

Parasitization of bats by bat flies (Streblidae) in fragmented habitats

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Abstract

Parasites represent a large fraction of the world's biodiversity. They control host population sizes and contribute to ecosystem functioning. However, surveys on species diversity rarely include parasitic species. Bats often present traits favoring parasite diversity, such as large home ranges, long life spans, and large colonies. The most conspicuous bat parasites are the highly host-specific, blood-sucking bat flies (Diptera: Streblidae, Nycteribiidae). Recent studies have found a direct effect of habitat alteration on the abundance of bat species. We expected, therefore, that changes in the host community in response to anthropogenic habitat modification will also result in changes in the associated parasite community. We captured bats in three different habitats in Central Panama between 2013 and 2015. We recorded information on prevalence and intensity of bat fly parasitization of the seven most commonly captured bat species. Prevalence and intensity were both significantly influenced by roost type, abundance, and host sex and age. We found that habitat variables and matrix type significantly influenced the prevalence and intensity of parasitization, while the direction of the responses was host species- and parasite species-specific. In general, roosting conditions and behavior of host bats appear to be fundamental in explaining changes in prevalence and intensity of parasitization between different habitat types, as bat flies are bound to the roost during their reproductive cycle. Habitat alterations affect next to the host community composition also the availability of possible roost structures as well as microclimatic conditions, which all three reflect in parasitization.

Abstract in Spanish is available with online material.

KEYWORDS

bat flies, bats, Central America, ectoparasites, habitat fragmentation, Streblidae

1 | INTRODUCTION

Parasites are highly speciose, with species numbers approaching the number of free-living species (Price, 1980; Windsor, 1998).

Parasites can affect their hosts in many ways, inducing regulative negative feedback loops that maintain the stability and integrity of ecosystems and contribute to ecosystem functioning (Brooks & Hoberg, 2001; Frainer, McKie, Amundsen, Knudsen, & Lafferty,

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2018; Hudson, 2005). Among other functions, parasites may control host population sizes (Anderson & May, 1979) by reducing reproduction, increasing predation risk, and even altering host morphology and mating behavior (Frainer et al., 2018). In spite of their ecological importance, few parasite taxa have been studied in detail, while for most groups estimates of parasite species richness and diversity are lacking (Poulin, 2014). Despite being key components of biodiversity (Christe, Morand, & Michaux, 2006), parasites are underrepresented both in taxonomic studies and in species diversity surveys (Wibbelt, Speck, & Field, 2009).

Diversity of parasites is influenced by several host-dependent traits such as host longevity, home range, and group size (Krasnov, Poulin, & Morand, 2006). Bats (Chiroptera) are the second most speciose mammalian order after rodents. They show nightly commuting flight distances of up to 100 km (Medellin et al., 2018) and have a very long life expectancy compared to other similar-sized mammals (Seim et al., 2013). Some species roost in large—often multispecies—assemblages of thousands or even millions of individuals (Kunz & Lumsden, 2003; Luis et al., 2013). Bats show great variation in these traits, which in turn likely drives the great diversity found in bat-associated parasites.

The obligate, blood-sucking bat flies (Diptera: Nycteribiidae and Streblidae) are certainly the most conspicuous ectoparasites of bats. They are highly host-specific, spend most of their life on their host, and die within hours if separated (Dittmar, Morse, Dick, & Patterson, 2015; Overall, 1980). They only leave their bat host to deposit a 3rd instar larvae, which has developed within its mother's oviduct and pupates directly on a surface within the bat's roost (Dittmar et al., 2015). Many bat flies are strictly bound to a single bat species, while their bat hosts in turn can be associated with a small number of different bat fly species (Dick & Gettinger, 2005; Wenzel, 1976; Wenzel, Tipton, & Kiewlicz, 1966). Morphological adaptations of bat flies to different habitats on the bat host (Dick, 2005; Hiller, Honner, Page, & Tschapka, 2018), such as the furry body or the hairless wing membranes, reflect resource partitioning among parasites and allow for the coexistence of various bat fly species on a single host individual (Dick & Gettinger, 2005; Patterson, Dick, & Dittmar, 2009; Tello, Stevens, & Dick, 2008; Wenzel, 1976; ter Hofstede, Fenton, & Whitaker, 2004; Wenzel et al., 1966). Bat flies most likely comprise a monophyletic clade, currently including the monophyletic family Nycteribiidae within the polyphyletic family Streblidae (Dittmar et al., 2015; Dittmar, Porter, Murray, & Whiting, 2006). Corresponding to the diversity patterns of their hosts, bat flies are most diverse in tropical regions (Stevens, 2004). More than 80% of the nycteribiids are found in the Old World tropics, mainly in the Indo-Malayan and Australasian regions, while 70% of the streblids occur in the Neotropics (Haelewaters, Hiller, & Dick, 2018), where they mostly parasitize the highly diverse family of Neotropical leaf-nosed bats (Phyllostomidae) (Dick & Gettinger, 2005; Wenzel, 1976; Wenzel et al., 1966).

Phyllostomids are not only the most commonly caught bats in the Neotropics (Kalko, Handley, & Handley, 1996; Meyer & Kalko, 2008; S. D. Brändel personal communication), but are also the ecologically

