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Parasite dispersal risk tolerance is mediated by its reproductive value

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Parasite dispersal theory draws heavily upon epidemiological SIR models in which host status (susceptible (S), infected (I), or recovered (R)) is used to study parasite dispersal evolution. In contrast to these extrinsically host-centric drivers, in this study we focus on an intrinsic driver, the parasite's reproductive value (predicted future offspring) as a regulator of the extent to which the individual will engage in risky dispersal behaviour. As a model system we use the honeybee *Apis mellifera* and its ectoparasite, the mite *Varroa destructor*. Mite reproduction happens exclusively inside cells of bee brood, and newly emerged fecund mites may parasitize either a homocolonial brood cell (low risk dispersal) or emigrate to a new bee colony via phoretic attachment to mature forager bees (high risk dispersal). In an empirical bioassay, prepartum mites (high reproductive value) and postpartum mites (low reproductive value) were offered a choice of newly emerged homocolonial worker bees (low risk), homocolonial pollen forager bees (high risk), or heterocolonial pollen foragers (high risk). A preference for newly emerged bees was earlier and more strongly sustained among prepartum mites. This suggests comparatively greater dispersal risk tolerance among postpartum mites with lower reproductive value. A dangerous bid for dispersal may be adaptive if the individual has already successfully reproduced and the rewards for successful dispersal are sufficiently large.

The choice between staying at a proven resource and dispersing to a new one is a high stakes decision for all parasites. Modern strategies for dispersal can be viewed as evolutionary optima balancing its benefits, such as improving conditions for reproduction (Ruxton & Rohani, 1999), avoiding kin competition (Cote & Clobert, 2010) and avoiding inbreeding (Crespi & Taylor, 1990), against its risks, such as energetic costs (Stirling, Fairbairn, Jensen, & Roff, 2001) and direct mortality (Bowler & Benton, 2009). Moreover, it is increasingly understood that dispersal is not a simple diffusion event, but rather a product of interacting dynamics at population margins.

Dispersal at the level of parasites is often studied with epidemiological 'SIR' models, which categorize hosts as susceptible (S), infected (I) or recovered (R) (Anderson & May, 1979, 1982). Parasite transmission from I to S hosts is regulated by a few powerful drivers, including host density (Kermack & McKendrick, 1927; Peel et al., 2014), host genetic diversity (Lively, 2010), genetic relatedness of other parasites on near-neighbour hosts (Lion & Boots, 2010) and relative opportunities for local versus global transmission (Boots & Sasaki, 1999). Such host-centric SIR models have been successfully used to explain disease dynamics in systems as diverse as rabies in fox (Anderson, Jackson, May, & Smith, 1981) and Ebola in humans (Pandey et al., 2014).

In the case of a relatively long-lived parasite capable of multiple broods, it is likely that dispersal regulation includes drivers intrinsic to parasite state. One of these is kin structure of parasites at the population level (Cote, Clobert, & Fitze, 2007; Hamilton & May, 1977; Kubisch, Fronhofer, Poethke, & Hovestadt, 2013). Theory predicts that dispersal will be selected for if inclusive fitness gains (reduced competition) exceed dispersal costs for the emigrant (Hamilton & May, 1977).

Another likely intrinsic dispersal driver is reproductive value at the individual level. An individual's reproductive value, defined as predicted future reproductive success based on the individual's age and sex (Fisher, 1930; Williams, 1966), has been used in applications as diverse as parental investment theory (Albrecht & Klvaňa, 2004; Ghalambor & Martin, 2001; Redondo & Carranza, 1989), mate selection (Wolf & Schulman, 1984), evolution of senescence (Hamilton, 1966) and for predicting success of colonists (MacArthur & Wilson, 1967).

