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Contrasting effects of body condition on ectoparasite abundance in a social bat: different roles of season and host sex

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ABSTRACT

Understanding the interplay between host species ecology and parasite dynamics is crucial for comprehending disease transmission patterns, population structures, and ecosystem health. In most host-parasite systems, host body condition is of primary importance in ectoparasite host choice. Bats were considered an exception, as previously several studies suggested that bat ectoparasites showed no or minimal dependence on host body condition. We investigated the relationships between host condition and ectoparasite abundance in multiple populations of European bent-winged bats (*Miniopterus schreibersii*) and their arthropod ectoparasites (mites, nycteribiid bat flies and ixodid ticks). We found weak correlations between individual host condition and combined ectoparasite abundance, with seasonal fluctuations in both, and a single seasonal peak in parasite abundance. However, when treated individually, single ectoparasite groups showed contrasting answers to changes in body condition. Body condition had a significant positive effect on wing mite abundance and a significant negative effect on the prevalence and intensity of nycteribiid bat flies, overall with no effect on tick infestation. These responses moreover showed also seasonal differences, highly correlating with the life-stages of the two host's sexes. Our long-term, large-scale study of European bent-winged bats and their arthropod ectoparasites was able to detect major influences exerted by hosts' body condition on ectoparasites' host choice. Here we showed that bat populations undergo dynamic changes in their body condition during the active period of their annual cycle, with ectoparasites evolved to differentially exploit peaks or troughs of these changes.

1. Introduction

Parasites show extremely wide morphological and behavioral adaptations to the parasitic lifestyle and each host species may be parasitized by several parasites (Dobson et al., 2008). They consume the hosts' energy resources and mostly use their hosts' body as habitat. Parasites as a group show varying intensity in host specificity (i.e., the capacity to exploit multiple host species), with most species being adapted to a single or few, morphologically similar and likely phylogenetically close host species (Poulin and Morand, 2000). Most ectoparasite species are arthropods, and they consume either their hosts cuticle or they penetrate the skin and rely on their hosts' blood. Due to their lifestyle, parasites may reduce their hosts' energy reserves, decrease their immunity, modify the activity budgets or cause disease and even the hosts' death (Nelson et al., 1977; Fitze et al., 2004;). In addition to direct effects, most hematophagous ectoparasites may pose an indirect risk through transferring pathogens between subsequent hosts during serial blood feeding (disease vector capacity, Lefèvre et al., 2022).

Host-parasite relationships are multi-faceted, with both sides showing a series of evolutionary adaptations for/against host colonization, parasite dispersion or antiparasitic defense (Dobson et al., 2008). Thus, patterns of ectoparasite infestations are complex processes and depend on many variables, both intrinsic (related to the ecology of the parasite or the host) as well as extrinsic (environment, season) among multicellular organisms in general (Nelson et al., 1977) and mammals in particular (Dáttilo et al., 2020). Par-

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asite infestation may depend on the host taxon, as well as individual size, sex, age, health status or condition. Generally, a larger size means more parasites (especially in the case of external parasites), both in number as well as diversity (Morand et al., 2007). Among most mammalian species males tend to host more diverse and more numerous parasite assemblages (Morand et al. 2004), however this is mostly different among bats (Zahn and Rupp, 2004; Christe et al., 2000, 2007; Sándor et al., 2019). Also, sex-biased parasitism may vary within a species, depending on seasonal host behavior, reproductive- and health status or even local reproductive output, but may also be affected by the parasite life stage or the mode of ectoparasite transfer (Sándor et al., 2024a). A host's age may also affect infestation success due to learned parasite avoidance or host defense behaviors (Webber et al., 2015), but acquired immunity also may be important (Lilley et al., 2014).

The importance of body condition for animals is multifaceted and positively correlates with their fitness by affecting survival and reproduction by having direct relationship to the individual's health, longevity, behavior or its social interactions (Jakob et al., 1996). It is also an effective index to assess information on the health of not just individuals but populations; therefore it can be a useful tool for conservation and management purposes (Stevenson and Woods, 2006). Host individuals with better condition have a higher chance of survival and reproduction, and may offer more resources for parasites. Body condition also correlates with the immunocompetence and other defense mechanisms of animals (such as grooming), therefore hindering infection by parasites (Alonso-Alvarez and Tella, 2001; Debeffe et al., 2016). As a result, parasites have to choose a strategy to overcome the trade-off between better resource with good defense mechanisms, and scarcer resources with weak defenses (Sánchez et al., 2018). The understanding of the connection between body condition and parasite infection represents a complex research area, as numerous studies reveal inconsistent or contradictory outcomes across various taxa (McLean and Speakman, 1997; Christe et al., 2000; Lourenço and Palmeirim, 2007; Rughetti and Toffoli, 2014; Budischak and Cressler, 2018; van Beest et al., 2023). In the case of bats, there are studies which have shown that ectoparasites tend to exploit the weaker and immunologically less competent individuals (McLean and Speakman, 1997; Lučan, 2006; Warburton et al., 2016). On the other hand, there are results which show that in some cases bat hosts with better condition have more parasites (Christe et al., 2003; Reckardt and Kerth, 2007; Tai et al., 2022). Also, some studies did not find any connection between body condition and parasite load (Postawa and Szubert-Kruszyńska, 2014; Postawa and Nagy, 2016).