most diverse in their feeding habits. Different species feed on insects, small vertebrates, nectar, fruits, and even blood (Giannini & Kalko, 2004). The diversity in their foraging behavior makes them an important component of natural systems, as they perform critical ecosystem functions such as arthropod predation, pollination, and seed dispersal (Cunto & Bernard, 2012; Jones, Jacobs, Kunz, Willig, & Racey, 2009). Phyllostomid bats show guild-dependent reactions to habitat alterations (Meyer & Kalko, 2008; Rocha et al., 2017; S. D. Brändel personal communication). While specialized, gleaning animalivorous forest species decrease in abundance with the loss of pristine, old growth forest, frugivorous species that are more generalized in their habitat and roosting requirements show increased numbers in response to anthropogenic change (Meyer & Kalko, 2008; S. D. Brändel personal communication). These guild-specific responses to habitat change allow us to use the diversity and abundance of phyllostomid species as biological indicators for habitat health (Medellin, Equihua, & Amin, 2000). In general, changes in the host community will also cause changes in the associated local parasite community. Therefore, parasite communities may also be indicative of the general health of an ecosystem (Hudson, Dobson, & Lafferty, 2006; Marcogliese, 2005). In the case of parasites with a high host specificity and direct development, such as the bat fly families Nycteribiidae and Streblidae, parasite communities may be excellent indicators for the health of host populations (Bush, Reed, & Maher, 2013). Using a dataset from the 1970s, Pilosof, Dick, Korine, Patterson, and Krasnov (2012) showed that the intensity of parasitization of bats was positively or negatively correlated with anthropogenic disturbance, depending on the host species. Recent studies from Costa Rica and Mexico further showed bat flies respond differently to habitat fragmentation, depending on the host species and the sex of the host individual (Bolívar-Cimé et al., 2018; Frank, Mendenhall, Judson, Daily, & Hadly, 2016). This suggests complex interactions between bat flies and their mammalian hosts, where various variables may influence the parasites' life cycle and natural history.

In this study, we focus on the response of bat flies to habitat alteration based on a standardized sampling of bats in three different habitat types: continuous forest, forest fragments surrounded by water, and forest fragments in an agricultural matrix. By including intrinsic factors and habitat characteristics, we cover a wide range of variables known to affect parasitization by bat flies (Bolívar-Cimé et al., 2018; Patterson, Dick, & Dittmar, 2008a; Pilosof et al., 2012) with the aim of disentangling the effects of habitat fragmentation on the prevalence and intensity of parasitization. We expect that bats using more permanent roosting structures will harbor more bat flies as these offer more stable host populations (Patterson et al., 2008a) as well as microclimatic conditions favoring parasite development (Dube, Hund, Turbek, & Safran, 2018). Female and juvenile bats should be infested with bat flies more often and in higher intensities as they roost predominantly in year-round stable groups together with their offspring, offering parasites a reliable food source (summarized in Frank et al., 2016). Further, as habitat fragmentation has been shown to

cause chronically elevated stress levels, impairing the hosts' immune systems and making them more receptive to parasitization (Christe, Arlettaz, & Vogel, 2000; Guerrero, 1994b; Lourenço & Palmeirim, 2008; Seltnann et al., 2017), we expect to find bats infested with bat flies more often and in higher intensities in the fragmented habitats compared to continuous forest sites.

2 | METHODS

2.1 | Study area

Bats were captured with mistnets between 2013 and 2015 in Central Panama in continuous forest ($n = 5$ sites) and in forest fragments surrounded by agricultural landscape ($n = 3$, 1.5–51 ha) or water ($n = 6$, 5.2–17.5 ha) (see Figure S1). Differences between fragment types are principally due to the respective interpatch landscape. Continuous forest sites located in the protected area of the Barro Colorado Nature Monument were treated as a control group to both types of fragments. For each capture location, we estimated three vegetation structure variables (canopy cover, canopy height, and understory density), and at the six positions, our mistnets were located. To assess canopy cover, we took readings facing N, S, E, and W with a hand-held convex densiometer (Forestry Suppliers, Inc.). Canopy height was measured using a laser distance meter (Leica, DISTO classic5 Hand Lasermeter). We further estimated the understory density at five different altitudinal levels by using a self-made densiometer adapted after Nudds (1977) with each field subdivided into nine rectangles.

Nets were checked in intervals of 15–20 min, and the captured bats were kept in individual soft cotton bags until processing. We recorded standard body measurements as well as age, sex, and reproductive status. Additionally, wings as well as the dorsal and ventral pelage of every bat were thoroughly examined for bat flies. Whenever possible, all bat flies on an individual bat were collected with entomological forceps and stored in individual vials containing 96% ethanol. In cases when the bat flies were not collected, the presence or absence of bat flies was noted. All collected bat flies were counted and identified in the laboratory to species level (Guerrero, 1993, 1994a, 1994b, 1995a, 1995b, 1996, 1997, 1998; Wenzel, 1976; Wenzel et al., 1966). A manuscript listing all host-parasite associations is currently in preparation by the authors. In this study however, we focused our analysis on the seven most commonly captured bat species in all three habitat types: *Artibeus jamaicensis*, *A. lituratus*, *Carollia castanea*, *C. perspicillata*, *Dermanura rava*, *D. watsoni*, and *Uroderma bilobatum* (Hiller, Brändel, Honner, Page, & Tschapka, 2019a).

2.2 | Data analysis

All statistical analyses were performed using the open source statistical software R (R Core Team, 2019, version 3.4.4). To identify

the variables influencing the presence and the intensity of parasitization by bat flies, we used generalized mixed effect models (glmer() and glmer.nb(), package lme4, Bates, Sarkar, Bates, & Matrix, 2017).

We included host sex, host *reproductive stage*, type of *landscape*, *canopy height* and *canopy cover*, *understory density*, host *abundance*, and *longevity of roost used by host bats* as explaining variables. We combined age and reproductive status of the bat hosts as non-reproductive (=NR) juveniles, NR subadults, NR adults, and reproductive adults (scrotal males or pregnant and lactating females), to avoid creating unique variable combinations, as, for example, juveniles can never be reproductively active. The variables *canopy* and *understory* were extracted for each capture location from principal component analyses, containing measurements of canopy height, canopy cover, and understory density (prcomp(), R-package stats). Host *abundance* is a relative measure, based on the capture rate of a single species during a standardized mist netting study (S. D. Brändel personal communication), and is here used as a proxy for the abundance of a given bat species. The variable *roost duration* described the endurance of roost types reported to be used by each bat species and is based on values suggested by Patterson, Dick, and Dittmar (2007) for bats in Venezuela. Hereby, each roost type has been ranked into one of six categories based on duration and enclosure, with Rank 1 = 0–10¹ days, Rank 2 = 11–10² days... Rank 6 = 100 001–10⁶ days. Both obligate tent-roosting *Dermanura* species (Rodríguez-Herrera et al., 2007) captured during this study do not occur in Venezuela; wherefore, we used the value reported for the closely related species *D. glauca* and *D. gnoma*. To control for differences in magnitude, all metric variables were standardized in our analyses. Finally, we included the random intercept *capture location* nested within *landscape* to address spatial autocorrelation as suggested by Zuur, Ieno, and Elphick (2010) as well as the random intercept *bat species* nested within *capture locations* to account for variability of parasitization within a host species between capture locations.