In this study, we investigate an association between a parasite's reproductive value and its propensity to engage in risky dispersal

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behaviour. We use the western honeybee *Apis mellifera* and its ectoparasite, the mite *Varroa destructor*, as a model system. This host–parasite relationship is man-assisted and no older than the mid-19th century (Danka, Rinderer, Kuznetsov, & Delatte, 1995). However, each species now shows signs of co-adaptation (Fries & Bommarco, 2007; Seeley, 2007); indeed the taxonomic epithet *destructor* is contextual to *A. mellifera* (Anderson & Trueman, 2000). The mite reproduces exclusively inside cells of bee brood. Emerged fecund females may either parasitize a new cell of brood in the same colony, often aided by brief phoretic attachment to a young house bee, or emigrate to a new bee colony and access a new population of host brood. This emigration is accomplished by phoretic attachment to adult forager bees who may subsequently enter an alien bee colony. This bee behaviour, called drifting, can be understood as either a bid by the drifter for reproductive opportunity (Neumann, Radloff, Pirk, & Hepburn, 2003) or a simple accident of navigation (Free, 1958). But from the perspective of the obligate mite parasite, a decision for extracolonial dispersal certainly constitutes the riskier choice.

Our study of the regulatory effect of mite reproductive value on dispersal risk tolerance was accomplished with laboratory behavioural assays comparing high- and low-risk host choices in pre- and postpartum varroa mites. Because most female varroa mites complete fewer than two reproductive cycles (DeRuijter & Calis, 1988; Fries, Camazine, & Sneyd, 1994), prepartum mites have a higher reproductive value. We predicted that this cohort would exhibit lower risk tolerance by preferentially parasitizing low-risk hosts, in our case, young homocolonial bees. In contrast, we predicted that postpartum mites would exhibit higher risk tolerance and parasitize older forager bees, either homocolonial or heterocolonial, at a comparatively higher rate.

METHODS

Collecting and Marking Mites

We collected mites from infested bee colonies maintained by the University of Georgia using one of two methods. The first method involved the use of a bee repellent (Bee Go, Cloverland Products, Inc., Pearl City, IL, U.S.A.) to drive adult bees into a box measuring 46.4 × 41.3 × 30.5 cm (Aliano & Ellis, 2005). The bees were then dusted with powdered sugar inside the box to dislodge and capture mites. The second method involved dusting the tops of all frames with powdered sugar and collecting mites as they fell through screen bottom boards onto plastic boards placed under the colony. Living mites were brought into the laboratory and housed on water-moistened filter paper suspended inside a clean glass quart (~1 litre) jar. Jars with mites were maintained in an incubator at 32 °C and ~40% relative humidity while marking was completed. Marking was accomplished the same day mites were collected. All mites were marked with correction fluid using the protocol described in Kirrane et al. (2012). After marking, mites were inoculated into brood cells containing 10-day-old honeybee larvae (see below).

Preparing Honeybee Worker Larvae for Inoculation

Ten days prior to mite inoculation, queens from four test colonies were individually caged on an empty drawn deep comb for 24 h to ensure uniform age of developing larvae. Queens were moved to a new frame every 24 h; each frame was labelled with the date eggs were laid. This was done for four consecutive days. Frames with 10-day-old larvae were removed from their colonies; adult bees were brushed off in the field before frames were brought back to the laboratory for inoculation. A scalpel was used to make a slit in the capping, a marked mite was placed inside the cell, and the slit was gently pushed back into place. A sheet of transparency film was used to map the inoculated larvae to aid in mite recovery. Frames were returned to the parent colony immediately after mite inoculation. This procedure was performed for each of the four test colonies. Inoculations continued for 4 days and were performed in a darkened room at 32 °C at ~40% relative humidity to improve survivorship of mites and honeybee larvae.

Mites were recollected 10 days after inoculation when bee larvae were 20 days old. Frames were removed, adult bees brushed off and the frames brought back to the laboratory. With the aid of the mapped transparency films, cells of inoculated brood, now pupae, were manually uncapped with forceps. All cells containing marked mites and their offspring were collected for experimental trials.

Only marked postpartum mites and their unmarked prepartum daughters were used in the study. Unmarked prepartum mites are assumed to have never reproduced while marked postpartum mites are assumed to have reproduced at least once. Only mites originating from a cell with a marked mite were used in the study. To control for honeybee larvae that may have already contained a postpartum mite in addition to the marked inoculated mite, each mite was inspected carefully, and the marked mite as well as any mites that were obviously lightly sclerotized, were used. No unmarked, darkly sclerotized mites were mistakenly used as prepartum mites.