Bats have a long evolutionary history, with the first representatives of the order known from the Eocene, ca. 52 million years ago, with species morphologically highly similar to extant species (Rietbergen et al., 2023). The reduced capacity for removing parasites due to highly specialized limbs, the pronounced sociality and their habit of sharing communal spaces frequently and for long periods of time, coupled with the longevity of the host itself create ideal conditions for many ectoparasites. Bats are regularly infested by a high number and a diverse array of arthropods, with whole phylogenetic groups exclusively occurring only in the order Chiroptera. Among the regularly occurring hematophagous groups, the spinturnicid mites (Acari: Mesostigmata: Spinturnicidae) are the most common, while many bats also host nycteribiid flies (Diptera: Nycteribiidae) and ticks (Acari: Ixodidae). In the case of most ectoparasites, prevalence and even infestation intensity is high, with each individual bat hosting several ectoparasite individuals (Christe et al., 2003; Reckardt and Kerth, 2007; Tai et al., 2022). Thus, bats and their ectoparasites offer an ideal study system to test hypotheses of host-parasite relationships.

Here we intended to assess the effect of host condition on parasite abundance in a multispecies host-parasite system, using a bat host (Eurasian bent-winged bat, *Miniopterus schreibersii*) and its ectoparasites (wing mites, ticks and nycteribiid flies). Eurasian bent-winged bats offer ideal conditions for studying host-parasite interactions. The species is a highly social, cave-dwelling bat, with both sexes using underground roosts together. In this way, one can test for sex-dependent differences in parasite abundance, while controlling for environmental conditions, which is not the case in most mammalian species, where sexes do not share the same roost. The species hibernates in caves and small-scale seasonal migrations are the norm, thus the seasonal effects of differing environmental conditions may also be tested in a single population. Hibernation and energy-intensive seasonal movements may affect individuals discretely, thus local congregations may host bats with varying condition levels in the spring and/or pre-hibernation sites. We hypothesized that the two sexes allocated different levels of resources to parasite defence according to their life-cycle stage, and thus were likely to show seasonal changes in parasite infestation patterns, with higher parasite infestation levels for females in the maternity period. Males, on the contrary, were expected to show a peak of parasite abundance during the mating period (autumn), when investment in sexual activities may suppress antiparasitic defence capabilities. We also expected that host condition will have the highest effect on parasite abundance during the most critical period of the hosts' life (e.g., during the maternity period for females and during the swarming period for males).

2. Materials and methods

Data were collected in eastern Europe, mostly in Romania, but also in Bulgaria, during the period between 2015 and 2022. Bats were captured close to permanent underground roosts, belonging to three main types: natural caves, mine shafts and buildings. Captures were made only during the active period of European bent-winged bats, to avoid harmful disturbance during sensitive periods for bats such as hibernation and lactation. Thus, bat captures were performed primarily before birth/lactation (*spring season*, chiefly mid-April to mid-May, and *autumn season*, late-July to mid-October). Bats were captured close to the entrances using harp traps, and after extraction from the traps, they were individually held in sterile, clean cloth bags. The age, sex and reproductive status were recorded for each animal and morphological measurements were taken: wing-length = forearm length to 0.1 mm accuracy (size) and body mass to 0.01 g accuracy. We calculated the body condition index (BCI) for hosts using the ratio of body mass and forearm length (Labocha et al., 2014). Each bat was individually screened for ectoparasites over the whole-body surface. Ectoparasites were recorded as a cumulative total for all mites observed on wing membranes, based on counts on both wings, while larger ectoparasites (nycteribiid flies and ixodid ticks) were removed by forceps and stored in 97% ethanol in coded vials for each individual host and ectoparasite group. Ticks and bat flies were identified in a laboratory, under a binocular microscope using morphological keys (Estrada-Peña et al., 2018; Theodor, 1967). Data of ectoparasites (species, developmental stage for ticks and sex for flies and adult ticks) were recorded and combined in an Excel database with the data on hosts.

Database manipulation and statistical analyses were performed in the R statistical environment (R version 4.3.2, 31.10.2023, R Core Team (2023)) using Windows 10. For data manipulation we used the *plyr* package (Wickham, 2011); to calculate confidence intervals and parasitological indices the *prevalence* (Devleesschauwer et al., 2014) and *misty* packages (https://CRAN.R-project.org/package=misty) were used; for comparing datasets we used the *car*

package (Fox and Weisberg, 2018) and for construction of Generalized-Linear Mixed Models (GLMM) we used the *glmmTMB* package (Brooks et al., 2017). Statistical data visualization was performed with the *ggplot2* package (Wickham, 2016). We used the Kolmogorov-Smirnov test to test normal distribution, while the F test was used to compare variances. We used the Wilcoxon test to compare bat condition data. A $P < 0.05$ was considered significant.

2.1. Data accessibility

All the primary data analyzed in this study together with the statistical scripts used are available on the Mendeley Data Repository (https://doi.org/10.17632/2p3vb6tynh.1).

3. Results

In this study we used the combined morphological and parasitological data collected from 1981 sampled *M. schreibersii*, captured at 21 individual locations. Most captured host animals were adults (93.7%), while we also sampled 124 juveniles. The sex ratio was slightly male biased (male/female ratio: 1.17), although the difference was not significant. Bats showed wide variations in body condition, with significant differences both seasonally, as well as among the sexes. Both sexes emerged from hibernation in poor condition, with males being in a marginally better state. However, the BCI increased more sharply in females during spring, while it drastically decreased post-partum, followed by a sharp increase once again in autumn (Fig. 1). For males, body condition did not follow this trend: their weight peaked in late July, followed by a gradual, slow decrease towards the end of the active season. Overall, males had significantly higher BCIs than

females (respectively, 0.287, 95% confidence interval (CI): 0.285–0.289 versus 0.283 95% CI: 0.280–0.285, $P < 0.001$, Fig. 2). There was no significant difference between juveniles and adults (we pooled the data together). The difference between spring and autumn BCIs of bats did not differ, however the difference between sexes was significant in both seasons. Females showed a seasonal decline in BCI, with their spring BCI significantly higher than in autumn (0.293 (95% CI: 0.290–0.297) versus 0.273 (95% CI: 0.271––0.276, $P < 0.001$). Males showed an opposite trend, with higher BCIs during autumn (0.292 (95% CI: 0.289–0.294) versus 0.274 (95% CI: 0.271–0.276, $P < 0.001$, Fig. 1).

