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From trees to fleas: masting indirectly affects flea abundance on a rodent host

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Abstract

Mast seeding causes strong fluctuations in populations of forest animals. Thus, this phenomenon can be used as a natural experiment to examine how variation in host abundance affects parasite loads. We investigated fleas infesting yellow-necked mice in beech forest after 2 mast and 2 non-mast years. We tested 2 mutually exclusive scenarios: (1) as predicted by classical models of density-dependent transmission, an increase in host density will cause an increase in ectoparasite abundance (defined as the number of parasites per host), versus (2) an increase in host density will cause a decline in flea abundance ("dilution," which is thought to occur when parasite population growth is slower than that of the host). In addition, we assessed whether masting alters the relationship between host traits (sex and body mass) and flea abundance. We found a hump-shaped relationship between host and flea abundance. Thus, the most basic predictions are too simple to describe ectoparasite dynamics in this system. In addition, masting modified seasonal dynamics of flea abundance, but did not affect the relationship between host traits and flea abundance (individuals with the highest body mass hosted the most fleas; after controlling for body mass, parasite abundance did not vary between sexes). Our results demonstrate that pulses of tree reproduction can indirectly, through changes in host densities, drive patterns of ectoparasite infestation.

Key words: *Apodemus flavicollis*, *Fagus sylvatica*, indirect effects, pulsed resources, Siphonaptera

INTRODUCTION

Masting, or synchronized, intermittent production of large seed crops by populations of perennial plants (Kelly & Sork 2002) provides pulsed resources that can satiate consumers (Zwolak *et al.* 2022) and trigger far-ranging effects in food webs (Clark *et al.* 2019). So far, most research focused on the impact of masting on granivores, and subsequent cascading effects on predators and their alternative prey (King 1983; Jędrzejewska & Jędrzejewski 1998; Ostfeld & Keesing 2000; Bogdziewicz *et al.* 2016b; Szymkowiak & Thomson 2019). Parasites have been relatively neglected in this regard (but see Pedersen & Greives 2008; Vandegrift & Hudson 2009), with a notable exception of ticks, due to

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concerns about tick-borne diseases that affect humans (Ostfeld *et al.* 1995; Jones *et al.* 1998; Ostfeld *et al.* 2006; Bogdziewicz & Szymkowiak 2016; Bregnard *et al.* 2021). Yet, masting has a considerable potential to inform parasite ecology. Pulses of massive seed production cause drastic changes in host densities. These changes can be used as a natural experiment on the parasitic effects of overcrowding. Such experiments are vital because host density plays a central role in theories on parasite transmission and population dynamics (Anderson & May 1978; McCallum *et al.* 2001; Roberts *et al.* 2002). Masting can be used to evaluate these theories with empirical data. In addition, the link between host density and parasite abundance (i.e. the number of parasites per host: Bush *et al.* 1997) is highly relevant in applied science. As an example, there is a concern that overcrowding of hosts in nature reserves can increase transmission rates, with negative effects on the viability of host populations (Lebarbenchon *et al.* 2006).

Most of our knowledge about parasite population dynamics comes from research on endoparasites, especially endoparasitic worms (Dobson & Hudson 1992; Arneberg *et al.* 1998). However, the link between host and parasite abundance might be different in ecto- versus endoparasites. In contrast to endoparasites, ectoparasites rarely affect host survival or reproduction (Raveh *et al.* 2015—although exceptions certainly exist: Brown & Brown 2004; López-Olvera *et al.* 2015). Consequently, the relation between host and ectoparasite population dynamics is thought to be mostly one-way, with lower potential for feedbacks. In addition, many species of hosts can prevent excessive build-up of ectoparasites through increased grooming (Hart 1990). This behavior can form a ceiling on the parasite abundance and has a relatively low cost that includes trade-offs with other behaviors (e.g. vigilance: Raveh *et al.* 2011). In endoparasites, the ceiling is usually through competition for space and resources in intestinal track of the host, and by increased mortality of heavily parasitized hosts (Coltman *et al.* 1999; Lello *et al.* 2004); thus, high endoparasite loads come with stronger negative impacts on hosts. These differences suggest that studying ectoparasites is essential if our goal is to verify whether there are robust, wide generalizations about the links between host and parasite abundances.