The two cohorts of mites were placed on water-moistened filter paper suspended inside pint-sized (~0.5 litre) glass jars and placed in an incubator at 32 °C and ~40% relative humidity. Mites were used in trials the day of collection.

Collecting Worker Honeybees

The same four colonies that produced pre- and postpartum mites were used as source colonies for adult honeybees. Mite-free, newly emerged teneral workers (NEW) found when searching for marked mites were used as NEW bees. Pollen foragers were collected directly off the comb; only bees with pollen in their corbicula were used.

Each of the four test colonies was positioned at least 3.2 km from each other or any other known colony to minimize the chance of bees drifting between the four colonies.

Bees were housed in new Ziplock® plastic food boxes with air holes and provided 1:1 sugar water. They were held in an incubator at 32 °C and ~40% relative humidity until used. Bees were used within 24 h of collection. Bees were immobilized with CO_2 for placement into petri dishes and examined for phoretic mites as they were being added. Bees found with phoretic mites were not used.

Mite Trials

Mite choice trials were conducted over four consecutive days utilizing a different mite source colony each day. Each petri dish trial consisted of a Fisherbrand® 100 × 15 mm petri dish containing one mite and three bees. The mite was given a choice of three living bees: (1) a homocolonial NEW bee, (2) a homocolonial pollen forager and (3) a heterocolonial pollen forager from one of the other three test colonies. Each combination was replicated three times for each mite type (Table 1).

Bees were immobilized with CO_2, inspected for phoretic mites, and once deemed mite free, placed equidistant from each other around the sides of the petri dish. Bees had either their right, left, or both forewings clipped for cohort identification. Clipping occurred just prior to being placed in the petri dish. Petri dishes were placed

Table 1
Experimental design for live mite host choice assay

Bee/mite source colony	Bee/mite source colony							
	1		2		3		4	
	Mite type		Mite type		Mite type		Mite type	
	Prepartum	Postpartum	Prepartum	Postpartum	Prepartum	Postpartum	Prepartum	Postpartum
1	–	–	$NEW_{2,}$ $F_{2,}$ $F_{1,}$ (3)	$NEW_{2,}$ $F_{2,}$ $F_{1,}$ (3)	$NEW_{3,}$ $F_{3,}$ $F_{1,}$ (3)	$NEW_{3,}$ $F_{3,}$ $F_{1,}$ (3)	$NEW_{4,}$ $F_{4,}$ $F_{1,}$ (3)	$NEW_{4,}$ $F_{4,}$ $F_{1,}$ (3)
2	$NEW_{1,}$ $F_{1,}$ $F_{2,}$ (3)	$NEW_{1,}$ $F_{1,}$ $F_{2,}$ (3)	–	–	$NEW_{3,}$ $F_{3,}$ $F_{2,}$ (3)	$NEW_{3,}$ $F_{3,}$ $F_{2,}$ (3)	$NEW_{4,}$ $F_{4,}$ $F_{2,}$ (3)	$NEW_{4,}$ $F_{4,}$ $F_{2,}$ (3)
3	$NEW_{1,}$ $F_{1,}$ $F_{3,}$ (3)	$NEW_{1,}$ $F_{1,}$ $F_{3,}$ (3)	$NEW_{2,}$ $F_{2,}$ $F_{3,}$ (3)	$NEW_{2,}$ $F_{2,}$ $F_{3,}$ (3)	–	–	$NEW_{4,}$ $F_{4,}$ $F_{3,}$ (3)	$NEW_{4,}$ $F_{4,}$ $F_{3,}$ (3)
4	$NEW_{1,}$ $F_{1,}$ $F_{4,}$ (3)	$NEW_{1,}$ $F_{1,}$ $F_{4,}$ (3)	$NEW_{2,}$ $F_{2,}$ $F_{4,}$ (3)	$NEW_{2,}$ $F_{2,}$ $F_{4,}$ (3)	$NEW_{3,}$ $F_{3,}$ $F_{4,}$ (3)	$NEW_{3,}$ $F_{3,}$ $F_{4,}$ (3)	–	–

