family member weekly. For *Mating*, the dominant females were in estrus during a single randomly selected week of the period December and the half of January. We assumed that the dominant females also could mate with a maximum of 2 extra dominant males beyond their mate (Morrell, 1971; Murdoch et al., 2008; Ralls et al., 2001; White et al., 2000). These 2 extra males were randomly selected from the set of alive non-relative dominant males from neighbor family groups (those whose home ranges are 2960 m apart from the boundary of the dominant female’s home range), whose mating couple was not in estrus during week *w*, and that have not had more than 2 extra-pair copulations already in the current mating season (Morrell, 1971; Murdoch et al., 2008; Ralls et al., 2001; White et al., 2000). The set of females in estrus during week *w* determined the extra pair mating in random order. We assumed that dominant males mating with an extra-pair dominant female returned to their own home range and current den. For *Nurse*, dominant females nursed their pups up to 9 weeks after their birth, at which time the pups became subdominants in the model (Morrell, 1971; Murdoch et al., 2008).

Aggressive interactions between individuals from different families that might result in inter-family transmission are rare (see Supplementary Material 3d). Therefore, there was no aggressive contact allowing inter-family sarcoptic mange transmission (Devenish-Nelson, 2012; Koopman et al., 2000; Morrell, 1971; Murdoch et al., 2008). On the other hand, based on our observations, infested foxes do contact relatives in and outside dens. Finally, disperser individuals did not contact other foxes as they moved across home ranges, and they had social contact only if they became a dominant individual (Devenish-Nelson, 2012; Koopman et al., 2000; Morrell, 1971; Murdoch et al., 2008; Supplementary Material 3b and 3d).

### 2.3.2. Den-associated sarcoptic mange transmission

Sarcoptic mange could also be transmitted when infested and S foxes shared a den (*Share*; within-den fox-to-fox transmission), or when an S fox used an unoccupied but infested den (*Denfox*; fox-den-fox transmission). Each potential transmission was determined by Bernoulli trials as previously explained.

For *Denfox* transmission, we assumed that the contamination of a den always occurred when any infested SJKF occupied it and remained as such after the infested individual(s) moved to another den based on the mite’s off-host within-den survival (see ‘*Scenarios of S. scabiei den-associated transmission*’ and Table 3). Mites remained infective while alive off-host (Arlian et al., 1984b). *Change* determined if a family changed dens in week *w* (Table 2). When the *j*<sup>th</sup> family changed dens, its members could occupy any den located within the surface of the corresponding home range, including those belonging to other families present in the area of overlap with neighbor home ranges (Frost, 2005; Koopman et al., 1998; Morrell, 1971; Ralls et al., 2001; Spiegel et al., 1996; White et al., 2000).

For *Share* transmission, relative foxes sharing a den were assumed to have within-den contact weekly. The relatives sharing a den in week *w* were determined when a family changed dens (*Change*). The dominant pair ‘decided’ to share a den; the dominants ‘chose’ to share a den with

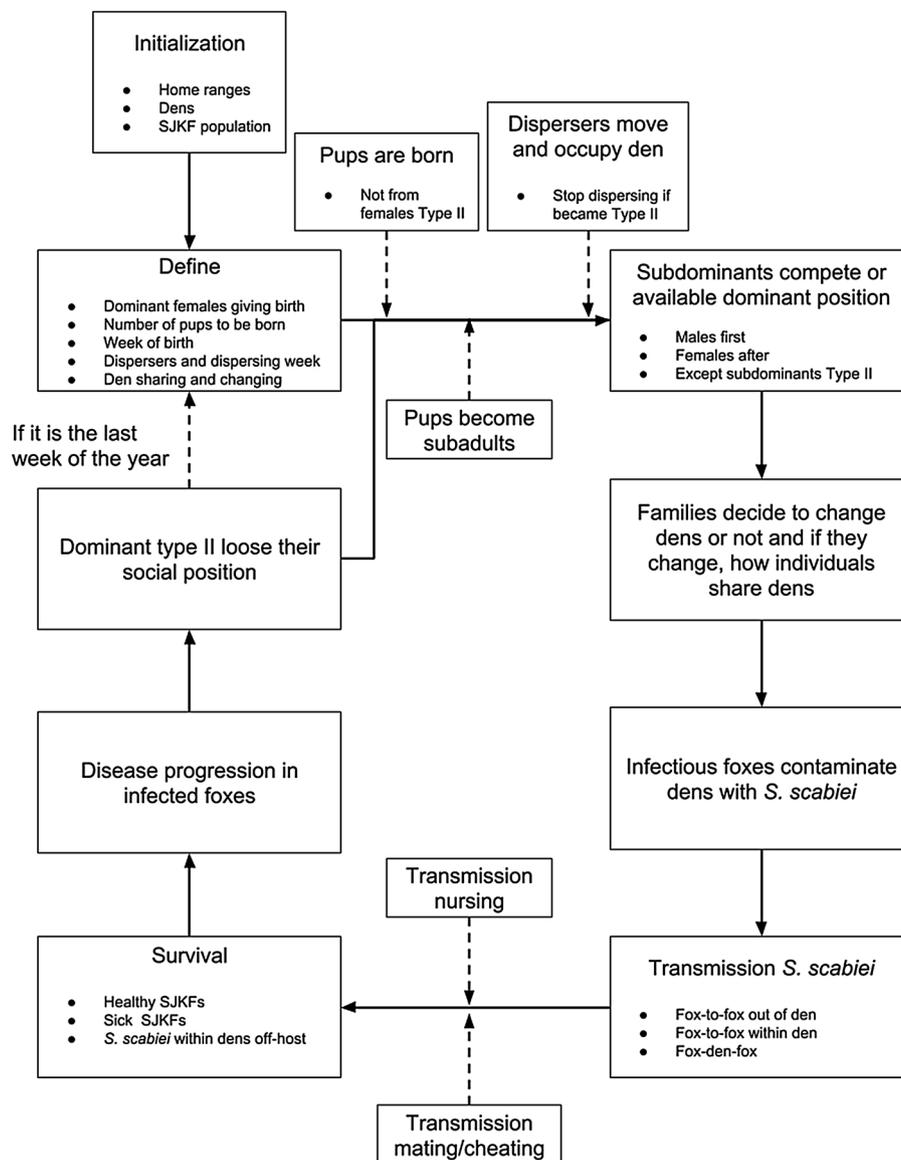


Fig. 2. Model events. Dashed arrows indicate seasonal events, while solid arrows indicate weekly events. Each simulation starts in the ‘Initialization box’ while each year simulated began in the ‘Define’ box.

subdominants; and finally, the subdominants ‘decided’ to share a den or not. These ‘decisions’ were random, based on *ShareD*, *ShareDS*, and *ShareSS*, respectively (Table 2).