There are 2 most basic and mutually exclusive predictions on the effects of host population density on the abundance of directly transmitted parasites. First, there can be a positive relationship between parasite and host abundance. A major mechanism of this relationship is increased transmission of parasites in dense host populations (Anderson & May 1978; Roberts *et al.* 2002). In addition, high host densities can lead to increased competition for food, lower body condition, and therefore greater susceptibility to infestation (Krasnov *et al.* 2005). In most systems, empirical studies support the positive relationship between host and parasite abundance (Arneberg *et al.* 1998; Chapman *et al.* 2005; Young *et al.* 2015).

Alternatively, increased host population density can negatively affect parasite abundance ("dilution"). If host densities rapidly increase, the infestation rates might decline, as parasites, especially those with relatively long life cycles, are temporarily diluted among hosts. This pattern has also been found by empirical studies, although perhaps not as frequently as the first one (Krasnov *et al.* 2007; Godfrey *et al.* 2008; Renwick & Lambert 2013; Zwolak *et al.* 2013; Samsing *et al.* 2014).

In addition to host abundance, parasite levels depend on characteristics of individual hosts. Sex and body mass are among the most widely studied and ecologically important individual traits of animals. These traits also affect infestation with parasites (Dziemian *et al.* 2015; Young *et al.* 2015; Hammond *et al.* 2019). Sex of the host can affect parasite loads through its effects on hormone levels (testosterone has immunosuppressive properties: Trigunaite *et al.* 2015) and behavior: in many species, males have larger home ranges than females (e.g. Ostfeld 1990; Fisher & Owens 2000; Perry & Garland 2002), and thus increased chances of encounter with parasites. High body mass presents larger food resource for parasites (translating into higher parasite abundance: Harrison *et al.* 2010; Meagher *et al.* 2019), but also indicates better condition and higher ability to resist infestation (potentially resulting in lower parasite abundance: Beldomenico *et al.* 2008; Beldomenico & Begon 2010). However, the surplus of food resulting from resource pulses can weaken the link between sex and space use (South *et al.* 2007) or between body mass and condition (Hertel *et al.* 2018). Thus, we predicted that host sex and body mass will have a reduced impact on parasite abundance after mast versus non-mast years.

We tested these notions in a study system consisting of fleas infesting yellow-necked mice [*Apodemus flavicollis* (Melchior, 1834)] in a beech (*Fagus sylvatica*) forest. We conducted 4 years of rodent trapping and parasite surveys over contrasting conditions of seed availability and rodent abundance (2 post-mast years of high rodent abundance, interlaced with 2 years of population crashes that occurred after seed production failures). We found that the most basic predictions are insufficient to describe the relationship between host and parasite populations in this system. Instead of a linear trend, we found a hump-shaped relationship between yellow-necked mouse and flea abundance. We also determined that hosts with the highest body mass tended to host the most fleas, host sex did not affect flea loads, and, contrary to our predictions, masting did not influence these patterns.

MATERIALS AND METHODS

Natural history

European beech (*F. sylvatica*) is a large (30–40 m tall), monoecious broadleaved tree that is widely distributed and economically important in Europe (Packham *et al.* 2012). Beech is flowering in April–May and seeds fall in autumn, often after first frosts (Packham *et al.* 2012). Seeds are relatively large (12–18 mm long: Packham *et al.* 2012), highly nutritious (see Grodziński & Sawicka-Kapusta 1970), and consumed by a wide range of granivores (Packham *et al.* 2012). Beech masts every 2–12 years; in the long term, average interval between mast events varies between 4 and 8 years (Pidek *et al.* 2010). Mast years are typically followed by a complete seed production failure next year (Bogdziewicz *et al.* 2020).

Yellow-necked mouse is a common rodent in forests of Europe and western Asia (Pucek 1981). Adults weigh between 20 and 60 g and measure between 80 and 130 mm in length (head and body; tail is again as long). The yellow-necked mouse is solitary, nocturnal, and omnivorous. Home ranges of males are considerably larger than those of females (Stradiotto *et al.* 2009). Yellow-necked mice are considered tree seed specialists (Selva *et al.* 2012), and abundance of the yellow-necked mouse strongly fluctuates in response to tree masting (Zwolak *et al.* 2016a,b). Typically, after autumn masting, the abundance of mice is high in the spring and summer the following year, and crashes to very low numbers 2 years after masting (Zwolak *et al.* 2016a, 2018). The post-mast increases are associated with high overwinter survival and winter breeding (Jansen 1982; Pucek *et al.* 1993). Causes of the subsequent crashes probably involve density-dependent inhibition of maturation and breeding, or the action of natural enemies, such as predators, disease, or parasites (Pucek *et al.* 1993; Elias *et al.* 2006; Pedersen & Greives 2008).