Besides the “all-species approach,” we assessed individual host species responses by using the same model structure, however omitting the variable *roosting* as well as the random intercept *bat species*. We further omitted levels of categorical variables if they were represented by fewer than 10 individuals to avoid statistical restrictions. We further conducted analyses for the three most common bat fly species (*Megistopoda aranea* and *Aspidoptera phyllostomatis* on *A. jamaicensis*, and *Trichobius joblingi* on *C. perspicillata*) using the same model structure as for intensity analyses on host species level.

Before fitting the models, we conducted extensive data exploration, following Zuur et al. (2010). We included collinear variables following Bolker (2019) and Graham (2003). We created a list of candidate models, ranked by AICc (dredge(), package MuMIn (Barton, 2018), and generated for the best fits ($\Delta AIC < 2$) an average model (model.avg(), package MuMIn). For each candidate model, we calculated pseudo R-squared values to estimate goodness of fit (r.squaredGLMM(), R-package MuMIn (Barton, 2018)).

3 | RESULTS

3.1 | Prevalence of parasitization

We recorded the presence or absence of bat flies in 3,456 individual bats and found prevalence values between 6.8% (*D. watsoni*) and 69.3% (*C. perspicillata*) (Table 1). Our analyses revealed three candidate models that explained equally well the prevalence of parasitization in a combined dataset of all host bat species (Table S1). Model averaging resulted in three variables significantly affecting the prevalence of parasitization by bat flies, namely host sex, abundance, and roost duration (Table 2). Males were less frequently parasitized than females, while roost longevity had a significant positive effect, with bat species using more permanent roosts showing a higher parasite prevalence. Further, bat abundance had also a significant positive effect on prevalence, with more abundant bats showing a higher bat fly prevalence.

We excluded subadult bats of *A. lituratus*, *C. castanea*, and *U. bilobatum* as well as individuals of *C. perspicillata* captured on islands for analyses on host species level due to insufficient sample sizes ($n < 10$). For both *Dermanura* species, the null model was the best model. All candidate models used in the following analyses can be found in Table S1.

Like in the all-species approach, host sex had a significant effect on prevalence in *A. jamaicensis* and *A. lituratus*, with females having more bat flies than males. Age had a significant effect only in *C. castanea* with juveniles having a lower prevalence than non-reproductive adults. Next to these intrinsic factors, host abundance had a significant negative effect on prevalence for *A. jamaicensis* and *C. perspicillata*. The variable canopy had a significant positive effect on prevalence for *A. jamaicensis* while it had a significant negative effect for *C. castanea*. The only host species showing a matrix effect was *A. jamaicensis*, with significantly lower prevalence in forest fragments surrounded by agricultural matrix and significantly higher prevalence in fragments surrounded by water, both compared to continuous forest.

3.2 | Intensity of parasitization

Complete parasite loads were collected from a total of 1,283 bats, amounting to 2,674 individual parasites obtained from 11 species. The intensity of parasitization varied greatly between host bat species, ranging from a mean of 1.1 (*D. watsoni*) to 2.9 (*C. perspicillata*) bat flies per host bat (Table 1). We identified six candidate models explaining equally well the intensity of bat fly infestation in our all-species approach (Table 3). Model averaging resulted in three variables significantly explaining the infestation intensity: reproductive status/age, sex, and roost longevity. Specifically, juvenile bats had more parasites than non-reproductive adults, and adult females had more parasites than adult males. Further, the more stable the roosting structure used by a bat species, the higher was its bat fly load.

For analyses on host species level, we had to exclude individuals of *C. perspicillata* captured on islands due to insufficient sample size ($n < 10$). For *C. castanea*, the null model was the most explanatory model. For the bat species roosting in foliage and in leaf tents (*A. lituratus*, *D. rava*, *D. watsoni* and *U. bilobatum*), we found a very low prevalence of parasitization: There were so few with bat flies that we could not conduct further meaningful analyses ($n = 30$, $n = 12$, $n = 9$, and $n = 31$, respectively).

Artibeus jamaicensis and *C. perspicillata* mirrored the results of the “all-species approach,” with juveniles having significantly more parasites than non-reproductive adults. Additionally, *A. jamaicensis* males showed lower infestation levels than females. Further, understory density had a negative effect on parasitization intensity in *A. jamaicensis*, with higher infestation rates at lower understory density. Finally, *A. jamaicensis* showed, as in the prevalence analysis, a matrix effect, with animals from fragments surrounded by agricultural matrix being less infested than individuals caught in continuous forest sites.

3.3 | Parasite species-specific response

Due to sample size, an analysis on parasite species level was only possible for bat flies of the two most common bat species: *A. jamaicensis* (streblid flies *M. aranea* and *A. phyllostomatis*, 49.5% and 48.3% of total amount, respectively) and *C. perspicillata* (streblid fly *T. joblingi*, 85.3%). The results we obtained in the model for *T. joblingi* differed from the results of the model including all bat fly species on *C. perspicillata*. We found a significant influence of host sex, with female *C. perspicillata* being infested by bat flies to a higher degree than male *C. perspicillata*. Both bat fly species of *A. jamaicensis* (*M. aranea* and *A. phyllostomatis*) mirrored this result and further showed a significant effect of reproductive status, with juveniles presenting significantly higher parasite load than non-reproductive adults. Understory density was only significantly affecting the intensity of parasitization with *A. phyllostomatis*, with lower intensity at higher levels of understory density. Interestingly, no matrix effect was detected for parasitization by neither *M. aranea* nor *A. phyllostomatis*, while there was a significant habitat effect for the total bat fly count of *A. jamaicensis*.