Den changing and den sharing were assigned at the family level. The probabilities of den sharing and changing differed across the year and fox types following (Koopman et al., 1998). For a detailed description of *Change* and *Share* modeling, refer to Supplementary Material 4. Pups occupied the same den as the dominant female.

Given our uncertainty regarding sarcoptic mange transmission, we modeled the system considering a wide range of direct and indirect transmission probabilities parameterizing the Bernoulli distributions of *Social*, *Mating*, *Nurse*, *Share*, and *Denfox*. These probabilities were also random variables obtained from uniform distributions (Table 2). A random value defined the corresponding transmission probability for the  $s^{\text{th}}$  simulation. We assumed that infested carcasses did not remain within dens as our observations suggest that terminally ill animals isolate themselves. Further, we explored 4 possibilities for the weekly *S. scabiei* survival off-host within dens (see ‘Scenarios of *S. scabiei* den-associated transmission’ section).

### 2.3.3. Disease progression and survival of infested SJKFs

The E individuals progressed to type I foxes after 2 weeks and type I individuals became type II foxes after 8 weeks. Foxes with 4 weeks as type II died due to sarcoptic mange (Cypher et al., 2017; Mörner and Christensson, 1984; Newman et al., 2002; Stone et al., 1972).

Following findings in urban infested red foxes (*Vulpes vulpes*), we assumed that dominant type II foxes lost their dominance and did not mate as a result of their weakness, and therefore, behaved as subdominants (Soulsbury et al., 2007). The dominant position thus became available, triggering the competition described in Supplementary Material 3d. For similar reasons, female dominants type II did not give birth or nurse (Soulsbury et al., 2007). Subdominants type II could not compete for a dominant position nor disperse. However, our field experience indicates that infested SJKFs are not avoided or driven off from the family, and they continue to share dens with relatives.

Finally, dispersers becoming type I individuals were assumed to continue dispersing; however, dispersers becoming type II stopped dispersing, they remained in the last home range they reached, and they did not compete if a dominant position was available. In this home range they occupied dens by themselves until they died.

**Table 2**  
 Summary of sarcoptic mange-associated transmission processes included in the model and their potential outcomes, the probabilistic distribution determining the outcomes, the parameter values of the probability distributions, and the source(s) supporting the value(s) of the corresponding parameters.

Process	Random variable	Space of the random variable	Probability distribution and parameters	Parameter value	References
Reproduction	<i>Mate</i> : week of the mating period in which the dominant female of the $j^{\text{th}}$ family mates.	$Mate = \{1, 2, 48, \dots, 52\}$	$Mate \sim \text{Uniform}(a,b)$ $a$ is the first week of the mating period $b$ is the last week of the mating period	$a = 1$ $b = 7$	Murdoch et al., 2008; White and Ralls, 1993
Den changing and sharing	<i>Change</i> : the $j^{\text{th}}$ family changes the dens currently occupied during week $w$	$Change = \{\text{Yes}, \text{No}\}$	$Change \sim \text{Bern}(p_{\text{Change}})$ $p_{\text{Change}}$ is the weekly probability to change dens in week $w$	$p_{\text{Change}} = 0.272$ week 1-18 $= 0.137$ week 48-52 $= 0.371$ otherwise	Koopman et al., 1998
	<i>ShareD</i> : the dominants in the $j^{\text{th}}$ family move to a new den together when they change den in week $w$	$ShareD = \{\text{Yes}, \text{No}\}$	$ShareD \sim \text{Bern}(p_{\text{ShareD}})$ $p_{\text{ShareD}}$ is the probability the dominants move to a new den together when they change den in week $w$	$p_{\text{ShareD}} = 0.9$ week 1 - 18 $= 0.9$ week 48 - 52 $= 0.4$ otherwise	
	<i>ShareDS</i> : the dominants in the $j^{\text{th}}$ family move to a new den together with the subdominants when they change den in week $w$	$ShareDS = \{\text{Yes}, \text{No}\}$	$ShareDS \sim \text{Bern}(p_{\text{ShareDS}})$ $p_{\text{ShareDS}}$ is the probability the dominants move to a new den together with the subdominants when they change den in week $w$	$p_{\text{ShareDS}} = 0.45$ week 1 - 5 $= 0$ week 6 - 18 $= 0.4$ week 19 - 47 $= 0.45$ otherwise	
	<i>ShareSS</i> : the subdominants in the $j^{\text{th}}$ family move to a new den together when they change den in week $w$	$ShareSS = \{\text{Yes}, \text{No}\}$	$ShareSS \sim \text{Bern}(p_{\text{ShareSS}})$ $p_{\text{ShareSS}}$ is the probability the subdominants move to a new den together when they change den in week $w$	$p_{\text{ShareSS}} = 0$ week 1 - 5 $= 0.85$ week 6 - 18 $= 0.55$ week 19 - 47 $= 0$ otherwise	
Den-independent sarcoptic mange transmission	<i>Social</i> : the transmission of sarcoptic mange from I or II SJKF to S individuals through social interactions during week $w$	$Social = \{\text{Yes}, \text{No}\}$	$Social \sim \text{Bern}(p_{\text{Social}})$ $p_{\text{Social}}$ is the probability that a fox type I or type II infests S relatives as a result of their social interactions during week $w$	$p_{\text{Social}} \sim \text{Uniform}(0.15, 0.3)$	These values are unknown and, therefore, we used a range of values that are reasonable for the biology of the species, their contact rates, the average size of the family groups, and the infectiousness of the mite
Den-associated sarcoptic mange transmission	<i>Mating</i> : the transmission of sarcoptic mange from I or II SJKF to S individuals when they mate during week $w$	$Mating = \{\text{Yes}, \text{No}\}$	$Mating \sim \text{Bern}(p_{\text{Mating}})$ $p_{\text{Mating}}$ is the probability that a dominant fox type I infests S dominants of the opposite sex as a result of mating during week $w$	$p_{\text{Mating}} \sim \text{Uniform}(0.9, 1)$	
	<i>Nurse</i> : the transmission of sarcoptic mange from I or II female dominants to S pups nursing during week $w$	$Nurse = \{\text{Yes}, \text{No}\}$	$Nurse \sim \text{Bern}(p_{\text{Nurse}})$ $p_{\text{Nurse}}$ is the probability that a dominant female type I infest her S pups as a result of nursing during week $w$	$p_{\text{Nurse}} \sim \text{Uniform}(0.95, 1)$	
	<i>Share</i> : the transmission of sarcoptic mange from I or II SJKF to S individuals when using a common den during week $w$	$Share = \{\text{Yes}, \text{No}\}$	$Share \sim \text{Bern}(p_{\text{Share}})$ $p_{\text{Share}}$ is the probability that a fox type I or type II infests S individuals when they use a common den during week $w$	$p_{\text{Share}} \sim \text{Uniform}(0.4, 0.7)$	
	<i>Denfox</i> : the transmission of sarcoptic mange from a contaminated den to an S SJKFs occupying it during week $w$	$Denfox = \{\text{Yes}, \text{No}\}$	$Denfox \sim \text{Bern}(p_{\text{Denfox}})$ $p_{\text{Denfox}}$ is the probability that an S individual occupying an infested den during week $w$ gets infested with <i>S. scabiei</i>	$p_{\text{Denfox}} \sim \text{Uniform}(0.3, 0.6)$	