Fleas (Insecta, Siphonaptera) are laterally flattened, wingless, periodic ectoparasites of higher vertebrates, with preference for small, burrowing mammals. Their hind legs are long and highly adapted for jumping. Flea life cycle consists of several larval stages followed by complete metamorphosis (Bitam *et al.* 2010). In most species, worm-like larvae are not parasitic and feed on organic matter found in the host nest, while the adults rely on blood meals. Between blood meals, adult fleas may occur on the host itself ("fur fleas"), or in host dens or other resting places ("nest fleas") (Krasnov *et al.* 2008). The transmission of fleas is direct and results from synchronous or asynchronous use of the same nests by different hosts, and from physical contact. Fleas are important vectors of numerous diseases (viral, bacterial, and rickettsial) and parasites (protozoans and helminths) (Bitam *et al.* 2010).

Study sites

We conducted this research over 4 years (2010–2013) in Gorzowska Forest, located in Western Poland (52.77°N, 15.07°E, elevation 60–80 m). The study area is situated in a temperate climate zone. It receives an average annual precipitation of 523 mm, and its mean monthly temperatures range from −4°C in January to 23°C in July. We selected 12 stands located in beech forests (8 used in 2010–2012; 12 in 2013). The stands were single-aged, about 80 years old, and managed for wood. Mast years occurred in 2009 and 2011, with seed production of about 300 seeds per m^2 during both events (counted on the ground: see Hilton & Packham 1997; Chianucci *et al.* 2021). In 2010 and 2012, beech did not produce viable seeds. See Zwolak *et al.* 2016a,b for further details on study sites and seed production.

Trapping procedure

The trapping was conducted each year of the study during June–September, in 5-day sessions at monthly intervals. At each stand, we established an 8 × 8 trapping grid, with 10-m spacing between trap points (0.49 ha). At each trap point, we placed one wooden live trap ("dziekanówka" type, widely used in Poland; size 21 × 8 × 9.5 cm; produced by A. Marcinkiewicz, Rajgród, Poland) baited with rolled oats and sunflower seeds. The traps were checked every morning (starting at ∼0800) and evening (starting ∼1800). We recorded species and sex of all captured animals, visually estimated their reproductive status (dividing males into scrotal vs. non-scrotal, and females into pregnant vs. lactating vs. not pregnant/lactating), weighted them using Pesola$^{\text{TM}}$ scales, and marked with uniquely numbered Monel ear tags (National Band & Tag Company, Newport, USA). Finally, captured yellow-necked mice were placed for 1–2 min in white cotton bags, and their fur was gently ruffled. Then, we released mice, and collected fleas that escaped onto the bag. This method has been successfully used before (Kowalski *et al.* 2014), but to provide additional validation, we carefully combed the fur of 100 individual mice for additional fleas. We found a high correlation between flea abundance measured with the cotton bag method, and the cotton bag plus combing method (Pearson's $r = 0.90$, 95% CI: 0.85–0.93).

Yellow-necked mice, followed by bank voles (*Myodes glareolus*) were the most common species captured (Zwolak *et al.* 2016a). Since both yellow-necked mice and bank voles feed on seeds and increase in abundance after beech masting, their abundances were highly correlated (Zwolak *et al.* 2016b). Other, relatively rare species included field mice (*Apodemus agrarius*), harvest mouse (*Micromys minutus*), voles (*Microtus* spp.), and shrews (*Sorex araneus* and *S. minutus*) (Zwolak *et al.* 2016a).

Flea identification

Fleas collected from yellow-necked mice were preserved in vials filled with 70% ethyl alcohol. A random subset of fleas was identified to species ($n = 837$; species identification was conducted in 3 out of 4 years of the study: 2010, 2011, and 2013). These individuals were processed with the O'Mahony's method and mounted on microscope slides using Canada balm (Rosický 1957). The fleas were identified to species using morphological features and keys developed by Rosický (1957), Skuratowicz (1967), Beaucournu and Launay (1990), and Brinck-Lindroth and Smit (2007).

Statistical analyses

To analyze the effects of masting on yellow-necked mouse abundance, we used a generalized linear mixed model (GLMM) with the number of unique individuals captured at a given site in each trapping session as the response variable. Explanatory variables included masting (categorical variable: yes or no) in interaction with month (categorical variable with 4 levels). Site was included as a random intercept effect. We used quasipoisson error distribution and log link function.