4 | DISCUSSION

In this study, we addressed the effects of intrinsic factors as well as of habitat fragmentation on the prevalence and intensity of parasitization of Neotropical bats by bat flies. We focused on the six phyllostomid bat species most commonly captured with a mistnetting approach in three landscapes varying in degree of fragment isolation. In our “all-species approach,” neither the surrounding matrix nor the habitat variables showed a significant effect on prevalence and intensity of parasitization. Significant effects were detected only at the host species level. The detected effects varied between host species, suggesting species-specific effects on parasitization (Pilosof et al., 2012).

TABLE 1 Summary of bat species used in analyses showing number of bats examined, number of parasite samples collected and resulting values for prevalence (% of infested bats), and mean intensity (number of bat flies recorded per infested bat) over the three habitat types, as well as associated roost duration (adapted from Patterson et al., 2007)

Bat species	Number of bats examined	Number of bats with bat flies	Prevalence (%)	Number of parasite samples	Total bat fly count	Mean intensity	Roost duration and protection
<i>A. jamaicensis</i>	2,201 (1236/965)	1,038 (653/385)	47.2 (52.8/39.9)	910 (576/334)	1844 (1245/599)	2.0 (2.2/1.8)	2.00
Continuous	1,027 (590/437)	500 (314/186)	48.7 (53.2/42.6)	445 (282/163)	915 (609/306)	2.1 (2.2/1.9)	
Agricultural matrix	241 (142/99)	63 (47/16)	26.1 (33.1/16.2)	60 (45/15)	99 (81/18)	1.7 (1.8/1.2)	
Islands	933 (504/429)	475 (292/183)	50.9 (57.9/42.7)	405 (249/156)	830 (555/275)	2.0 (2.2/1.8)	
<i>A. lituratus</i>	302 (163/139)	32 (26/6)	10.6 (16.0/4.3*)	30 (26/4)	35 (30/5)	1.2 (1.2/1.3*)	1.33
Continuous	137 (78/59)	13 (10/3)	9.5 (12.8/5.1*)	12 (10/2)	13 (11/2)	1.1 (1.1/1.0*)	
Agricultural matrix	54 (25/29)	7 (6/1)	13* (24.0*/3.4*)	7 (6/1)	9 (7/2)	1.3* (1.2*/2.0*)	
Islands	111 (60/51)	12 (10/2)	10.8 (16.7/3.9*)	11 (10/1)	13 (12/1)	1.2 (1.2/1.0*)	
<i>C. castanea</i>	216 (93/123)	92 (39/53)	42.6 (41.9/43.1)	87 (38/49)	160 (71/89)	1.8 (1.9/1.8)	4.16
Continuous	101 (48/53)	35 (19/16)	34.7 (39.6/30.2)	34 (19/15)	55 (29/26)	1.6 (1.5/1.7)	
Agricultural matrix	97 (38/59)	46 (16/30)	47.4 (42.1/50.8)	44 (16/28)	88 (37/51)	2.0 (2.3/1.8)	
Islands	18 (7/11)	11 (4/7)	61.1 (57.1/63.6*)	9 (3/6)	17 (5/12)	1.9* (1.7*/2.0*)	
<i>C. perspicillata</i>	293 (164/129)	203 (117/86)	69.3 (71.3/66.7)	192 (110/82)	549 (343/206)	2.9 (3.1/2.5)	3.91
Continuous	127 (71/56)	87 (49/38)	68.5 (69.0/67.9)	82 (46/36)	243 (153/90)	3.0 (3.3/2.5)	
Agricultural matrix	160 (89/71)	113 (65/48)	70.6 (73.0/67.6)	108 (62/46)	300 (184/116)	2.8 (3.0/2.5)	
Islands	6 (4/2)	3 (3/0)	50.0* (75.0*/0*)	2 (2/0)	6 (6/0)	3.0* (3.0*/NA)	
<i>D. rava</i>	98 (42/56)	12 (4/8)	12.2 (9.5*/14.3*)	12 (4/8)	15 (5/10)	1.3 (1.3*/1.3)	1.00
Continuous	29 (11/18)	5 (1/4)	17.2* (9.1*/22.2*)	5 (1/4)	8 (2/6)	1.6* (2.0*/1.5*)	
Agricultural matrix	32 (16/16)	1 (1/0)	3.1* (6.3*/0)	1 (1/0)	1 (1/0)	1.0* (1.0*/NA)	
Islands	37 (15/22)	6 (2/4)	16.2* (13.3*/18.2*)	6 (2/4)	6 (2/4)	1.0* (1.0*/1.0*)	
<i>D. watsoni</i>	132 (46/86)	9 (2/7)	6.8* (4.3*/8.1*)	7 (2/5)	8 (3/5)	1.1* (1.5*/1.0*)	1.00
Continuous	54 (20/34)	3 (1/2)	5.6* (5.0*/5.9*)	2 (1/1)	3 (2/1)	1.5* (2.0*/1.0*)	
Agricultural matrix	68 (24/44)	6 (1/5)	8.8* (4.2*/11.4*)	5 (1/4)	5 (1/4)	1.0* (1.0*/1.0*)	
Islands	0 (0/0)	0 (0/0)	NA	0 (0/0)	0 (0/0)	NA	
<i>U. bilobatum</i>	10 (2/8)	46 (13/33)	21.5 (13.5/28.0)	45 (13/32)	63 (19/44)	1.4 (1.5/1.4)	1.00
Continuous	214 (96/118)	13 (3/10)	23.6 (13.0*/31.3)	13 (3/10)	22 (8/14)	1.7 (2.7*/1.4)	
Agricultural matrix	55 (23/32)	4 (4/0)	6.9* (9.5*/0)	4 (4/0)	4 (4/1)	1.0* (1.0*/NA)	
Islands	58 (42/16)	29 (6/23)	28.7 (19.4*/32.9)	28 (6/22)	37 (7/30)	1.3 (1.2*/1.4)	

Note: Numbers in parenthesis reflect sex-dependent values (females/males) while an asterisk (*) marks values with $n < 10$.