**Table 3**Summary of the scenarios simulated with respect to direct and indirect den-associated *S. scabiei* transmission and its survival.

Scenario	Sub scenario	Within-den fox-to-fox transmission	Fox-den-fox transmission	<i>S. scabiei</i> off-host within den survival
A	–	No	No	–
B	–	Yes	No	–
C	1	No	Yes	1 week <sup>a</sup>
	2	No	Yes	2 weeks in the cold season <sup>b</sup> 0 week in the warm season <sup>b</sup>
	3	No	Yes	1 week during the cold season in dens of the group 1 <sup>1</sup> 3 weeks during the cold season in dens of the group 2 <sup>2</sup> 2 weeks during the cold season in dens of the group 3 <sup>3</sup> 0 week during the warm season in dens of the group 1 <sup>4</sup> 3 weeks during the warm season in dens of the group 2 <sup>5</sup> 1 week during the warm season in dens of the group 3 <sup>6</sup>
D	1	Yes	Yes	1 week across dens and seasons
	2	Yes	Yes	2 weeks across dens in the cold season 0 weeks across dens in the warm season
	3	Yes	Yes	1 week during the cold season in dens of the group 1 <sup>1</sup> 3 weeks during the cold season in dens of the group 2 <sup>2</sup> 2 weeks during the cold season in dens of the group 3 <sup>3</sup> 0 week during the warm season in dens of the group 1 <sup>4</sup> 3 weeks during the warm season in dens of the group 2 <sup>5</sup> 1 week during the warm season in dens of the group 3 <sup>6</sup>

<sup>a</sup> We assumed 15 °C in the den's soil and 45% relative humidity inside dens (Arlian et al., 1989, 1984a).

<sup>b</sup> We assumed 10 and 20 °C in the den's soil and 75 and 25% relative humidity inside dens each season (Arlian et al., 1989, 1984a).

<sup>1</sup> Dens located in 'Open', 'Transition', 'Industrial', and 'Linear' land types and assuming within den temperature 15 and 45% relative humidity.

<sup>2</sup> Dens located in 'Residential', 'Commercial', and 'Manicured' land types and assuming within den temperature 10 and 90% relative humidity.

<sup>3</sup> Dens located in 'Water catchment basins' and assuming within den temperature 15 and 75% relative humidity.

<sup>4</sup> Dens located in 'Open', 'Transition', 'Industrial', and 'Linear' land types and assuming within den temperature 20 and 25% relative humidity.

<sup>5</sup> Dens located in 'Residential', 'Commercial', and 'Manicured' land types and assuming within den temperature 10 and 90% relative humidity.

<sup>6</sup> Dens located in 'Water catchment basins' and assuming within den temperature 15 and 10% relative humidity.

#### 2.4. Scenarios of *S. scabiei* den-associated transmission

We simulated a susceptible population: i) for 8 years in the absence of the mite; and ii) for 3 years (156 weeks) but introducing *S. scabiei* in the 45<sup>th</sup> week (before the beginning of the mating season). Further, we simulated an already infested population for 8 years. The second scenario simulated an epizootic, while the third simulated an enzootic period. These 2 periods have been recognized in infested urban populations of species taxonomically related with SJKF (Baker and Harris, 2000; Newman, 2001; Soulsbury et al., 2007). We introduced a single E individual in week 45 of the first year simulated because it is the estimated infestation moment for the first case of sarcoptic mange found in Bakersfield considering the progression of its illness. The introduction occurred in the northernmost part of the City, where the first case was detected (Cypher et al., 2017). We selected week 156 as the cut-off for this period because preliminary simulations showed that, in our model, the incidence generally reached its peak at this point, and up to this moment there are more cases than expected.