All flea species were pooled for analyses because our hypotheses concerned total flea burden. To analyze the effects of changes in host abundance on fleas, we used a GLMM with flea abundance (per host) as the response variable. Explanatory effects included host abundance (the number of unique yellow-necked mice captured in a given trapping session at a given site: linear and quadratic effect), masting, and month. Using the sum of yellow-necked mouse and bank vole abundance as an explanatory variable (an index of total host density: see e.g. Stanko *et al.* 2002; Young *et al.* 2015) did not improve model fit (evaluated with Akaike Information Criterion). To verify whether masting affects the relationship between flea and host abundance or the temporal dynamics of flea abundance, we included interactions between host abundance and masting, and between month and masting. Random intercepts included host ID (i.e. unique individual mouse) and study site. Model diagnostics revealed temporal autocorrelation of residuals; thus, we also included first-order autoregressive (AR1) temporal correlation structure in the model. We used negative binomial error distribution (log link function).

Parasite abundance is a function of prevalence (the fraction of hosts infected) and mean intensity (mean number of parasites in infected hosts: Bush *et al.* 1997). We also analyzed prevalence separately to check if this measure reveals new patterns. Flea prevalence was estimated in the same manner, but the model had binomial error distribution (log link function).

Effects of host individual traits on flea abundance were modeled with body mass, sex, and their interactions with mast as explanatory variables. Random intercepts involved host and study site. The model included temporal autocorrelation and had quasipoisson error distribution (log link function). Effects of host individual traits on flea prevalence were estimated using a similar model, but with binomial error distribution (logit link function).

We analyzed data in R (R Core Team 2021). Generalized linear mixed models were implemented with package *glmmTMB* (Brooks *et al.* 2017) and evaluated with packages *performance* (Lüdecke *et al.* 2021) and *DHARMa* (Hartig 2022). We used package MuMIn (Bartoń 2020) to calculate coefficients of determination (pseudo-R^2, Nakagawa & Schielzeth 2013) for abundance models; in logistic regression (prevalence models), R^2 is less useful because it can be very low even for perfect regression relationships (Mittlböck & Schemper 1996). Marginal R^2 represents variance explained by fixed factors and conditional R^2 variance explained by both fixed and random factors (Nakagawa & Schielzeth 2013).

RESULTS

Host abundance

Yellow-necked mouse abundance was about 5 times higher during summers after mast years, relative to summers after non-mast years ($\chi^2 = 175.1$, df = 1, $P < 0.0001$; Fig. 1). The monthly dynamics were also influenced by masting (interaction mast × month: $\chi^2 = 26.4$, df = 3, $P < 0.0001$). After mast years, the

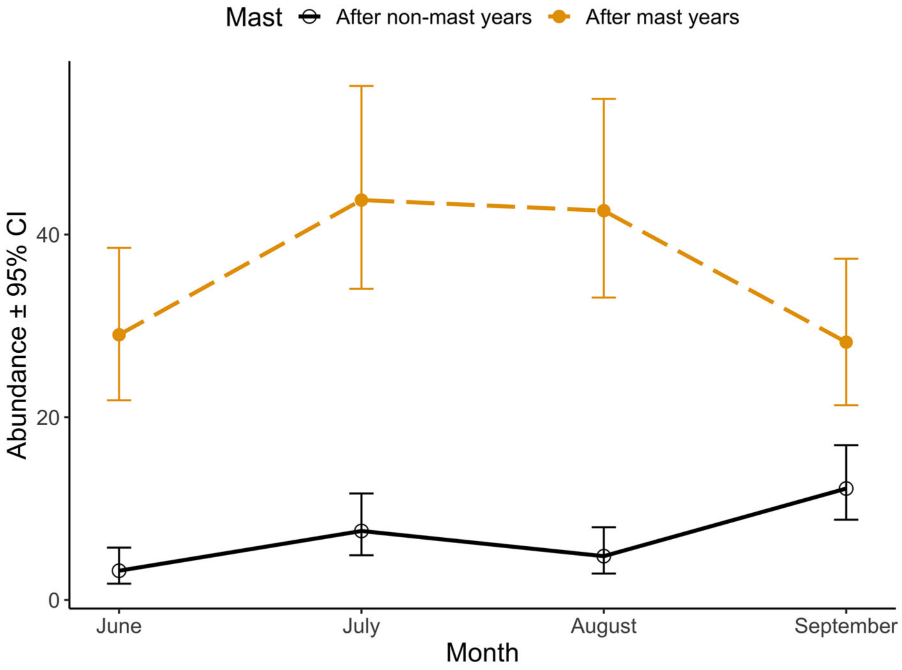

Figure 1 Monthly dynamics of yellow-necked mouse abundance (per trapping grid, 0.49 ha) after mast (dashed line) and non-mast (solid line) years. The estimates are from a quasipoisson generalized linear mixed model (see Materials and Methods) and whiskers represent 95% confidence intervals.