The combined (all three parasite groups) prevalence reached 81.02% (95% CI: 79.23–82.69). We collected 1754 ticks belonging to two species and a total of 2190 bat flies from eight different species (Table 1). Ticks were found on 35.18% (95% CI: 33.11–37.31) of the bats, with a mean intensity of 2.52 (95% CI: 2.33–2.70). Most ticks (n = 1743) were *Ixodes simplex* (126 females, 688 nymphs and 929 larvae), while 0.6% belonged to *Ixodes vespertilionis* (two nymphs and nine larvae). Bat flies had a prevalence of 49.57% (95% CI: 47.37–51.77) and a mean intensity of 2.23 (95% CI: 2.12–2.34). The most numerous bat fly species collected was the host specific *Nycteribia schmidlii* (n = 1438), followed by two polyxenous species, *Penicillidia conspicua* (n = 612) and *Penicillidia dufourii* (n = 106). In smaller numbers we also collected *Nycteribia latreillii* (n = 16), *Nycteribia pedicularia* (n = 14), *Nycteribia vexata* (n = 2), *Phthiridium biarticulatum* (n = 1) and *Basilia nana* (n = 1). A total of 4192 mites were counted on the wing membranes of bats with a prevalence of 46.95 (95% CI: 44.76–49.15) and a mean intensity of 4.08 (95% CI: 3.80–4.35). The combined parasite distribution showed a single-peak increase followed by a slow decrease (Fig. 3). However, when treated separately, all three ectoparasite
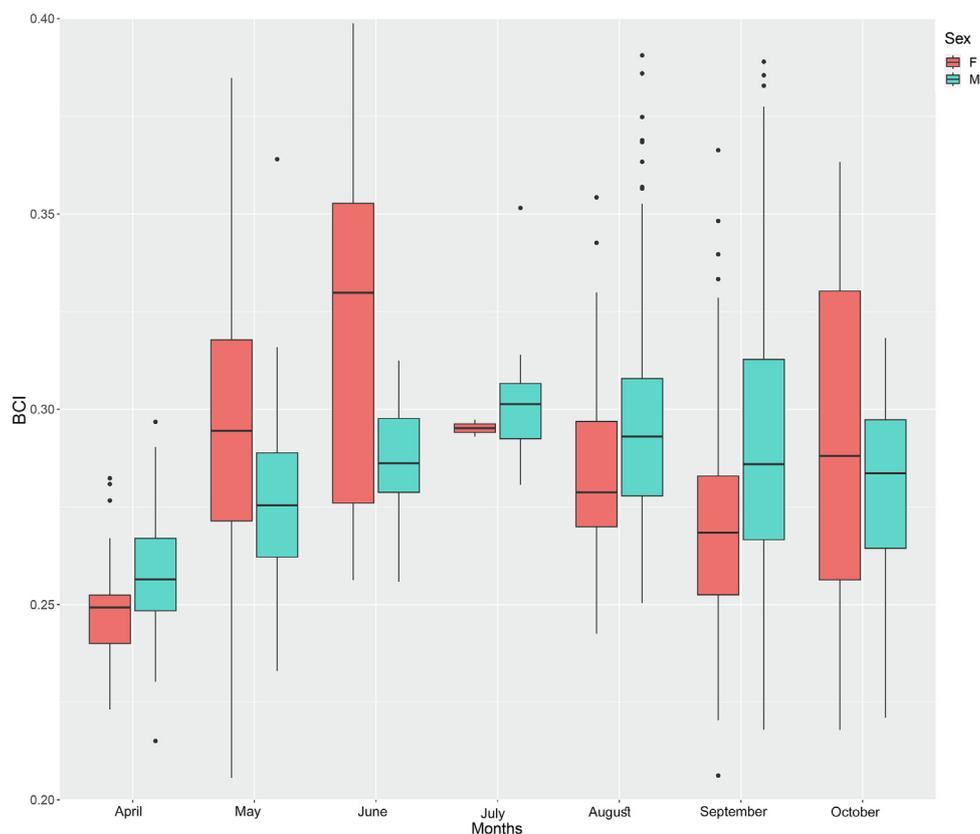