$NEW_{bee/mite\ source\ colony}$: newly emerged worker bee; $F_{bee/mite\ source\ colony}$: pollen forager bee. Numbers in parentheses = starting number of petri dish trials for each combination of mite type and bees.

on tables in a darkened room outfitted with red lights to minimize disturbance. The room was maintained at 32 °C and ~40% relative humidity during trials. Petri dish trials followed procedures from Kuenen and Calderone (1997). For each petri dish trial, mite choice was recorded once every 15 min for 4 h. If a mite or bee died before the 4 h ended, data were no longer taken for that dish. Each mite was used for only one assay. The inclusion of time in the design is predicated on the assumption (Del Piccolo, Nazzi, Della Vedova, & Milani, 2010; Kuenen & Calderone, 1997) that if a mite finds itself on a preferred host, then it is likely to stay there, whereas if it initially attaches to an inferior host, then there is a higher probability that it will relocate to another host over the course of a trial. A mite's choice was considered positive if it was phoretically attached onto a bee; if a mite was not phoretically attached to a bee at any time point, then that petri dish trial was not included in analyses for that time point. At each time point, there were some mites that were not on any bee; such petri dish trials were not included in statistical analyses for that time point.

Statistical Analyses

Analysis of mite choice over time used a repeated measures multinomial mixed effects model performed by the software package SAS/STAT® v. 9.3 (SAS Institute, Cary, NC, U.S.A.). We used a GLIMMIX procedure recognizing bee type as the response variable, individual petri dish trial as a random effect, the type of mite used in the trial (pre- or postpartum) as a fixed effect, and the continuous variable time within trial as a fixed effect. The repeated measures within a petri dish necessitated the use of petri dish trial as a random effect. Initially the colony of origin for the mite and homocolonial bees was considered for inclusion as a fixed effect, but was shown statistically nonsignificant ($P = 0.3813$). Observations for which the mite was not located on a bee, or for which the mite had died, were removed from analysis. Preliminary analysis showed that on average both pre- and postpartum mites favoured newly emerged worker bees over other bee choices; therefore, we calculated probabilities for a mite's presence on any bee type for each time point relative to the probability of the mite being on a new bee.

RESULTS

The fixed effect of time on mite choice of bee was significant ($F_{2,609} = 14.74$, $P < 0.0001$). On average, mite type was not significant with respect to choice of bee ($F_{2,110} = 0.56$, $P = 0.5712$); however, there was a strong interaction effect on mite choice between mite type∗time ($F_{2,609} = 5.03$, $P = 0.0068$).

Over time, postpartum mites demonstrated a trending preference for newly emerged homocolonial bees (Fig. 1, Table 2); this was significantly the case when the comparison was against heterocolonial pollen foragers ($t_{609} = 3.03$, $P = 0.0025$), but the comparison was not significant against homocolonial pollen foragers ($t_{609} = 1.57$, $P = 0.1163$).

Prepartum mites also demonstrated a trending preference for newly emerged homocolonial bees over time (Fig. 2, Table 3); in contrast to the postpartum mites, this was true whether the comparison was against heterocolonial pollen foragers ($t_{609} = 3.40$, $P = 0.0007$) or homocolonial pollen foragers ($t_{609} = 3.69$, $P = 0.0002$).

The interaction between mite type∗time is apparent when comparing Figs 1 and 2; a divergent preference for newly emerged homocolonial bees was earlier and more strongly sustained in prepartum mites than in postpartum mites. Moreover, when we compared mite choice over time between pre- and postpartum mites, we found that the probability of a prepartum mite choosing a pollen forager decreased significantly faster than for postpartum mites. This was true for both heterocolonial pollen foragers ($t_{609} = 1.94$, $P = 0.05$) and homocolonial pollen foragers ($t_{609} = 2.82$, $P = 0.005$).

DISCUSSION

Our results indicate strong differences in risk tolerance between prepartum and postpartum varroa mites, an effect consistent with our hypothesis that differences in dispersal risk tolerance are mediated by reproductive value. Prepartum mites, with higher reproductive value, exhibit low risk tolerance and a more discriminating preference for 'safe' house bees. In contrast, postpartum mites, with comparatively lower reproductive value, show a greater tolerance for 'riskier' forager bees.