abundances peaked in June and July; after non-mast years, the abundance was highest in September (Fig. 1). The coefficient of determination (R^2) for this model equaled 0.747 (marginal) and 0.790 (conditional).

Flea abundance and prevalence

We collected a total of 3725 fleas from 1273 infested mice (prevalence 59%). We identified 7 flea genera and 10 species (Table S1, Supporting Information). *Ctenophthalmus agyrtes* accounted for 48% of fleas, *Ctenophthalmus solutus* for 34%, and *Megabothris turbidus* for 7%. Other species contributed less than 5% of individuals. The abundance ranking was similar across years (Table S1, Supporting Information).

The abundance of fleas had a hump-shaped relationship with host abundance (Table 1A; Fig. 2). After accounting for changes in mouse abundance, masting did not affect flea populations (Table 1A). However, the monthly dynamics of flea abundance differed between mast and non-mast years (Table 1A). After non-mast years, flea abundance declined over the summer, but after mast years, the highest flea abundance occurred in August (Fig. 2). Marginal R^2 for this model equaled 0.149, and conditional $R^2 = 0.283$. Flea prevalence mirrored the temporal patterns of flea abundance, but was not influenced by mouse abundance (Table 1B).

Mice with higher body mass were more heavily parasitized by fleas (body mass effect in Table 2). Host sex did not affect flea abundance nor prevalence (sex effect in Table 2). Masting had a significant effect on flea prevalence, and marginally non-significant on flea abundance (Table 2; note that this effect was most likely mediated by mast-related changes in host abundance: Table 1). Contrary to our predictions, masting did not modify the effects of host body mass or sex on flea abundance or prevalence (although the mast x body mass interactions approached significance: Table 2; Fig. 3). The host traits model explained relatively little variation in flea abundance: marginal R^2 equaled 0.096, and conditional $R^2 = 0.843$.

DISCUSSION

We found that tree reproductive cycle influenced ectoparasite abundance on their rodent hosts. Most likely, the effect of masting was indirect, mediated through changes in host population density. However, the hump-shaped relationship between host and parasite abundance reported in this study was more complex than the linear relationships outlined in our predictions. The abundance

Table 1 Determinants of abundance (A) and prevalence (B) of fleas parasitizing yellow-necked mice (*Apodemus flavicollis*)

Predictor	χ^2	df	*P*-value
(A)	Flea abundance		
Host abundance (quadratic effect)	12.1	2	**0.002**
Masting	0.6	1	0.443
Month	81.9	3	**<0.0001**
Host abundance (quadratic effect) × masting	3.2	2	0.199
Masting × month	22.5	3	**<0.0001**
(B)	Flea prevalence		
Host abundance (quadratic effect)	2.6	2	0.271
Masting	1.91	1	0.167
Month	48.7	3	**<0.0001**
Host abundance (quadratic effect) × masting	5.12	2	0.077
Masting × month	9.47	3	**0.024**

Significant effects are in bold.