Because of our uncertainty with respect to den-associated sarcoptic mange transmission ( $p_{Share}$ ,  $p_{Social}$ ), we simulated 4 scenarios that included or excluded within-den fox-to-fox transmission (direct transmission) and fox-den-fox transmission (indirect transmission), while allowing for out-of-den direct transmission: Experiment A – no within-den direct transmission and no indirect transmission ( $p_{Share}$  and  $p_{Denfox} = 0$ ); Experiment B – only within-den direct transmission ( $p_{Denfox} = 0$ ); Experiment C – only indirect transmission ( $p_{Share} = 0$ ); and Experiment D – both types of transmission. Further, due to our uncertainty on *S. scabiei* within-den off-host survival, we simulated 3 options for Experiments C and D. Sub-experiment 1: mites survived equally across temperature seasons and across dens for 1 week; sub-experiment 2: mites survived differentially across temperature seasons but homogeneously across land types where dens were located, with 2 and 0 weeks off-host survival in the cold and warm season, respectively; and sub-experiment 3: mites survived heterogeneously across seasons and land types following the definitions and assumptions in Table 3.

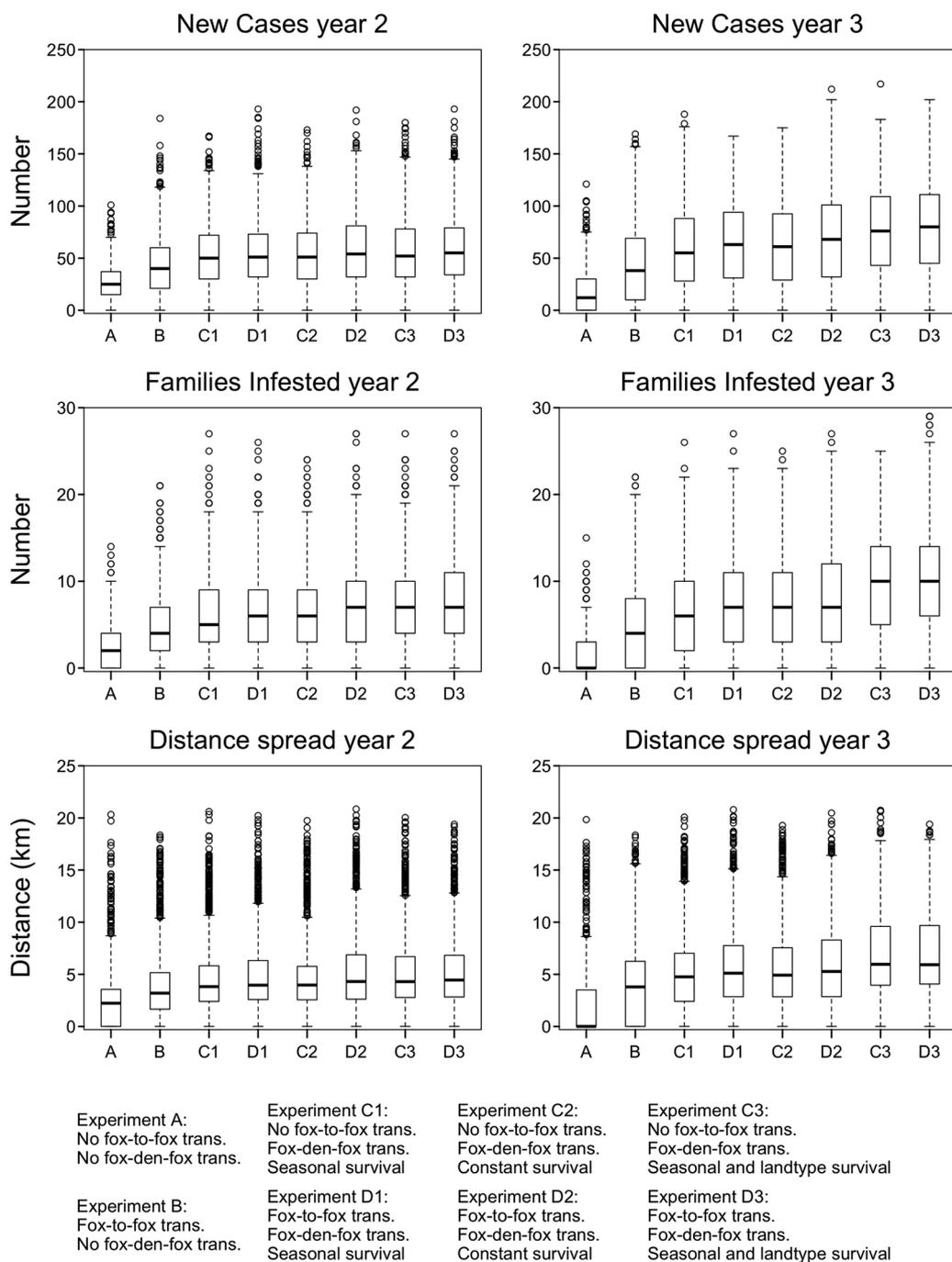
These different sub-experiments were chosen because off-host survival of *S. scabiei* depends on temperature and relative humidity (Arlian et al., 1989, 1984a). Therefore, mite survival may be heterogeneous throughout the year but also across dens depending on the land type in which they are located (a watered park versus an industrial site). The cold season (December - April) and warm season (May - November) were based on historical ground temperatures in the Mojave Desert, the previously reported difference between the soil temperature of an unoccupied kit fox den and temperature in the area, the published relative humidity of an occupied kit fox den at different environmental temperatures, and the similar temperatures between the Mojave desert and Bakersfield (Girard, 2001; Golightly, 1981; Your weather service, 2017a,b).

In total 16 experiments were conducted, 8 in each period. This set of scenarios allowed us to compare sarcoptic mange spread, establishment, and persistence in the SJKF population when den-associated transmission does not occur against several plausible scenarios when it is feasible. Further, when den-associated transmission was possible, we were able to assess if mechanistic differences in within-den off-host *S. scabiei* survival, whose current nature is unknown, could modify sarcoptic mange dynamics.

#### 2.5. Initialization and simulations

The simulations were initialized with one random generation of home ranges and dens, and an initial fox population. For the details on the initial populations to simulate the scenario without sarcoptic mange and the epizootic period see Supplementary Material 5. For the enzootic period, the initial population was a randomly selected population that remained infested with *S. scabiei* at the end of the epizootic period (at least one E, type I, or type II individual) under any experiment. Dens occupied by infested individuals started the enzootic period as contaminated.