Dispersal in the mite *V. destructor* is usually explained as a product of extrinsic, host-centric drivers of the kind classically explained by SIR models (see Introduction). However, in the honeybee superorganism, host state must be considered for at least three levels: colony density at a landscape scale, colony state and the state of individual bees within a colony. There is evidence that *V. destructor* is sensitive to cues across all three levels.

At the landscape scale, host (colony) spatial density is an important dispersal regulator, with evidence that mite dispersal and virulence are encouraged in high-density apiaries like those used in modern beekeeping (Frey & Rosenkranz, 2014; Greatti, Milani, & Nazzi, 1992; Nolan & Delaplane, 2017). At the colony level, decreasing ratios of bee brood cells to mites can promote resource-limited reproductive competition (Eguaras, Marcangeli, & Fernandez, 1994), a condition especially acute in late season when brood area in bee colonies is naturally contracting. Competition is a strong driver for dispersal evolution, especially when conditions at population margins encourage high kinship (Cote et al., 2007; Hamilton & May, 1977; Kubisch et al., 2013). Although genetic variation is low in the two most globally dispersed clones of *V. destructor* (Solignac et al., 2005), local genetic variation remains detectable between apiaries, between

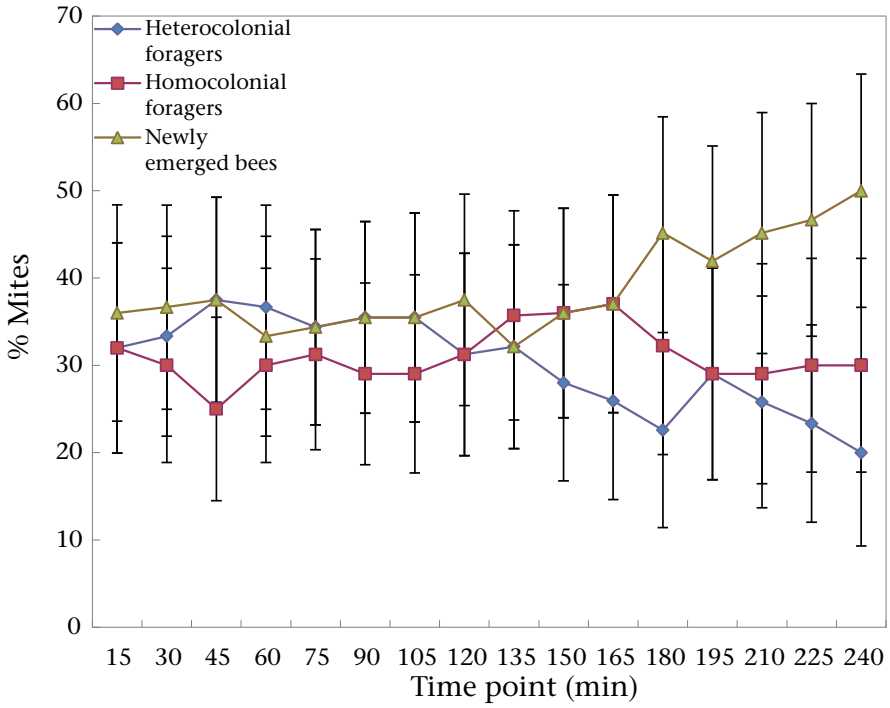

Figure 1. Mean ± SE percentage of postpartum mites on different bee types (heterocolonial foragers, homocolonial foragers, newly emerged homocolonial workers) over 240 min.