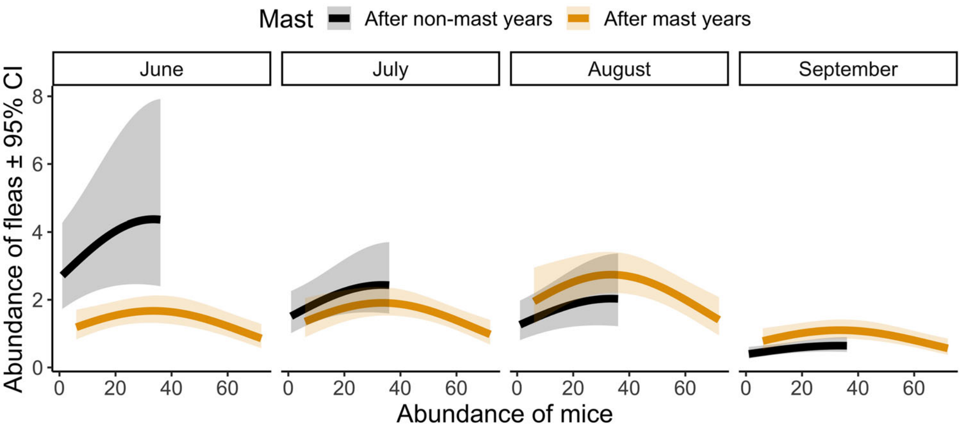

Figure 2 Hump-shaped relationship between flea and host abundance, estimated across months (June–September) and after mast (yellow) versus non-mast (black) years. Lines denote estimates from a negative binomial generalized linear mixed model. Shaded regions denote 95% confidence intervals.

of fleas had a positive relationship with yellow-necked mouse abundance when host densities were low to intermediate (<40 individuals/site). This is in agreement with basic models of density-dependent transmission (Anderson & May 1978). Yet, contrary to the mass-action model, when host densities were high (>40 individuals/grid), the relationship changed to negative, and flea abundance declined. Furthermore, even though some rodent densities recorded in this study were extremely low, we did not find a host density threshold, which would be necessary for parasite persistence, as predicted by basic theoretical models (Anderson & May 1978; McCallum *et al.* 2001; see also Renwick & Lambin 2013).

Such a hump-shaped pattern of abundance is infrequent in host–parasite interactions. Studies typically find a positive relationship between host and endoparasite abundance (reviewed by Arneberg *et al.* 1998). In contrast, studies on ectoparasites often found a negative relationship (Stanko *et al.* 2002; Renwick & Lambin 2013; Zwolak *et al.* 2013; but see e.g. Young *et al.* 2015). Few researchers reported more complex patterns (e.g. curvilinear increase to a plateau: Krasnov *et al.* 2002a). Perhaps the dominance of linear trends in published studies reflects that most investigations have been limited to first-order effects of host abundance. Moreover, to detect the hump-shaped relationship, it is necessary to