TABLE 2 Obtained parameters of the averaged candidate models ($\Delta AIC < 2$) addressing the prevalence of parasitization by bat flies for the all-species approach as well as on bat species level

		Landscape matrix		Sex		Reproductive status/age					Canopy	Understory	Abundance	R	Roost duration
		agriculture	water	M	NRJ	NRSA	NRJ	NRSA	R	Abundance					
All species	Intercept	-0.3084	-0.4892	-0.4064	0.1487	-0.1719	-0.1639	0.5297	0.0366	-0.1503	0.6598				
	Estimate	0.2101	0.3212	0.0800	0.1177	0.1458	0.0973	0.1336	0.1032	0.1461	0.0748				
	SE	0.2102	0.3213	0.0801	0.1178	0.1459	0.0974	0.1337	0.1033	0.1461	0.0748				
	Adj. SE	1.4670	1.5220	5.0770	1.2630	1.1790	1.6830	3.9630	0.3540	1.0280	8.8220				
	p-Value	.1423	.1279	<.0001	.2067	.2385	.0924	<.0001	.7231	.3037	<.0001				
<i>A. jamaicensis</i>	Intercept	0.0038	-0.5770	-0.5618	0.2636	-0.1686	-0.0939	0.2108	0.0359	0.2108	-				
	Estimate	0.1252	0.2314	0.0952	0.1368	0.1603	0.1203	0.0581	0.0556	0.0782	-				
	SE	0.1253	0.2315	0.0952	0.1369	0.1604	0.1204	0.0581	0.0556	0.0783	-				
	Adj. SE	0.0300	2.4930	5.8990	1.9260	1.0510	0.3260	2.5030	0.6460	2.6920	-				
	p-Value	.9760	.0127	<.0001	.0541	.2933	.7442	.0123	.5180	.0071	-				
<i>A. lituratus</i>	Intercept	-1.5789	-	-1.3899	-0.1311	-	-0.7409	0.0786	-	-0.2008	-				
	Estimate	0.2494	-	0.4940	0.6238	-	0.4518	0.1927	-	0.1943	-				
	SE	0.2503	-	0.4960	0.6264	-	0.4537	0.1935	-	0.1952	-				
	Adj. SE	6.3090	-	2.8020	0.2090	-	1.6330	0.4060	-	1.0290	-				
	p-Value	<2e-16	-	.0051	.8342	-	.1024	.6845	-	.3035	-				
<i>C. castanea</i>	Intercept	-0.2337	-	-	-1.2144	-	0.1759	-	-	-0.3625	-				
	Estimate	0.2322	-	-	0.5482	-	0.3106	-	-	0.1620	-				
	SE	0.2336	-	-	0.5515	-	0.3124	-	-	0.1630	-				
	Adj. SE	1.0000	-	-	2.2020	-	0.5630	-	-	2.2240	-				
	p-Value	.3171	-	-	.0277	-	.5730	-	-	.0262	-				
<i>C. perspicillata</i>	Intercept	1.0129	0.1442	-0.0903	0.9796	0.2021	-0.5458	-0.4582	0.3128	-0.4099	-				
	Estimate	0.2615	0.4219	0.2754	0.5793	0.6989	0.2867	0.2276	0.2094	0.3047	-				
	SE	0.2626	0.4238	0.2766	0.5818	0.7019	0.2879	0.2286	0.2100	0.3055	-				
	Adj. SE	3.8580	0.3400	0.3270	1.6840	0.2880	1.8960	2.0040	1.4890	1.3420	-				
	p-Value	.0001	.7337	.7440	.0922	.7734	.0580	.0451	.1360	.1796	-				
<i>D. rava</i>	Null model as best model														
<i>D. watsoni</i>	Null model as best model														
<i>U. bilobatum</i>	Intercept	-1.4343	-2.3523	0.6915	-	-	-	0.6155	-0.5512	0.2859	-				
	Estimate	0.5839	1.3923	0.4123	-	-	-	0.3697	0.3016	0.5073	-				
	SE	0.5868	1.3988	0.4148	-	-	-	0.3718	0.3034	0.5105	-				
	Adj. SE	2.444	1.682	1.667	-	-	-	1.655	1.817	0.56	-				
	p-Value	.0145	.0926	.0955	-	-	-	.0978	.069	.5754	-				

Note: Significant results are presented in bold. ^a = sample size < 10, and ^b = eliminated during model averaging.

TABLE 3 Obtained parameters of the averaged candidate models ($\Delta AIC < 2$) addressing the intensity of parasitization by bat flies for the all-species approach, on bat species level, as well as on bat fly species level