Fig. 1. Monthly variation in mean body condition index (BCI) of European bent-winged bats (*Miniopterus schreibersii*) during the active period. Filled bars represent 75% quartiles; red females, aquamarine males. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
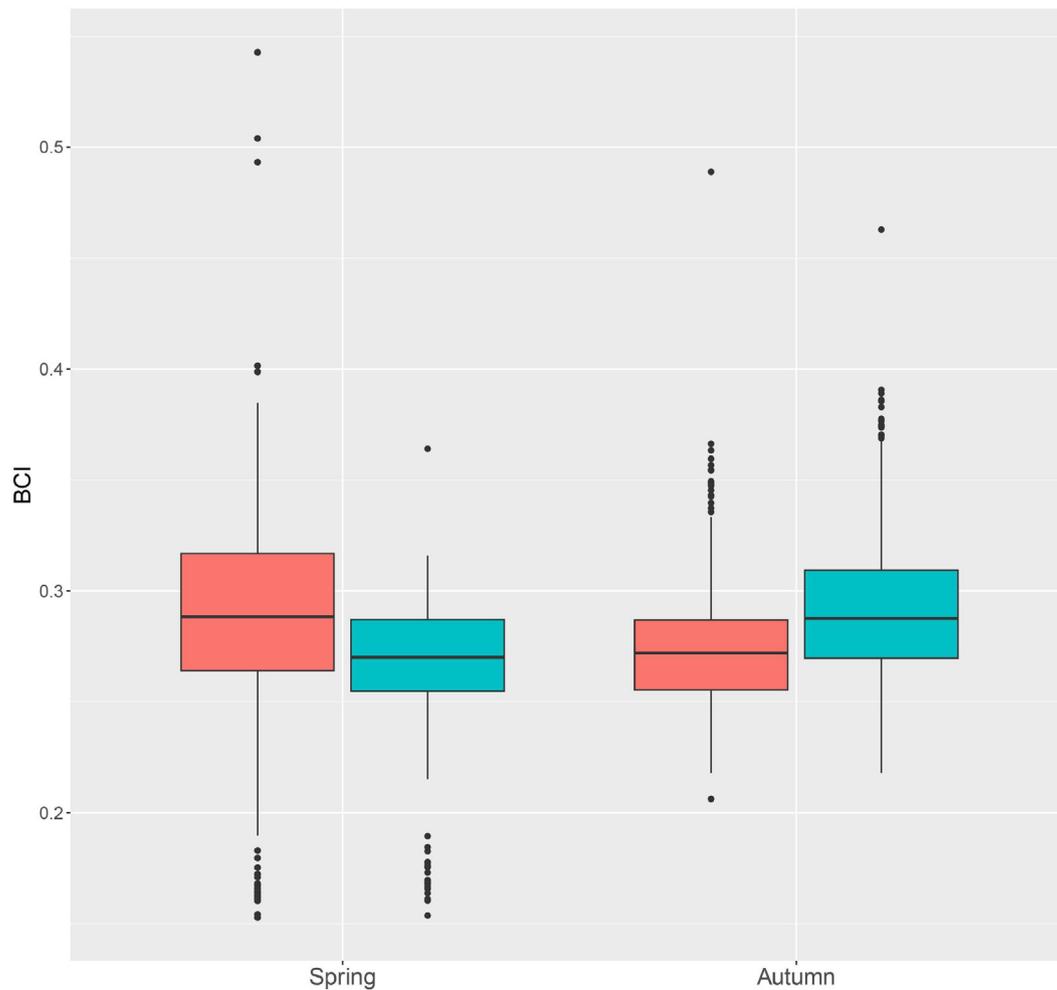
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Fig. 2. Mean body condition index (BCI) of European bent-winged bats (*Miniopterus schreibersii*) in the pre-maternity (*spring*: mid-April – mid-May) and mating (*autumn*: mid-July – mid-October) seasons. Filled bars represent 75% quartiles; red females, aquamarine males. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Morphological measurements (forearm length in mm and weight in g) of Eurasian bent-winged bats (*Miniopterus schreibersii*) and computed body condition index (BCI).

	Forearm length	Body mass	BCI
Mean	45.55	12.91	0.28
Variance	0.86	3.0	0.001
Minimum	40.28	6.8	0.15
Maximum	47.96	25	0.54

groups show a double-peak distribution, with peaks overlapping among groups only in June-July (Fig. 4).

GLMM models did not indicate BCI as a significant variable in the case of overall parasite infestation (all parasites combined) of hosts (Table 2, Fig. 5). The variables which affected overall parasitism were only host sex (males had fewer parasites, $z = -3.531$, $P > 0.001$) and season (infestation rates in spring were lower, $z = 2.813$, $P > 0.01$, Table 2). However, when parasite groups were analysed separately, body condition showed contrasting effects. It had a significant positive effect on mite abundance ($z = 2.016$, $P = 0.043$), and a significant negative effect on bat fly abundance ($z = -3.217$, $P < 0.01$), while it had no effect on tick abundance. Host sex influenced all three parasite groups, with male bats having significantly less mites than females ($z = -2.41$, $p = 0.016$), and fewer ticks ($z = -3.337$, $P < 0.001$), but more flies ($z = -1.868$,

$P = 0.06$). Season also determined parasite abundance, with more mites ($z = 16.524$, $P < 0.001$) and ticks ($z = -6.736$, $P < 0.001$), but less flies, during spring on both sexes ($z = -6.736$, $P < 0.001$, Fig. 4). Roost type was very important for ticks (mines; $z = 2.373$, $P = 0.017$) and fly abundance (bats in mines had fewer flies compared with those in buildings; $z = -1.803$, $P = 0.07$), while it had no effect on mite abundance. Host size, however, was important for mites, with slightly more mites observed on smaller bats (Figs. 6 and 7).