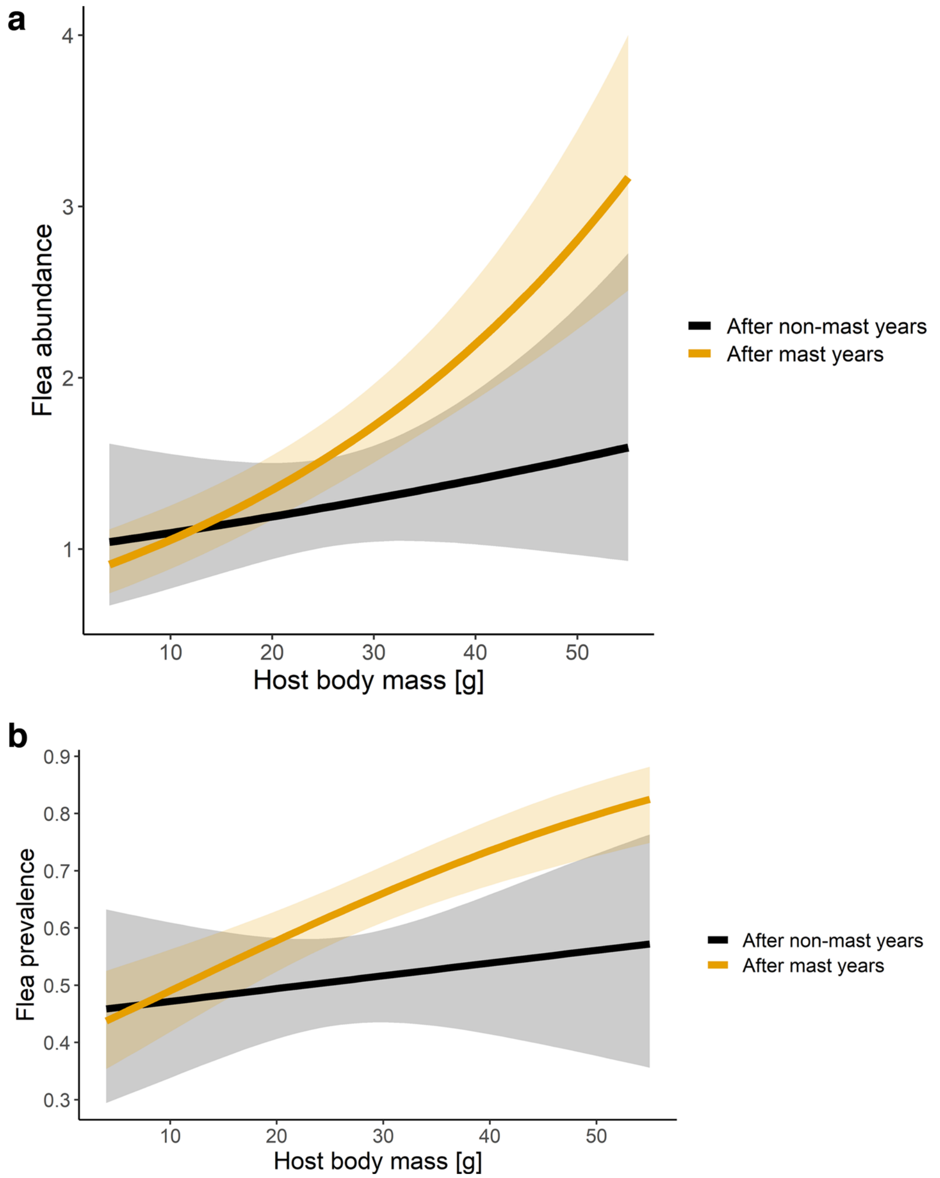

Figure 3 Relationship between host body mass, flea abundance (a), and flea prevalence (b). Lines represent estimates from negative binomial (b) and binomial (b) generalized linear mixed models. Shaded regions denote 95% confidence intervals. The interactions between host body mass and masting did not reach statistical significance (abundance: $P = 0.09$; prevalence: $P = 0.10$).

investigate a wide range of host densities (Fig. 1). This condition is fulfilled in masting systems, where densities of granivorous hosts can be extremely high after masting, but then typically crash to very low numbers (Ostfeld & Keesing 2000).

What could be the mechanism of non-linear changes in flea abundance? An increase in host density leads to increased contact rates among individuals, and higher probability of parasite transmission (Côté & Poulin 1995; Sih *et al.* 2018; Fernandes *et al.* 2021). In our study system, the potential for higher contact rates at high host densities is indicated by increased home range overlap that occurs in yellow-necked mice after mast years (Bogdziewicz *et al.* 2016c). Perhaps this effect caused an increase in flea abundance, which was reversed when fleas began to compete with each other (e.g. for high-quality feeding spots on the host: Hawlena *et al.* 2007), and when hosts started suffering from high

Table 2 Effects of individual host traits on abundance (A) and prevalence (B) of fleas parasitizing yellow-necked mice (*Apodemus flavicollis*) after mast and non-mast years

Predictor	χ^2	df	*P*-value
(A)	Flea abundance		
Body mass	47.12	1	**<0.0001**
Sex	0.05	1	0.829
Masting	3.81	1	0.051
Body mass × masting	2.87	1	0.090
Sex × masting	0.16	1	0.692
(B)	Flea prevalence		
Body mass	23.67	1	**<0.0001**
Sex	0.01	1	0.922
Masting	7.19	1	**0.007**
Body mass × masting	2.66	1	0.103
Sex × masting	0.54	1	0.463

Significant effects are in bold.

infestation levels. Skin inflammation (dermatitis) caused by flea bites triggers increased grooming (Eads *et al.* 2017), which causes flea mortality and plays a crucial role in host-mediated regulation of ectoparasite loads (Hawlena *et al.* 2007). It is unclear, however, why this effect would lead to a decline in flea abundance, rather than a plateau (Krasnov *et al.* 2002a).

An alternative explanation is that host population growth increases a proportion of "transient" individuals with no burrows (Gliwicz 1992). Burrows are necessary for flea reproduction and larvae development (Krasnov *et al.* 2002a). Thus, transient individuals can affect flea transmission, but do not participate in their life cycle (Krasnov *et al.* 2002a). A growing proportion of transient individuals in high density host populations might dilute flea abundances. We note, however, that an increase in the proportion of transient animals was thought to cause a decline in flea prevalence in Krasnov *et al.* (2002a), but in our study prevalence was unaffected by changes in host abundance. Nevertheless, an increase in transient hosts could act synergistically with increased grooming, leading to a decline in flea abundance at high rodent densities. Finally, changes in flea abundance with host numbers were unlikely to be driven by alterations in flea communities because flea species composition remained similar in the years of high and low rodent density (Table S1, Supporting Information).