	Landscape matrix			Sex		Reproductive status/age					Canopy	Understory	Abundance	Roost duration																																																													
	Intercept	Agriculture	Water	M	NRJ	NRSA	R	Canopy	Understory	Abundance					Roost duration																																																												
		Estimate	SE	Adj. SE	z Value	p-Value																																																																					
All species	0.6836	-0.1105	0.0389	-0.2130	0.3380	-0.0074	-0.0008	0.0163	-0.0537	0.0398	0.1498	0.0526	0.0828	0.0784	0.0444	0.0588	0.0334	0.0334	0.0409	0.0334	0.0317	0.0294	0.0526	0.0829	0.0785	0.0445	0.0588	0.0334	0.0334	0.0409	0.0334	0.0317	0.0295																																										
	12.9870	1.3340	0.4950	4.7900	5.7460	0.0910	0.0160	0.5130	1.6070	0.9730	5.0840	<.0001	.1820	.6200	<.0001	.9280	.9880	.1080	.3310	.1080	.6080	<.0001	0.6576	-0.2326	0.0528	-0.2522	0.3849	-0.0379	0.0545	-0.0653	0.0239	-	0.0592	0.1170	0.0580	0.0546	0.0693	0.0941	0.0675	0.0263	0.0265	0.0348	-	0.0593	0.1171	0.0580	0.0546	0.0694	0.0942	0.0676	0.0263	0.0266	0.0349	-	11.0880	1.9860	0.9100	4.6160	5.5440	0.4030	0.8060	0.7040	2.4590	0.6840	-	<.0001	.0470	.3629	<.0001	.6873	.4205	.4814	.0139	.4941	-
<i>A. jamaicensis</i>	Not enough individuals (n = 30)																																																																										
<i>A. lituratus</i>	Null model as best model																																																																										
<i>C. castanea</i>	Null model as best model																																																																										
<i>C. perspicillata</i>	1.0936	-0.0765	- ^a	-0.1888	0.2893	0.1132	-0.1526	-0.1451	-0.0903	-0.1384	-	0.1009	0.1389	- ^a	0.1056	0.1445	0.2058	0.1256	0.0756	0.0870	0.0756	0.0797	-	0.1015	0.1398	- ^a	0.1063	0.1455	0.2071	0.1264	0.0874	0.0761	0.0802	-	10.7790	0.5470	1.7760	1.9890	0.5470	1.2070	1.5830	1.1870	1.8080	-	<.0001	.5845	- ^a	.0757	.2275	.1134	.2351	.0706	-																						
<i>D. rava</i>	Null model as best model																																																																										
<i>D. watsoni</i>	Null model as best model																																																																										
<i>U. bilobatum</i>	Null model as best model																																																																										
<i>A. jamaicensis</i> – <i>M. aranea</i>	0.3505	-0.2005	-0.1156	-0.1569	0.2795	0.1139	0.0950	0.0527	-0.0323	-0.0220	-	0.0795	0.1452	0.0713	0.0737	0.0980	0.1245	0.0901	0.0356	0.0356	0.0344	-	0.0797	0.1455	0.0715	0.0738	0.0982	0.1248	0.0903	0.0357	0.0357	0.0345	-	4.4000	1.3790	2.1250	2.8470	0.9130	1.0520	0.6170	0.9050	1.5260	-	.0000	.1680	.1058	.0336	.2926	.5371	.3655	.1269	-																							
<i>A. jamaicensis</i> – <i>A. phyllostomatis</i>	0.5032	- ^b	- ^b	-0.1971	0.4182	-0.0016	0.0730	-0.0598	-0.0847	-0.0304	-	0.5032	0.0726	- ^b	0.0821	0.0994	0.1433	0.1011	0.0384	0.0384	0.0367	-	0.0728	0.1436	0.1014	0.0823	0.0997	0.1436	0.1014	0.0385	0.0385	0.0368	-	6.9090	- ^b	2.3950	4.1950	0.0110	0.7210	0.7190	2.2010	1.6260	-	<.0001	- ^b	- ^b	.0166	<.0001	.9913	.4712	.4721	.0277	.1040	-																					

(Continues)

TABLE 3 (Continued)

	Landscape matrix			Sex		Reproductive status/age						
	Intercept	Agriculture	Water	M		NRJ	NRSA	R	Abundance	Understory	Canopy	Roost duration
<i>C. perspicillata</i> - <i>T. joblingi</i>	Estimate	1.1063	-0.1773	- ^a	-0.2745	- ^b	- ^b	- ^b	-0.1398	-0.0972	-0.1108	-
	SE	0.0964	0.1285	- ^a	0.1319	- ^b	- ^b	- ^b	0.0820	0.0687	0.0907	-
	Adj. SE	0.0972	0.1297	- ^a	0.1332	- ^b	- ^b	- ^b	0.0826	0.0694	0.0917	-
	z Value	11.3870	1.3670	- ^a	2.0620	- ^b	- ^b	- ^b	1.6930	1.4010	1.2090	-
	p-Value	<.0001	.1717	- ^a	.0392	- ^b	- ^b	- ^b	.0905	.1611	.2268	-

Note: Significant results are presented in bold. ^a = sample size < 10, and ^b = eliminated during model averaging.

4.1 | Roosting behavior and host intrinsic variables

For all bat species, we identified the longevity of roost used, as well as intrinsic factors such as sex and reproductive status, as factors affecting the prevalence and intensity of parasitization (Frank et al., 2016; Patterson et al., 2007; Pilosof et al., 2012). The more stable the roost used by the host bats, the higher the prevalence and the intensity of parasitization by bat flies in Belize, Venezuela, and Mexico (Bolívar-Cimé et al., 2018; ter Hofstede & Fenton, 2005; Patterson et al., 2007). This relation can be explained by the life history of bat flies, which must leave their host bat to deposit a pupa on a surface within the roost (Dittmar et al., 2015; Wenzel et al., 1966). It is then critical for the freshly emerged fly imago to find a host. Here, more permanent roosts, such as caves or hollow trees, are more likely to harbor a stable host bat population with individuals to colonize, compared to more ephemeral and often smaller tent or foliage roosts. While some hollow trees and particularly cave roosts can be used by bats for hundreds of years, leaf tents are usually abandoned within weeks or months after construction (Kunz & Lumsden, 2003; Rodríguez-Herrera et al., 2007). Persistent roosts probably also provide more stable micro-environmental conditions that favor a successful development of parasites (Dube et al., 2018); however, no conclusive correlation has been shown so far for bat flies (Dittmar, Dick, Patterson, Whiting, & Gruwell, 2009; Lourenço & Palmeirim, 2008).

We detected further a clear sex bias in prevalence and intensity of parasitization in all species, with males being parasitized significantly less often and with fewer bat flies. This could be related to social organization of bats and the resulting roosting behavior. Social systems of most of the bat species studied consist of year-round persisting harems, comprising multiple females, their offspring, and commonly one harem male, while non-harem males roost solitarily or in small all-male groups (Chaverri, Gamba-Rios, & Kunz, 2007; Fleming, 1988; Lewis, 1992; McCracken & Wilkinson, 2000; Morrison, 1979; Muñoz-Romo, Herrera, & Kunz, 2008). Non-harem males of *A. jamaicensis* are often found in foliage roosts with less favorable microclimatic conditions than more enclosed and more permanent roosting structures, factors that likely may also affect the reproductive success of their parasitic bat fly parasites (Morrison, 1979, 1980). In addition, non-harem males frequently switch their day roosts, providing an inconsistent and unpredictable source of hosts for bat flies (Lewis, 1995).