The initial population for the 5<sup>th</sup> simulation was equivalent across experiments (see next). Each experiment was simulated 1000 times,



**Fig. 3.** The distribution of a) the number of new individuals infested with *S. scabiei*, b) the number of families infested at the end of each year, and c) the distance *S. scabiei* spreads by the end of each year, in each of the 8 transmission scenarios in the epizootic period.

which was adequate to stabilize point estimates and ranges for our outcomes of interest. Each simulation had a random set of transmission parameter values.

Home ranges and dens were also equivalent for the  $s^{\text{th}}$  simulation of each experiment, and they remained constant through each simulation.

**2.6. Outcomes of interest and data analysis**

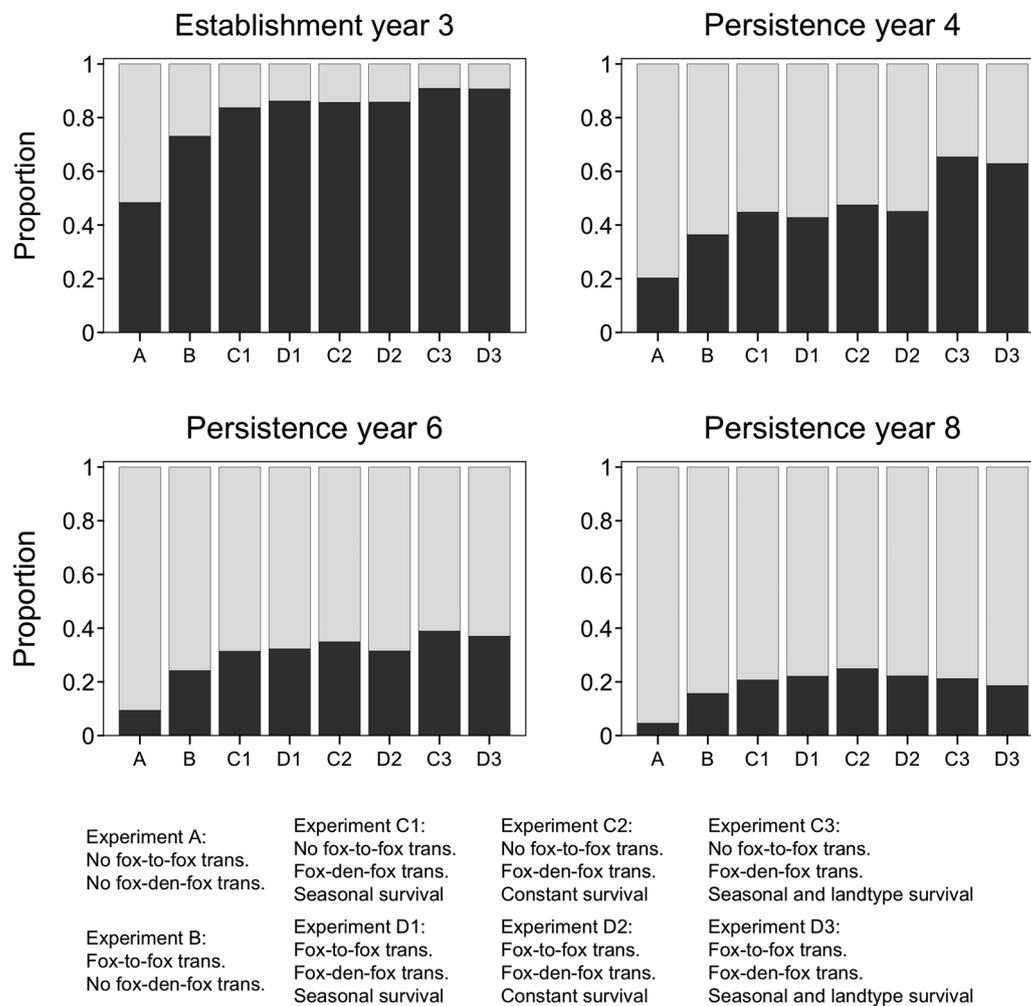
To assess the role of dens in the spread of sarcoptic mange, we tracked 3 outcomes during the epizootic period: i) the annual number of new cases (hereafter “new cases”); ii) the number of infested families at the end of each year (weeks 52, 104, and 156; hereafter “families infested”); and iii) the distance between the home range of initial

introduction and the furthest infested home range (the centroid) by the end of each year (hereafter “distance”). We computed the distributions of the 3 outcomes tracked per experiment.

Further, we computed for each experiment the proportion of simulations in which the disease remained in the SJKF population (at least a single E, type I, or type II individual in the population) at the end of the epizootic period (week 156; establishment), and at the end of the 4th, 6th, and 8th year of the enzootic period (weeks 208, 312, and 416; persistence).

**2.7. Sensitivity analysis**

We conducted a sensitivity analysis (SA) to identify disease-



**Fig. 4.** a) Proportion of simulations per experiment in which sarcoptic mange established in the SJKF population (contained at least one E, type I, or type II individual) by the end of the epizootic period (week 156; dark portion). b–d) Proportion of simulations per experiment in which sarcoptic mange persisted in the SJKF population (contained at least one E, type I, or type II individual) at the end of the fourth, sixth, and eighth year of the enzootic period (weeks 208, 312, and 416; dark portion).

associated parameters that influence sarcoptic mange spread, establishment, and persistence; and to assess major changes in the results when considering wider ranges of values for each transmission probability and the off-host survival of *S. scabiei* across seasons and land types. The disease-associated parameters in the SA included the 5 transmission probabilities (Table 2 and Supplementary Table 6.1) and parameters related with the length of mite off-host within-den survival (Supplementary Table 6.1). For each outcome of interest and each value of the parameter assessed we ran 500 simulations while the rest of the parameters were held constant at their mean values. We registered the values of the outcomes of interest obtained on the values of each parameter assessed, assuming a linear and monotonic relationship between them. Parameters whose coefficient absolute value was larger compared to the other ones were considered relevant for the corresponding outcome of interest. More details of the SA are provided in Supplementary Material 6.