We also detected that mast and non-mast years differed in the monthly dynamics of flea abundance and prevalence. Causes of seasonality in parasite infestations are complex and can be difficult to pinpoint (Altizer *et al.* 2006). In our study system, seasonality in flea abundance can result from direct weather effects on flea survival (Krasnov *et al.* 2001, 2002b), but also from seasonal changes in host social behavior, population structure, and immune defenses (Altizer *et al.* 2006). Masting can influence all these factors. First, beech masting is associated with specific weather conditions (Bogdziewicz *et al.* 2017; Nussbaumer *et al.* 2018), which can affect flea reproduction and survival, and contribute to the differences in monthly dynamics during mast and non-mast years. Furthermore, mast-related fluctuations in population size can affect host behavior (including space use: Bogdziewicz *et al.* 2016c), population structure (Falls *et al.* 2007), and body condition (Bogdziewicz *et al.* 2016b). Thus, determining the exact mechanism of the differences is challenging.

On the other hand, masting did not modify the influence of body mass on parasite loads (prevalence and abundance) and did not change the lack of relationship between flea loads and host sex. Thus, our prediction that masting modifies the influence of host traits on ectoparasite infestation was not supported. We found that host mass was positively associated with flea prevalence and abundance. In many species, larger individuals have more parasites (e.g. Young *et al.* 2015; Meagher *et al.* 2019), and the interaction between yellow-necked mice and fleas fits this pattern. The most popular hypotheses that explain such findings state that larger individuals represent an easier and higher quality target for parasites because such hosts eat more, range further, and provide parasites with more resources, or that there is a trade-off between growth and immunity that leaves larger hosts more vulnerable (van der Most *et al.* 2011).

In mammals, males often harbor more parasites than do females (Moore & Wilson 2002). In many cases, this difference is apparent even after accounting for sex-related differences in body size (Zwolak *et al.* 2013; Patterson *et al.* 2015; Hammond *et al.* 2019) and can be caused by the immunosuppressive effect of testosterone (Trigunaite *et al.* 2015), and by male–female differences in ranging or grooming behavior (Krasnov *et al.* 2012). In other species, males and females do not differ in parasite loads or the difference can be attributed to body size dimorphism (Moore & Wilson 2002). This seems to be the case with *Apodemus* mice and their ectoparasites: males tend to be more heavily infested than females, but they are also larger, and after taking into account the body size, the sex-bias in the ectoparasite abundance and prevalence vanishes (this study; Harrison *et al.* 2010;

Kowalski *et al.* 2014). This also explains why masting did not change this pattern. While changes in food resources associated with masting could, at least in theory, affect the magnitude of sex differences in immunocompetence (through effects on body condition) or in ranging patterns (Bogdziewicz *et al.* 2016b), they are unlikely to affect body size dimorphism because it results from sexual selection (Moore & Wilson 2002).

As a caveat, studying ecological responses to masting is inherently difficult because only multidecade data sets can contain numerous repetitions of masting events. Our research was based on a 4-year series of observations, which included 2 mast years. A longer time series would be needed to exclude the possibility of more complex dynamics, such as long time lags between peaks of the flea and rodent abundance. This remains an important direction for future studies.

Another apparent caveat is that our models explained relatively low proportion of variation in flea abundance. This indicates their limited predictive power. However, our goal was to test the hypothesized relationships between tree masting and flea populations. Thus, we divided the models into 2 groups (one focused on the effects of changes in host populations and another on the effects of hosts traits) rather than try to construct one, highly predictive model.

In conclusion, we documented non-linear changes in parasite abundance with increase in host density. Such a phenomenon indicates that mechanisms driving flea infestation are more complex than predicted by the basic epidemiological models or the dilution effect. Moreover, our results demonstrate that pulses of tree reproduction can drive patterns of ectoparasite infestation in granivorous hosts. While previous studies documented that masting, and subsequent increase in rodent host abundance, leads to a higher density of free-ranging ectoparasite stages (tick nymphs: Jones *et al.* 1998; Bregnard *et al.* 2021), this study is the first to document masting-related changes in ectoparasite infestation of individual hosts. Thus, it reveals another indirect effect of masting on interactions in forest food webs (Clark *et al.* 2019).

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Proportional abundance (in %) of fleas infesting yellow-necked mice in Gorzowska Forest in 2010 ($n = 216$), 2011 ($n = 490$), and 2013 ($n = 131$). Identification of flea species was not conducted in 2012. Percentages of the 3 most abundant species (each year and in total) are in bold.

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