Juvenile bats are more likely to be found in social groups with their mothers, in stable roosts with optimal conditions for bat fly development (Esbérard, Astúa, Geise, Costa, & Pereira, 2009), thus promoting parasitization by bat flies. Juveniles are generally preferred hosts for parasites, as they have thinner skin, are less experienced in grooming than adults, and have an immune system that is not yet fully developed (Bertola et al., 2005; Christe et al., 2000; Dick & Patterson, 2007). In our all-species model, as well as in the species-specific models for *A. jamaicensis* and *C. perspicillata* we found juveniles having significantly higher bat fly counts compared to adult bats. However, for prevalence of parasitization, we

detected a significant relationship only for juvenile *C. castanea*. This relationship was not positive as expected, but negative, indicating juveniles being less often infested by bat flies. Probably, this result is influenced by host behavior; for example, juvenile bats are moved by their mothers from their day roosts to separate night roosts (Kohles, Page, Dechmann, & O'Mara, 2018). Additionally, juveniles of the similar-sized *D. watsoni* are capable of longer flights at an age of ca. 40 days, gaining foraging and roosting independence, and were sequentially often found roosting alone (Chaverri & Kunz, 2006).

In addition to intrinsic variables of the hosts, we also found that bat abundance had a significant positive effect on bat fly prevalence in our "all-species approach." However, for *A. jamaicensis* and *C. perspicillata* we detected a significant negative effect of abundance on parasite prevalence. Various studies have shown that host abundance correlates positively with levels of parasitism in social hosts (Arneberg, Skorping, Grenfell, & Read, 1998; Patterson & Ruckstuhl, 2013; Rifkin, Nunn, & Garamszegi, 2012). This relation is commonly seen in directly transmitted parasites, while more mobile parasites, which actively seek their hosts, are often negatively correlated with host group size (Arneberg et al., 1998; Côté & Poulin, 1995; Patterson & Ruckstuhl, 2013; Pilosof et al., 2012). Bat flies might appear to be mobile parasites, although Côté and Poulin (1995) categorize their mode of transmission as functionally similar to that of contagious parasites which may be transmitted only through direct body contact. Furthermore, large amounts of variation in parasite loads remain often unexplained by host density alone (Rifkin et al., 2012). Abundance of *C. perspicillata* was highly correlated with the matrix type, while for *A. jamaicensis* abundance was similar in all three matrix types (S. D. Brändel personal communication), suggesting other factors not quantified in this study may have influenced parasite prevalence.

4.2 | Habitat variables and surrounding matrix

We detected a significant matrix effect only for *A. jamaicensis*, showing a higher bat fly prevalence in forest fragments surrounded by water and lower prevalence as well as lower intensity in forest fragments surrounded by agricultural landscape. This partly contradicts our hypothesis of bats captured in fragmented areas with higher anthropogenic influence presenting higher parasite loads than individuals living in pristine forests. In our study, the actual difference between the forest fragments surrounded by water and those surrounded by agriculture is not only matrix heterogeneity, but also the presence of anthropogenic influence. The forest fragments surrounded by Gatun Lake have been largely undisturbed for over 80 years, while the forest fragments surrounded by agriculture experienced a continuous anthropogenic influence (e.g., selective logging) (van Breugel et al., 2013; Leigh, 1999). While some bat species can survive or even thrive in altered habitats, their associated bat flies may not find these conditions favorable for successful reproduction. This relationship is especially clear in the case of *A. jamaicensis*. This bat species may roost in hollow trees but is also found roosting in foliage or in human-made structures (Morrison, 1979, 1980). On fragments surrounded

by water, we detected a high prevalence of bat flies on *A. jamaicensis*, likely because roosting resources are less abundant than they are in the continuous forest, given the limited size of the islands and their exposure to more extreme climatic conditions, due to increased edge effects (Harper et al., 2005; Meyer & Kalko, 2008). This might lead to bats crowding in the few remaining roosting opportunities, creating optimal conditions for bat flies to reproduce and recolonize. In the fragments surrounded by agricultural landscape, the number of large trees is greatly reduced through selective logging (Harper et al., 2005; Schulze, Seavy, & Whitacre, 2000) and is perhaps too low to sustain the parasite prevalence seen in continuous forest. In combination with the abundance of *A. jamaicensis* in all three habitat types, the lower prevalence and intensity of parasitization in fragments surrounded by agricultural matrix is probably not a result of limited host resources, but of restrictions on bat fly reproduction, such as unsuitable microclimatic conditions in the roosts the bats are inhabiting.

Canopy height and canopy density have positive effects on the prevalence of bat flies infesting *A. jamaicensis*, with higher rates of parasitization at capture sites with older, taller trees. In old growth forests, the understory density is often reduced, due to limited light levels at the forest floor, causing saplings to stay small and dormant (Leigh, 1999; Turner, 2001). In other words, these older forests provide more suitable tree cavities for roosting which therefore favor bat fly reproduction and transmission. This relationship is in accord with the negative relation we found between understory density and intensity of parasitization: Bat fly abundance on *A. jamaicensis* is higher in locations with lower understory density.

In contrast, we found a negative effect of canopy height and canopy cover on the parasite prevalence in *C. castanea*, which were more frequently parasitized in agricultural areas. Similar to *C. perspicillata* (which share bat fly species), this could be a product of higher host abundance in altered habitats (Côté & Poulin, 1995). *Carollia* species feed mostly on fruits from plants of early successional stages such as *Piper* spp. or *Vismia* spp. (Thies & Kalko, 2004), which are very common in altered habitats (van Breugel et al., 2013). The high abundance of suitable food plants may allow these bat species to become very abundant in altered habitats (Faria, 2006). Although *Carollia* species are also flexible in roost choice, they prefer stable roosting sites, such as hollow trees, crevices, or culverts (LaVal & Rodríguez-H., 2002; Patterson et al., 2007; Seim et al., 2013), which directly affects parasitization by bat flies. If roost availability in fragmented habitats is similar to that in continuous forest sites, the higher bat abundance can lead to a higher density of occupied roosts but also to increased crowding in especially favorable day roosts. Close host associations in turn may cause elevated stress levels (Creel, Dantzer, Goymann, & Rubenstein, 2013), promoting parasitization by bat flies (Gannon & Willig, 1995).