Table 2
Data for postpartum mites

Time (min)	Bee type			
	Newly emerged worker	Homocolonial forager	Heterocolonial forager	Grand total
15	9	8	8	25
30	11	9	10	30
45	12	8	12	32
60	10	9	11	30
75	11	10	11	32
90	11	9	11	31
105	11	9	11	31
120	12	10	10	32
135	9	10	9	28
150	9	9	7	25
165	10	10	7	27
180	14	10	7	31
195	13	9	9	31
210	14	9	8	31
225	14	9	7	30
240	15	9	6	30

Data are numbers of mites phoretic on target bee in petri dish trials. These are the source of percentages given in Fig. 1. There were 36 postpartum mites used in assays (see Table 1); when a mite was not phoretic on a bee it was not included in analyses for that time point. Three postpartum mites were never located on a bee at any of the 16 time points.

colonies within an apiary, and even within colonies (Dynes et al., 2016), suggesting that kinship-mediated dispersal could be selected for in this species. And finally, there is evidence that *V. destructor* modulates its dispersal strategy in response to individual bees. It is well established that phoretic *V. destructor* prefer young bees over older cohorts (Del Piccolo et al., 2010; Kraus, Koeniger, & Fuchs, 1986; Kuenen & Calderone, 1997; present study); this is generally understood as a strategy for optimizing the mite's chance for dispersing to an open cell of brood, as it is the younger bees that are more likely to linger in the brood nest.

Interestingly, there is evidence that *V. destructor* is sensitive to cues interacting across these host levels. Cervo et al. (2014) showed that phoresy-seeking mites become less 'choosy' of host bees in colonies with high mite populations; in such colonies the chemical profiles that mites use to discriminate nurse bees from foragers (Del Piccolo et al., 2010) become confounded. A greater tolerance for, or an inability to discriminate against, older forager bees could be adaptive if it promotes mite dispersal away from collapsing colonies.

In contrast to these emphases on host-centric drivers of dispersal evolution, our study focuses on the intrinsic factor parasite reproductive value. A dispersing mite subpopulation was implicated by Kuenen and Calderone (1997), who performed an assay similar to ours and with mites of unknown age, and found that mites chose forager bees 20% of the time. Our study suggests that such forager-choosing mite cohorts are biased towards older postpartum mites. The results of Cervo et al. (2014) suggest that an interaction of colony state and bee state can also tilt mite choice towards foragers. We did not characterize state of colony of origin in our laboratory assays; however, neither was colony of origin ($N = 4$) a significant effect in our analyses, reinforcing our confidence that mite effects in our study are unambiguous. It remains that postpartum mites exhibit a sharp reduction in reproductive success after the first reproductive cycle (DeRuijter & Calis, 1988; Fries et al., 1994); this reduction in reproductive value has the effect of lowering relative costs for risky behaviour. A dangerous bid for dispersal may be adaptive if the individual has already successfully reproduced and the rewards for successful dispersal are sufficiently large, in this case, uninfested honeybee brood, a virtually limitless reproductive resource for the risk-taker's progeny.

What the state of experimental science is suggesting at this point is that parasite dispersal is a product of complex interactions across drivers. In the case of the *A. mellifera*–*V. destructor* system, there are at least three levels of biological organization at which parasite dispersal is responsive to host state: colony spatial density, colony (superorganism) and individual bee. We know of at least one