4. Discussion

Our study revealed abundant ectoparasite infestations in all studied European bent-winged bat populations, independent of their life stage, condition or activity. Using the extensive dataset collected at several study sites, through seven active seasons of European bent-winged bats, we tested if ectoparasite host choice is determined by host body condition or other characteristics related to host ecology or habitat (such as sex, age, roost type and season). Body condition (indexed as BCI) was not a static measure in the studied populations, but reflected host sex, reproductive status or seasonal activity. Host sexes showed contrasting trends in body condition, with females showing two peaks in body weight (pregnancy and late swarming periods), while males showing a single peak (late July, Fig. 1) during the active season. Still,
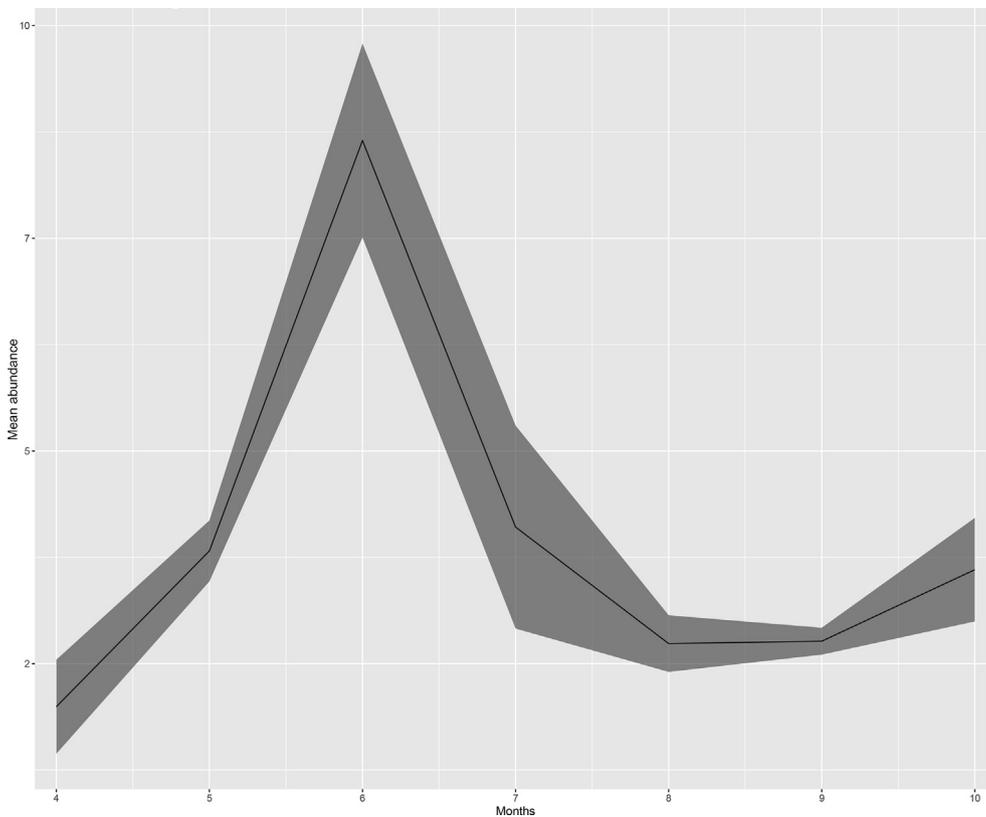
Fig. 3. Seasonal changes in cumulative abundance of ectoparasites (wing mites, ixodid ticks and nycteribiid flies; grey shadow covers 95% CI) on European bent-winged bats (*Miniopterus schreibersii*).
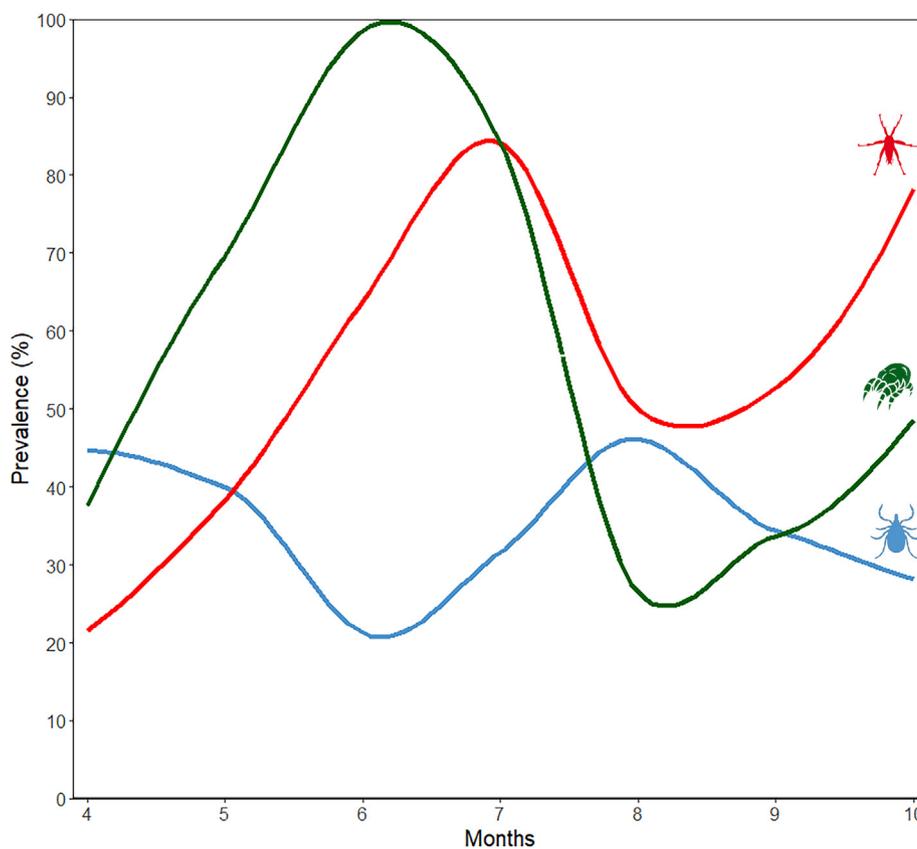

Fig. 4. Seasonal patterns of ectoparasite prevalence values in ectoparasites (wing mites, ixodid ticks and nycteribiid flies) hosted by European bent-winged bats (*Miniopterus schreibersii*). Green – wing mites; red bat flies (Nycteribiidae); blue short-legged battick (*Ixodes simplex*).

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Table 2

Effect of selected biotic and abiotic variables on cumulative ectoparasite infestation abundance of European bent-winged bats, *Miniopterus schrebersii* (negative binomial distribution general linear mixed model).