### 3. Results

The data of raw results is available at <https://doi.org/10.6084/m9.figshare.6728999.v1>.

#### 3.1. No disease

Without disease, the SJKF population remained stable for 8 years

(see the temporal series in Supplementary Material 7). The mean population sizes across the 3rd and 9th week of each year were 250 and 367 individuals, respectively (pre and post birth pulse). At the end of year 1, 2, 3 and 8, the population ranges were: 217–297, 214–301, 204–304 and 205–301, respectively. These results are consistent with the estimated SJKF population in Bakersfield (Cypher and Cypher, 2010; Cypher and Frost, 1999).

#### 3.2. Epizootic period

The distribution of new cases, infested families, and distance were practically identical for the first year across experiments. For the second year, the distributions were different for Experiment A (no den-associated transmission). This experiment yielded medians about half for these outcomes of interest compared with experiments that considered at least one den-associated transmission pathway. Moreover, Experiment B (no indirect transmission) favored lower values compared with the set of C and D Experiments (Fig. 3). Although the interquartile ranges of Experiment A and B overlapped, and the interquartile ranges of Experiment B and Experiments C–D overlapped, their median differences could be epidemiologically and logistically meaningful.

In contrast, the third year showed clear differences in the distribution of outcomes of interest. Experiment A favored lower values compared with the rest of the experiments (the median of families infested and distance of spread is close to zero). Experiment B caused larger

medians for the 3 outcomes of interest but again with interquartile ranges overlapping those from Experiment A. Experiments C1-3 and Experiment D1-3 consistently caused larger median spread and the interquartile ranges were located at higher values compared with Experiment A (Fig. 3). Interestingly, it was possible to observe an increasing trend of the median values of the outcomes of interest along the gradient of transmission complexity and off-host within-den *S. scabiei* survival (from Experiment A to D3). Finally, it is worth noting that the variation within individual simulations was generally larger than the variation across the different experiments.

The temporal series of the SJKF population, sarcoptic mange cases, families infested, and distance of spread across the 8 experiments during the epizootic period are shown in Supplementary Fig. 8.1.

Following the results for the spread of sarcoptic mange, the experiments could be classified into 3 groups with respect to the establishment of the disease. Experiment A yielded the lowest proportion of simulations resolving in established disease according to our definition (0.47). Experiment B resolved in  $\sim 0.7$ , simulations with established disease, 33% higher than Experiment A, whilst Experiments C1-3 and D1-3 had higher establishment probability, all above 0.8, about twice the establishment probability of Experiment A (Fig. 4a).

### 3.3. Enzootic period

The persistence of sarcoptic mange during the enzootic period declined constantly across experiments, but at different rates. Again, experiments could be grouped in 3: Experiment A resolved in a maximum persistence of  $\sim 0.2$  of the simulations by the end of year 4 (week 208) and in less than 0.05 after 8 years (week 416); Experiment B, C1-2, and D1-2 had lower rates of persistence with  $\sim 0.4$ , of the simulations presenting at least one infested individual by the end year 4 and  $\sim 0.2$  after 8 years in enzootic period. This is about 4 times larger than in Experiment A. Finally, Experiments C3 and D3 yielded persistence of sarcoptic mange in more than 0.5 of the total simulations by the end of year 4. However, these experiments presented high rates of sarcoptic mange extinction afterward, with faster declines in the second half of the enzootic period. This process caused the persistence of this disease by the end of the 8th year to resemble the results obtained in Experiment B (Fig. 4b–d).

The temporal series of the SJKF population, sarcoptic mange cases, families infested, and distance the disease spread across the 16 experiments are shown in Supplementary Fig. 8.2.

### 3.4. Sensitivity analysis

The spread-associated outcomes of interest by the first year were not sensitive to any parameter. With respect to den-associated transmission parameters,  $p_{\text{Denfox}}$  had one of the largest absolute coefficient values across outcomes of interest (the largest in 5 of 8). The  $p_{\text{Share}}$ , however, was a parameter of secondary importance, likely as a result of the relevance of the  $p_{\text{Social}}$  parameter, which determines transmission within the family regardless of whether the foxes are sharing den or not. Interestingly,  $p_{\text{Mate}}$  was primarily important for the incidence during the 2nd and 3rd year of the epizootic, for the establishment of disease at the end of this period, and to some degree for the persistence of sarcoptic mange at the end of the enzootic period. Finally, the number of days of *S. scabiei* survival off-host within dens located in 'Open', 'Transition', 'Industrial', and 'Linear' land types land types during the warm season was somewhat relevant for the establishment of *S. scabiei* at the end of the epizootic (Fig. 5).

## 4. Discussion

The identification of relevant transmission routes is crucial for efficient prevention, management planning, and control of diseases. However, to our knowledge, no previous model has explicitly included

dens, their spatial distribution, and the den sharing and den changing behavior of the hosts to assess the potential responsibility of dens in infectious disease dynamics. Here, we used an agent-based model to study the role of dens in *S. scabiei* dynamics for den-dwelling species. Specifically, we selected the urban population of San Joaquin kit fox in Bakersfield as a case study because it is an endangered den-dwelling species that is facing an epizootic of sarcoptic mange (Cypher et al., 2017), members of different family groups are rarely in contact (Koopman et al., 1998; Morrell, 1971; Ralls et al., 2007, 2001), the sequential use of dens by non-relative individuals may be the only relevant path by which the mite could cross the between-family barrier, and there are data available with respect to the denning behavior in this species.

The model considered the heterogeneous aggregation of hosts in family groups over space, daily and seasonal fox behavior, morbidity-associated behavioral changes, den environment, and subsequent within-den survival of *S. scabiei* when off-host. Further, within- and out-of-den direct transmission and fox-den-fox transmission were considered, and they were parameterized with wide but plausible probabilities. As a result, every fox had unique opportunities for transmission and infestation within and among family groups.