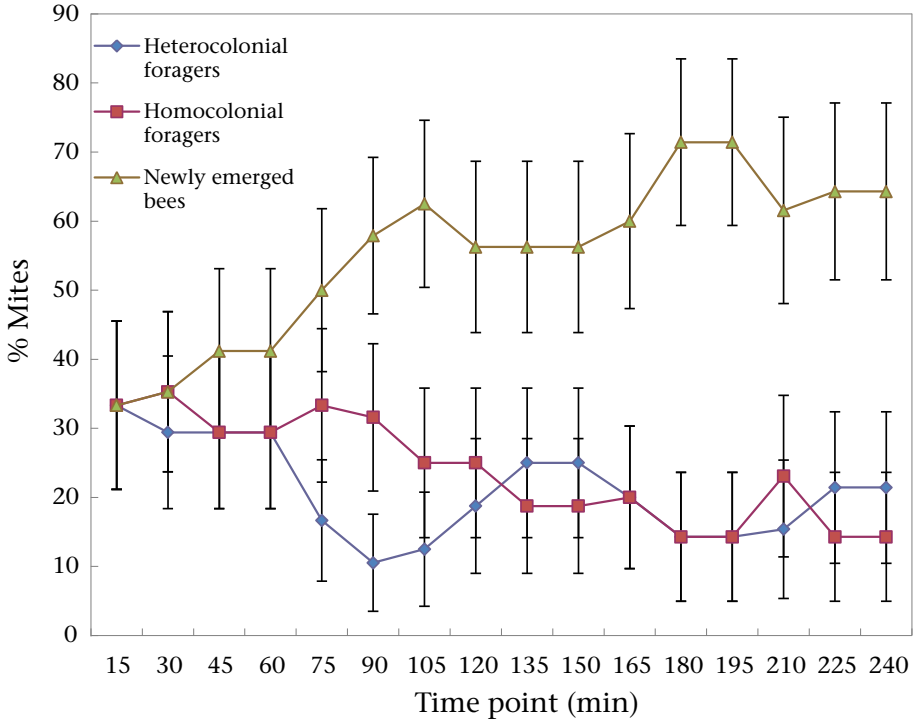

Figure 2. Mean ± SE percentage of prepartum mites on different bee types (heterocolonial foragers, homocolonial foragers, newly emerged homocolonial workers) over 240 min.

Table 3
Data for prepartum mites

Time (min)	Bee type			
	Newly emerged worker	Homocolonial forager	Heterocolonial forager	Grand total
15	5	5	5	15
30	6	6	5	17
45	7	5	5	17
60	7	5	5	17
75	9	6	3	18
90	11	6	2	19
105	10	4	2	16
120	9	4	3	16
135	9	3	4	16
150	9	3	4	16
165	9	3	3	15
180	10	2	2	14
195	10	2	2	14
210	8	3	2	13
225	9	2	3	14
240	9	2	3	14

Data are numbers of mites phoretic on target bee in petri dish trials. These are the source of percentages given in Fig. 2. There were 33 prepartum mites used in assays (see Table 1); when a mite was not phoretic on a bee it was not included in analyses for that time point. Nine prepartum mites were never located on a bee at any of the 16 time points.

interaction among these levels, colony∗bee (Cervo et al., 2014). We know of at least one intrinsic dispersal driver, mite reproductive value (this study), and have reason to predict a second, kin structure of mite populations (Cote et al., 2007; Hamilton & May, 1977; Kubisch et al., 2013). It seems likely that similar conditions will apply generally to other host–parasite systems.

The non-natural *A. mellifera*–*V. destructor* relationship makes a good model system for analysing these terms and interactions in general and reproductive value in particular. The mite is obligate on its bee host, restricted (at least outside of Asia) to *A. mellifera*, capable of multiple broods with a sharp drop in reproductive value after the first, and capable of dispersing to new hosts (bee colonies). Moreover, the dispersal is risky: on average, the number of phoretic mites per bee drops by nearly half in foragers returning to their colony compared to foragers leaving their colony (Kralj & Fuchs, 2006). Given that bee drift and robbing behaviour to other colonies are not default behaviours, it is plain that the majority of this difference represents mite field attrition and mortality. Also, a body of work on extrinsic drivers for *Varroa* dispersal is available for comparing with intrinsic drivers. And finally, the manageability of the bee host simplifies controlled experiments for testing this hypothesis and subsequent tests of fitness and costs.

Dispersal evolution is an active field of research, compelled in no small part by the expediencies of epidemics and biodiversity threats. Dispersal is not only a rapidly evolving trait, especially in invasive species (Alford, Brown, Schwarzkopf, Phillips, & Shine, 2009), but experimental science has exposed potential interactions, not only between extrinsic and intrinsic drivers of parasite dispersal, but also, as the honeybee superorganism example teaches us, across levels of biological organization.

In conclusion, we present evidence that dispersal in the parasitic mite *V. destructor* is a product not only of extrinsic host-centric drivers, but also the intrinsic driver parasite reproductive value. Postpartum mites with lower reproductive value showed a comparatively greater propensity to parasitize high-risk forager bees, affording these risk-takers opportunity to emigrate to new resources at a landscape scale. If Goodman (1982, p. 804) is correct that 'reproductive value, when properly formulated, is the fundamental quantity which is maximised at every optimisation of a life history', then we can expect parasites to evolve dispersal mechanisms that optimize trade-offs between risk taking and potential future reproduction. This study sustains that premise.

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