	Estimate	Std. Error	z value	P-value	
Intercept	1.30561	0.31363	4.163	<0.001	[a]
Condition	−0.03385	0.04532	−0.747	0.455	
Sex (male)	−0.14646	0.03691	−3.968	<0.001	[a]
Roost (cave)	0.26281	0.22287	1.179	0.238	
Roost (mine)	−0.32364	0.23308	−1.389	0.165	
Season (spring)	0.56342	0.05681	9.918	<0.001	[a]

[a] Highly significant result.
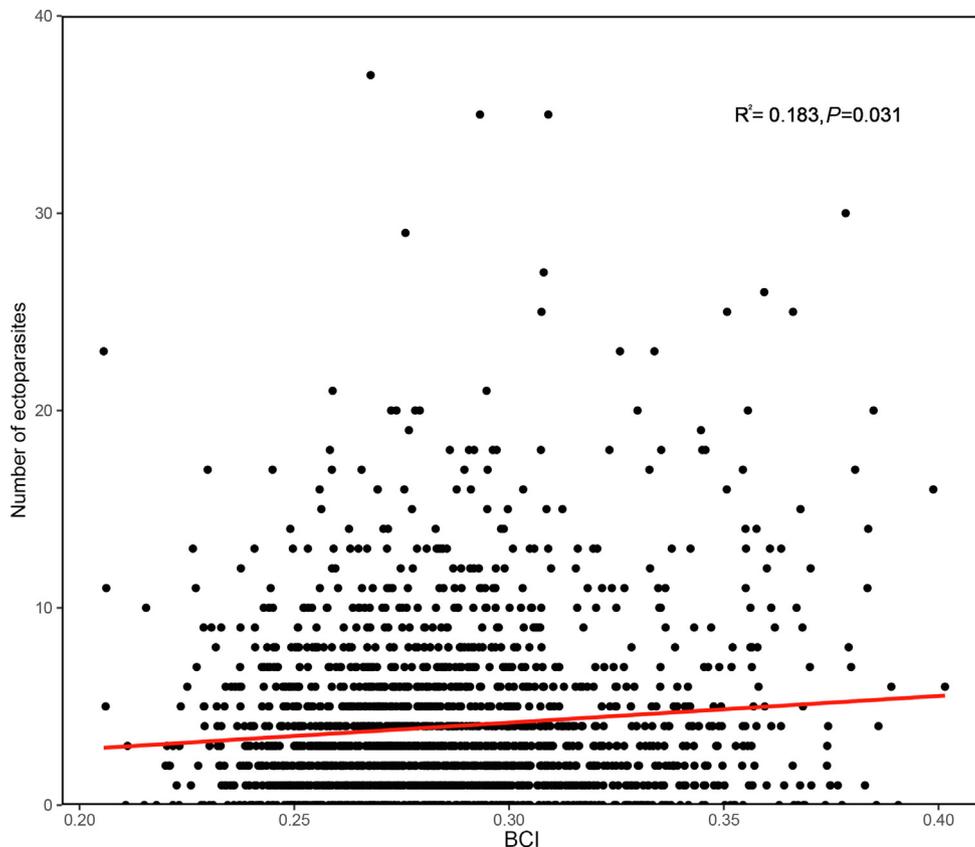
Fig. 5. Relationship between body condition (BCI) and cumulative ectoparasite abundance of ectoparasites (wing mites, ixodid ticks and nycteribiid flies) of European bent-winged bats (*Miniopterus schreibersii*).