Results from the simulations showed that, on average, it is unlikely that out-of-den direct transmission by itself (no den-associated transmission) could cause an extensive sarcoptic mange epidemic. The spread was inhibited, the disease extinguished about 50% of the time during the epizootic phase, and it rarely persisted after 8 years as enzootic although susceptible individuals were still available. The need for other transmission pathways for sarcoptic mange spread has been stated in the past for in urban red foxes as well (Devenish-Nelson et al., 2014). The inclusion of den-associated transmission, on the other hand, supported greater spread by several orders of magnitude in terms of new cases, the number of families infested, and distance of spread. The establishment of sarcoptic mange was up to twice more likely and the persistence was up to 4 times more likely (depending on *S. scabiei* off-host survival capabilities). Consistently, results of the SA showed that the metrics of spread, establishment, and persistence of sarcoptic mange were sensitive mainly to the den-associated indirect transmission parameter and to a certain degree to the den-associated direct transmission as well.

When the model allowed within-den direct transmission only (no fox-den-fox transmission), sarcoptic mange tended to spread, establish, and persist more often compared to simulations without any den-associated transmission. Higher risk of disease in social species has been proposed because of the enhanced interaction with conspecifics (Altizer et al., 2003; Cross et al., 2009). Although within-den direct transmission mainly supports the infestation of susceptible relatives in the model, it could cause a larger absolute number of infested dominant foxes, increasing the chances that infested individuals contact susceptible ones belonging to other families during the mating season. Similarly, it could also support a larger absolute number of infested subdominant foxes, creating more opportunities for recently infected individuals to successfully change of family group and spread the disease.

In those experiments allowing den-associated indirect transmission sarcoptic mange spread even more, while the establishment and persistence of this disease were substantially more likely versus scenarios with den-associated direct transmission only. Indirect transmission experiments with equivalent *S. scabiei* off-host survival but that differed with respect to the feasibility of within-den fox-to-fox direct transmission (feasible versus unfeasible), resulted in similar outcomes of spread, establishment, and persistence of sarcoptic mange. This suggests that the fox-den-fox transmission pathway could drive *S. scabiei* dynamics without regard to within-den fox-to-fox direct transmission. This pattern is likely explained because: i) fox-to-fox out-of-den direct transmission can cover the within-den direct transmission events if infestation does not occur through this later pathway and ii) only indirect

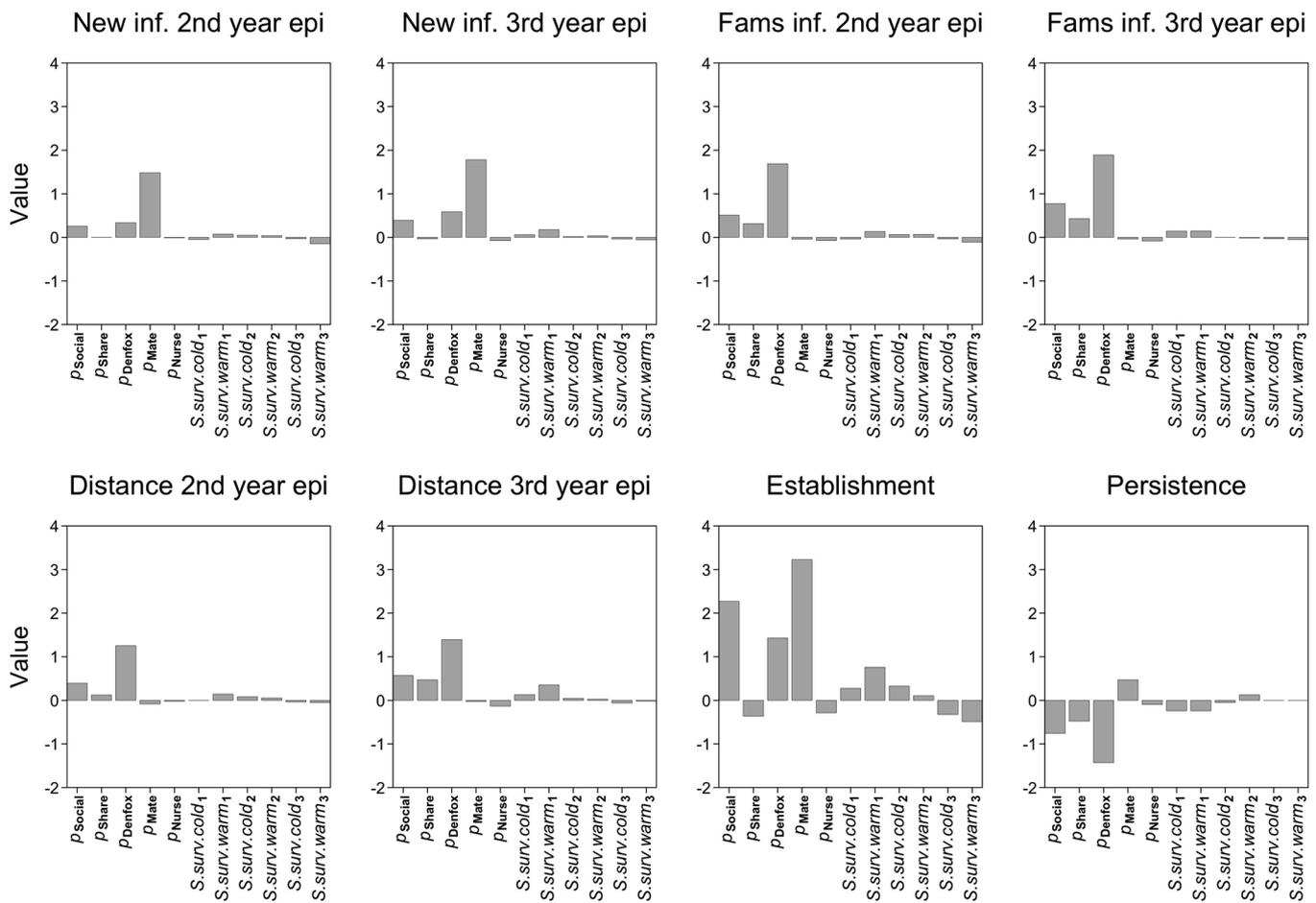


Fig. 5. Value of the coefficient term of each parameter assessed in the sensitivity analysis per outcome of interest. New inf. refers to “New infested”, Fams. inf refers to “Families infested”, and Persistent refers to the presence of sarcoptic mange at the end of the 8th year of the enzootic period.

transmission allows interfamily infestation associated with dens. This is consistent with SA results, were the outcomes associated with the spread after the first year are sensitive mainly to  $p_{\text{Social}}$ ,  $p_{\text{Denfox}}$ , and  $p_{\text{Mate}}$ .