4.3 | Bat fly species-specific responses

In our analyses of parasitization intensity, we combined the bat fly count of different species occurring on each host bat individual to

model the reaction of total parasite burden to habitat and intrinsic variables. Previous studies showed no or only slightly negative interactions between simultaneously occurring bat flies on a host individual, suggesting resource partitioning, for example, by using different parts of the body (Hiller et al., 2018; Tello et al., 2008). To assess if individualized responses by bat fly species are driving our results, we focused on the three most common bat fly species in our data set *T. joblingi* parasitizing *C. perspicillata*, and *A. phyllostomatis* and *M. aranea* parasitizing *A. jamaicensis*, which also differed in their proportional representation in the total bat fly community of their host species. *Trichobius joblingi* was the most common bat fly species on *C. perspicillata* and made up 85.3% of its total bat fly community. However, our model on intensity of parasitization by *T. joblingi* differed from the results of the model including all bat fly species of *C. perspicillata*. While in the latter model, juveniles hosted significantly more bat flies than subadults and adults, in the parasite species-specific model the variable age was dropped during model selection. We found a significant influence of host sex, with female bats being infested by more bat flies than male bats, which could be explained by social structure and life history of our study bat species (Chaverri et al., 2007; Fleming, 1988; Lewis, 1992; McCracken & Wilkinson, 2000; Morrison, 1979; Muñoz-Romo et al., 2008; Patterson, Dick, & Dittmar, 2008b). These higher values in females were also observed for the two equally common bat fly species parasitizing *A. jamaicensis* (*M. aranea* and *A. phyllostomatis*, 49.5% and 48.3%, respectively), each mirroring the result of the model combining all bat fly species on *A. jamaicensis*. Likewise, juvenile bats had significantly higher intensities of *M. aranea* and *A. phyllostomatis*. Further, *A. phyllostomatis* showed a negative response to understory density, which we also detected in our model combining all bat fly species of *A. jamaicensis*, while this effect was not visible for *M. aranea*. Finally, no matrix effect was found on bat fly species level, although present in the model combining all parasite species of *A. jamaicensis*.

Altogether, the results of our models for individual bat fly species differed clearly from the results among different bat species. This indicates that each parasite species is differently affected by habitat alteration and host intrinsic factors. However, it further suggests that our results using the combined bat fly count are likely not driven by a single parasite species and allow us to draw conclusions about the effect of habitat alteration on the total parasite burden of a bat species.

4.4 | Foliage and tent-roosting bats

In contrast to *A. jamaicensis* and the two *Carollia* species, which roost in the study area predominantly in caves and tree cavities, the remaining host bat species are foliage and tent-roosting species (*A. lituratus*, *D. rava*, *D. watsoni*, and *U. bilobatum*). In general, these species show low parasite prevalence and parasite load (ter Hofstede et al., 2004; Patterson et al., 2007), factors likely causing the null model to be the best explaining option in our analyses.

As such, we could not identify any of the available explaining variables as having a significant effect on prevalence and intensity of bat fly parasitization. These bat species are confronted with similar roosting options in all three habitats and readily use also ornamental plants for tent construction (Rodríguez-Herrera et al., 2007; Rose et al., 2017). They switch roosts rather frequently, due to the comparably short lifespan of their leaf tents (Herrera-Victoria, Zuluaga-Egas, Rojas-Díaz, Valenzuela, & Kattan, 2018; Rodríguez-Herrera, Ceballos, & Medellín, 2011), and are therefore less likely to experience changes in parasitization due to habitat alteration.

5 | CONCLUSION

In summary, we show that variables on host individual level (e.g., sex, reproductive status), host population level (host abundance), and habitat (e.g., landscape, canopy) have significant influence on the prevalence and intensity of parasitization by bat flies. However, these results are highly host species-specific and therefore complicate generalizations over all bat species. In addition, given the peculiar life cycle of these ectoparasitic insects (depositing a 3rd instar larva in their hosts' roost), the availability and microclimatic conditions of the roosting environment may be of great importance to parasitization by bat flies (Dittmar et al., 2009). Altered habitats with more extreme climate conditions might lead to faster desiccation of deposited bat fly pupae. Studies focusing on the ecology of bat flies, however, remain rare (Fritz, 1983; Marshall, 1971; Overall, 1980; Reckardt & Kerth, 2006) causing a lack of knowledge in the underlying processes. The detected effect of habitat alteration on parasitization lies therefore probably in its induced changes in roosting ecology on bat species level.

The response of bats to habitat alteration has recently caused them to become the focus of several studies, in part due to their importance as model organisms for topics related to eco-health and zoonoses (Brook & Dobson, 2015; Hiller, Rasche, et al., 2019b; Streicker et al., 2012). However, the importance of parasites to affect host populations directly by controlling reproductive success, as well as their potential role as vectors for pathogens (Morse et al., 2013; Xu et al., 2018), is often neglected and severely understudied. While bat flies are known vectors of *Polychromophilus* blood parasites (Witsenburg et al., 2015), and bats react to infections with blood parasites with elevated white blood cell counts (Cottontail, Wellinghausen, & Kalko, 2009), consequences on bat health remain to be explored. With an ever increasing anthropogenic influence worldwide, it is important to understand how the interactions between hosts and their parasites respond to habitat changes, as here shown on the example of bats and their bat flies. Based thereon, further predictions on the effects caused by habitat loss and fragmentation on species interactions and ecosystem health are possible.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8w9ghx3h5> (Hiller, Brändel, et al., 2019a).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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