females showed an overall better condition in spring than males (or females in autumn). Seasonal fluctuations in adult body weight (and BCI) were already recorded for several bat species (Dwyer, 1964; Beasley et al., 1984; Tai et al., 2022) and registered for European bent-winged bats (Serra-Cobo et al., 2000). An increase in body weight is likely determined by flight-related parameters in the case of bats. They rely on sustained, powered flapping flight; thus, wing load and aspect-ratio will limit individual changes in body-weight or condition (Norberg and Norberg, 2012). Even so, most adult individuals go through extensive, seasonal changes in BCI. These changes in body weight are caused by the build-up and depletion of energy reserves used for maintenence of metabolism during the wintering season or sustained specific activities linked to reproduction (i.e., pregnancy and lactation in females and swarming in males, Lyman, (1970)). With significant differences in BCIs recorded during along the active season (Fig. 2), we suspected that parasite host choice would be impacted by host condition. Contrary to our expectations we found weak correlations between host condition and overall parasite intensity (Table 2, Fig. 5), with a generalized effect of selection pressure on substandard and overweight individuals (Fig. 7). When treated separately, host selection by different parasite groups is not similar. We found major differences in host selection by the different parasite groups (flies, ticks and mites, Fig. 4) and in seasonality of abundance patterns among host sexes. Female hosts were more frequently parasitized than males, irrespective of their body condition (Fig. 1) or reproductive status (pregnant, post-partum), although this showed a seasonally decreasing trend (Fig. 3). This is a general pattern among bats; in most studied species females show higher parasite prevalence and intensity (Deunff and Beaucournu, 1981; Estrada-Peña and Serra-Cobo, 1991; Zahn and Rupp, 2004; Lučan, 2006; Lourenço and Palmeirim, 2007; Sándor et al., 2019, 2024a). This is partly caused by the overall gregarious habit of most bat females, at least during the pregnancy and pup-rearing periods due to energetic constrains (Lyman, 1970; Kerth, 2008). As such, for most ectoparasite species this period is ideal for propagulation, hence they evolved to overlap their reproduction with the host' reproduction in order to maximize chances
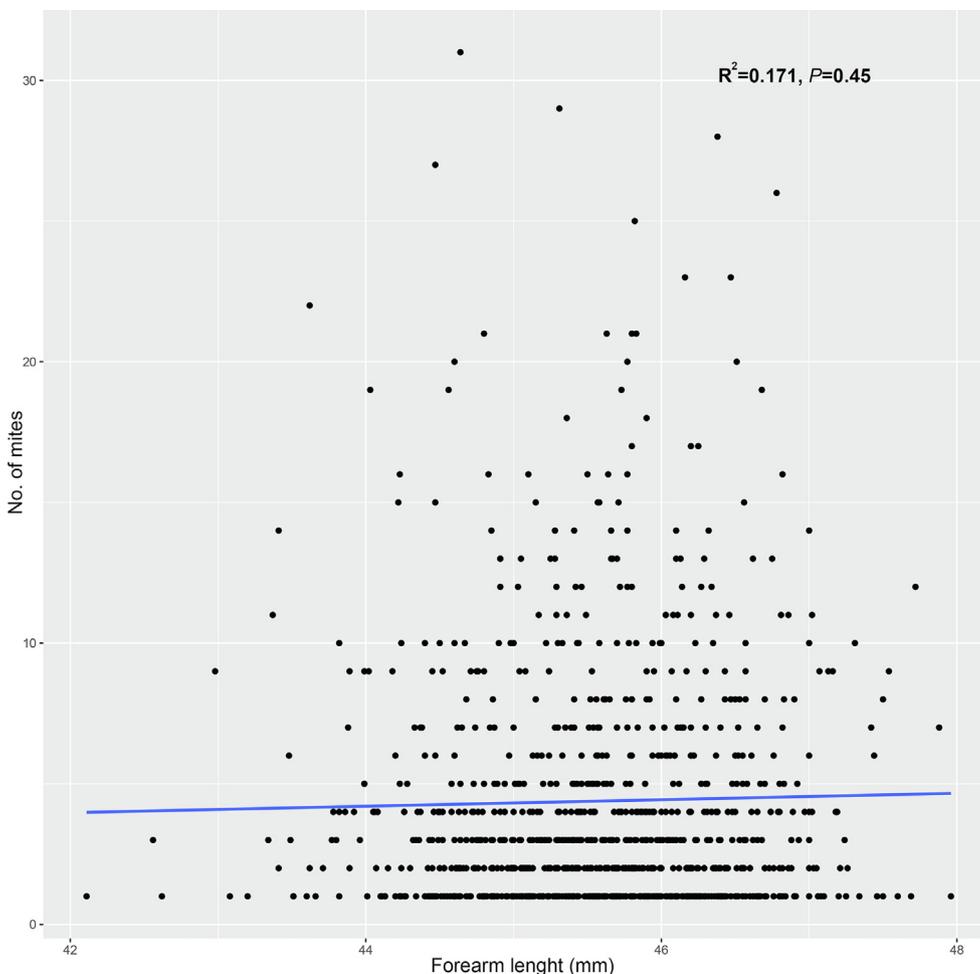
Fig. 6. Relationship between host size (forearm length in mm) and wing mite abundance.

for host transfer (Deunff and Beaucournu, 1981; Zahn and Rupp, 2004; Lučan, 2006; Lourenço and Palmeirim, 2008). On the contrary, in the case of most species, males tend to be solitary during this period (Dietz et al., 2009), thus their inherent parasite prevalence is lower in most cases (Sándor et al., 2019, 2024a). European bent-winged bats (together with other *Miniopterus* spp.), are an exception to this norm, as males are gregarious and stay together with females in the same roosts, throughout the year (Aulagnier and Presetnik, 2020). Even so, bent-winged bats in our study populations showed sexually determined parasite prevalences, thus underlining the importance of host sex in host choice of bat ectoparasites. It is interesting that the weakest effect of host sex on host choice was recorded in bat flies (Nycteribiidae) a pattern already documented for several other host species (Sándor et al., 2024).

Generally, host condition itself does not determine the combined ectoparasite abundance, although it was important for individual ectoparasite groups. Tick presence showed no link to body condition; however, the latter was important for the other two parasite groups. We recorded higher mite abundance on hosts with high BCIs. Higher mite intensity may be the result of better reproduction levels of mite groups on hosts with body condition above the average. However, increased prevalence should signal active host choice even in the case of mites. To elucidate this, experimental settings should be used.

Short-legged bat ticks (*I. simplex*) are nearly exclusive parasites of European bent-winged bats (Hornok, 2017; Sándor et al., 2018;

Péter et al., 2021). As their name suggests, these ticks have short legs and reduced mobility (Sándor et al., 2019), thus they likely show opportunistic host choice (they choose the closest/most available host, see also Sándor et al. (2024b)). In addition, after biting the host, all ixodid ticks are permanently fixed to their hosts until fully engorged (Sonenshine and Roe, 2014). In this way any potential transfer between hosts is fully excluded, thus host size or condition are either (i) likely totally irrelevant for their individual host choice; or (ii) not measurable using our approach, as represents an earlier and possibly different host condition (due to the feeding method, ticks stay attached for an individual to up to 5–8 days, (Sándor et al., 2019)). Mites on the other hand were shown to adjust their host selection according to host size (Presley, 2011; Postawa and Szubert-Kruszyńska, 2014), condition (Lourenço and Palmeirim, 2007) and sex (Zahn and Rupp, 2004; Lučan, 2006). They are known to easily commute between hosts (Christe et al., 2000), and are suggested to be good indicators of host health (Zahn and Rupp, 2004). Our study showed that not only host size *per se* (measured in wing length), but host condition itself is important for host choice in the case of mites and bent-winged bats.