Although the contamination of dens with *S. scabiei* and indirect infestation of susceptible individuals with dislodged mites present in the substrate of dens remains to be proven, research has shown that host-seeking infective mites can be recovered from the environment (Arlian et al., 1989, 1988, 1984a, 1984b; Arlian and Vyszynski-Moher, 1988), and that low temperatures and high relative humidity facilitating *S. scabiei* off-host survival (Arlian et al., 1989, 1984a) are promoted in dens (e.g., Anderson and Richardson, 2005; Roper, 1992), including those used by the kit fox (*Vulpes macrotis arsipus*; (Anderson and Richardson, 2005; Girard, 2001) and by the SJKF (A. Loreda, *in prep.*).

Furthermore, the data provided by our model are in agreement with previous studies reporting a relationship between the use of dens by carnivores and wombats (*Vombatus* sp.), and sarcoptic mange (Gerasimov, 1958; Kołodziej-Sobocińska et al., 2014; Skerratt et al., 2004, 1998); and between other infectious diseases and the use of burrows by wild mammals (Barnes et al., 1972; Caley et al., 1998; Centers for Disease Control and Prevention, 2015; Davis et al., 2008; Fairweather et al., 1987; Patterson et al., 2017; Rogers et al., 2003; Seery et al., 2003; Weber et al., 2013). Our results are also consistent with previous research identifying indirect transmission of sarcoptic mange in urban red foxes. Soulsbury et al. (2007) reported temporally concordant sarcoptic mange prevalence in these animals and in domestic dogs (*Canis familiaris*) due to indirect transmission, whilst the incorporation of indirect infestation in an agent-based model predicted

better the patterns of this disease in the same red fox population (Devenish-Nelson, 2012; Devenish-Nelson et al., 2014).

This collective evidence strongly suggests that indirect transmission is a relevant driver of sarcoptic mange as proposed for other infectious diseases in wild populations (Barlow et al., 2002; Berthier et al., 2000; Miller et al., 2006; Roche et al., 2009; Rohani et al., 2009; Sauvage et al., 2003). Neglecting this pathway can misguide surveillance and mitigation efforts (Lange et al., 2016), therefore, managers should consider den-associated transmission (direct and indirect) in den-dwelling species when dealing with sarcoptic mange and likely with other pathogens with an environmental infective stage. This transmission pathway is especially important in socially organized species, where direct contact is restricted to the family group (Loehle, 1995).

Although validation of results from our model with field data would be ideal, it was not possible because there has not been a consistent searching for cases (passively or actively) over time and space. Currently, it is possible to find cases and treat them, but not to assess temporal trends. Secondly, because the SJKFs in Bakersfield are being trapped and treated, it is very likely that the dynamics of sarcoptic mange during the epizootic and enzootic periods of our modeling are different compared to a treated population.

Sarcoptic mange in our model showed density dependence: as the population declined due to the disease also did the levels of disease. This would not be in agreement with the population collapse caused by *S. scabiei* in urban red foxes (Soulsbury et al., 2007), nor frequency-dependent transmission reported in these animals (Devenish-Nelson et al., 2014). Specific model conditions can explain this tendency. The denning behavior was parameterized with data from exurban SJKFs, but urban populations tend to behave differently with respect to non-

urban counterparts in manners that could affect pathogen dynamics (Bradley and Altizer, 2007; Brearley et al., 2013), whilst behavioral changes in many canids have also been reported (e.g., in coyotes [*Canis latrans*]; Murray et al., 2015). Furthermore, to simplify the model, home ranges were common for an entire social group and their shape and area were fixed over time. The inclusion of individual home ranges and changes in their form could create larger chances of overlap across families. Increasing their area would allow direct or indirect contact with families that originally were not in the overlap range. Field data from urban red foxes affected with sarcoptic mange in Bristol U.K. showed that family groups expanded their territory to encompass the space left by groups killed off by this disease (Baker and Harris, 2000), and individual foxes reduced their rest site fidelity (Newman et al., 2003). However, simulations of this infested population that included these features showed that inter-group contact rate remained unchanged and that direct transmission alone was unable to reproduce observed mange dynamics (Devenish-Nelson, 2012). These findings are concordant with our results.

As data is obtained for future development, the current model can be a useful tool to assess the role of dens in the dynamics of *S. scabiei* and to evaluate the potential results of management strategies in den-dwelling species. Practical management of dens could include their collapse, incineration, chemical treatment, and providing artificial structures to be used as dens with properties that impair *S. scabiei* off-host survival. However, potential management of dens should create conservative expectations in terms of disease control/eradication as our intra-experiment variability tended to be larger than the variability across experiments. In practical terms, there could be no difference in either sarcoptic mange dynamics or kit fox population impacts, whether or not the den is managed.

## 5. Conclusions

The simulations in the agent-based model of the urban San Joaquin kit fox population in Bakersfield, which explicitly included dens, their spatial distribution, environment, and the denning behavior of the foxes, showed that den-associated direct transmission (fox-to-fox within-den) and den-associated indirect transmission (fox-den-fox) increase the chances of *S. scabiei* to spread, to establish, and to persist in this population. Current results are in agreement with previous research supporting indirect transmission of sarcoptic mange and the relationship between den-use and the transmission of this disease, and they provide further understanding of one of the “critical questions” established by Martin et al. (2017): “What role does the burrow play in (sarcoptic mange) transmission?”

Managers dealing with *S. scabiei* in this species as well as in other den-dwelling species should consider the possibility of den-associated transmission as they could be targeted as part of the control strategies against this mite, although expectations for the use of this strategy alone should be conservative. The current model could be used to assess the outcomes of management strategies targeting dens.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.epidem.2019.01.001>.

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