Bat flies showed a strong negative relationship with host body condition in our study. These dipterans are highly mobile, easily and regularly switch between hosts and are the largest and most peculiar bat ectoparasites. They are known to cause considerable nuisance to their hosts, initiating strong behavioral responses (Dick and Patterson, 2006). By choosing a host with low body condition (constrained by metabolic challenges), they may reduce the
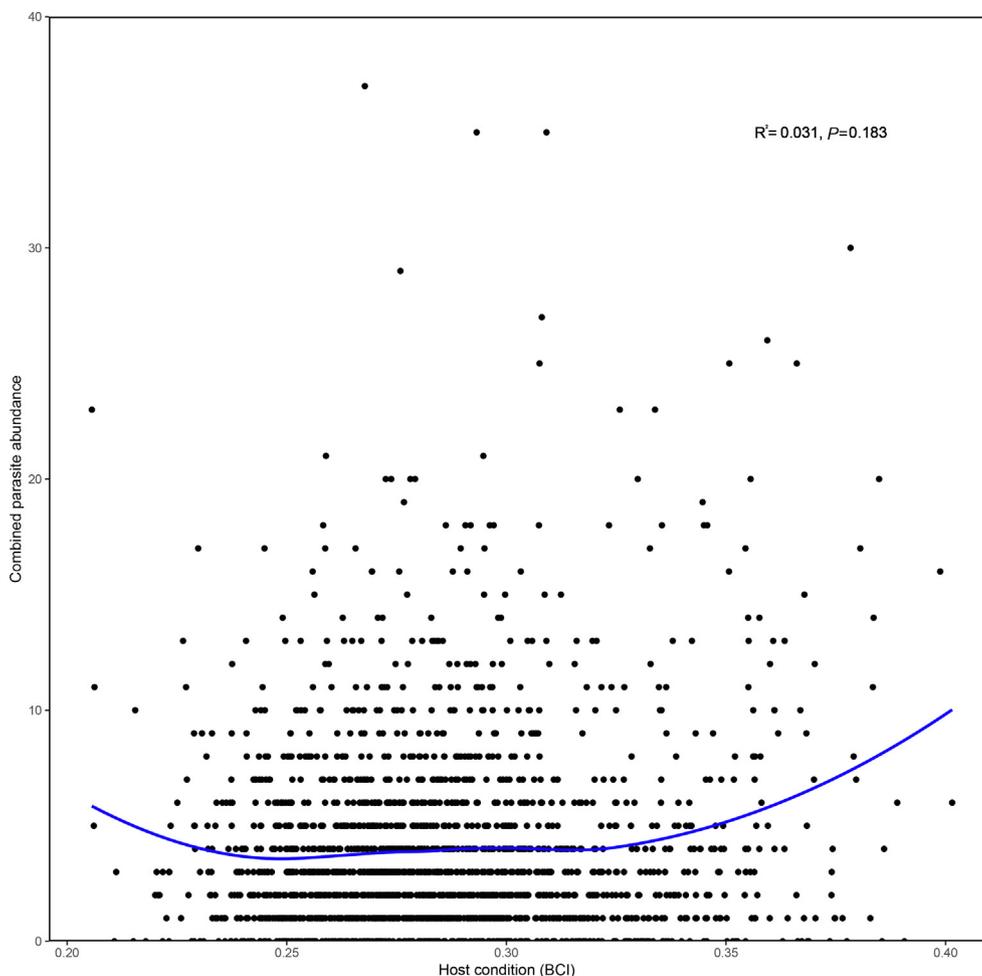
Fig. 7. Relationship between host condition and combined parasite abundance using non-parametric regression in the studied European bent-winged bat (*Miniopterus schreibersii*) populations, showing strong effect of the body condition index (BCI) of substandard and overweight individuals.

risk posed by host self-grooming, a considerable predation pressure (Sullivan et al., 1993; Ramanantsalama et al., 2018). In addition, bat flies were shown to increase their population size (and inadvertently their prevalence and especially their intensity) on their hosts in the boreal autumn (Sándor et al. 2024). This period overlaps with the swarming and pre-hibernation migration of the hosts, when males cover considerable distances and are constrained to reduce their self-grooming effort, due to mating (Suba et al., 2010; Fraser and McGuire, 2023). Bat flies were proven to show a predilection for choosing male hosts during these periods (Sándor et al. 2024), while these hosts also showed lower BCIs later in this season (Fig. 1), thus reinforcing the importance of lower host BCI.

In most host-parasite systems, host body condition is of primordial importance in ectoparasite host choice (Lehmann, 1993; Poulin, 2011). Bats were considered an exception, as previously several studies suggested that bat ectoparasites showed no or minimal dependence on host body condition (Christe et al., 2000; Zahn and Rupp, 2004; Dick and Patterson, 2006; Lučan, 2006; Lourenço and Palmeirim, 2007; Presley, 2011; Postawa and Szubert-Kruszyńska, 2014). The lack of such a relationship was suggested to be caused by opportunistic host choice (Zahn and Rupp, 2004), robust host defence (Lourenço and Palmeirim, 2007; Presley, 2011) and/or parasite ecology (Dick and Patterson, 2006; Postawa and Szubert-Kruszyńska, 2014). In contrast, our long-term, large-scale study of European bent-winged bats and their arthropod ectoparasites was able to detect major influences exerted by a host's body condition on ectoparasite host choice. Here we showed that bat populations undergo dynamic changes in their body condition during the active period of their annual cycle, with ectoparasites evolved to differentially exploit peaks or throughs in these changes.

CRediT authorship contribution statement

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tected areas which granted permission to work on their territory. This work was supported by the National Research, Development and Innovation Office of Hungary (PD143382 NKFIH, to ÁP, K-132794, to SH and ADS).

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