Host body size, not host population size, predicts genome-wide effective population size of parasites

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Abstract

The effective population size (N_e) of an organism is expected to be proportional to the total number of individuals in a population (Frankham, 1995). In parasites, we might expect the effective population size to be proportional to host population size and host body size, because both are expected to increase the number of parasite individuals (Barret et al., 2008). However, parasite populations are sometimes so extremely subdivided that high levels of inbreeding may distort these relationships (Huyse et al., 2005). Here, we used whole-genome sequence data from dove parasites (71 feather louse species of the genus *Columbicola*) and phylogenetic comparative methods to study the relationship between parasite effective population size and host population size and body size. We found parasite effective population size is largely explained by host body size but not host population size. These results suggest the subdivided nature of parasite populations, rather than the overall number of parasites, has a stronger influence on the effective population size of parasites.

Main Text

Introduction

The effective population size (N_e) of an organism has a profound impact on evolutionary processes, such as the relative contributions of selection and genetic drift to genomic change (4). For free-living organisms, it is expected that N_e is proportional to the total number of individuals in a population (1). While population size estimates can often be readily obtained for free-living species, estimating the population size of parasites can be more challenging because this usually requires sampling from individual hosts.

Typically, we might expect that the size of a parasite population is proportional to that of the host, because parasites rely on their hosts for survival and reproduction (2). However, population subdivision can influence measures of N_e for a species (5). Theoretical expectations generally predict that subdivided populations have a higher overall N_e than non-subdivided ones (4). On the other hand, in highly divided populations, levels of inbreeding can increase, such that the N_e of these subdivided populations is low (3).

In the case of parasites, populations can sometimes be so extremely subdivided that each individual host harbors a distinct parasite population, termed infrapopulation (7). This subdivision is particularly pronounced in the case of parasites that spend their entire lifecycle on the host (i.e., permanent parasites). For example, lice, which are permanent parasitic insects of birds and mammals, have highly structured infrapopulations subject to high levels of inbreeding (8). We might expect that infrapopulation size influences the effective population size of a parasite. This effective population size, in turn, could influence the amount of genetic variation within an infrapopulation, as has been shown for feather mites (9).

Host body size has been shown to strongly impact infrapopulation size, with larger-bodied hosts harboring larger parasite infrapopulations (10). For example, a positive effect of host body size on parasite abundance has been shown for avian feather lice, which feed on the feathers of their hosts (11). Thus, we would expect that feather lice on larger-bodied avian hosts would have higher N_e, reflecting their larger infrapopulation sizes. This relationship, in turn, should affect the degree of inbreeding and be evident in the genetic variation in lice of different infrapopulation sizes.

Thus, two factors may influence a parasite's N_e: 1) host population size and 2) host body size. We test the relative contributions of these two factors to parasite N_e by examining genome-wide variation in the wing lice (Phthiraptera: *Columbicola*) of pigeons and doves (Aves: Columbidae). Pigeons and doves vary dramatically in overall population sizes, with some species being among the most abundant birds on earth and others restricted to single small islands and highly endangered. In addition, pigeons and doves vary by over an order of magnitude in body mass, and smaller-bodied species have been shown to have smaller infrapopulations of these lice (10). Thus, pigeons and doves and their lice are an excellent system in which to examine the correlation between both host population size and host body size and parasite N_e. We used genome sequencing of 71 species of *Columbicola* to estimate a phylogeny for these parasites and examine the relationship between a genome-wide measure of effective population size (θ) and the overall population size and body size of their respective hosts, accounting for phylogeny.

Results

We found a strong positive relationship between θ, a metric directly proportional to N_e, and host body size (PGLS, Brownian: $R^2_{pred} = 0.44$, $p < 0.001$; Pagel's λ: $R^2_{pred} = 0.48$, $p < 0.001$; Fig. 1). In contrast, there was no significant relationship between θ and host population size (PGLS, Brownian & Pagel's λ: $p > 0.05$). Including host population size in the best model led to a small improvement in the overall model fit (PGLS, Pagel's λ including host population size, R^2_{pred} =

0.52), but the host population size term remained non-significant (PGLS, Pagel's λ model including host population size, $p > 0.05$).

Discussion

For parasites such as lice, hosts represent their habitat (10). Host body size largely explains parasite infrapopulation size (11). Genome scale data for parasitic lice of pigeons and doves revealed that metrics (θ), associated with effective population size (N_e), are also highly correlated with host body size. In contrast, there was little association between parasite effective population size and host population size. Thus, it appears that the smaller infrapopulation sizes on smaller-bodied hosts increase the amount of inbreeding to such a degree that N_e is also reduced on smaller bodied hosts, eliminating any effects of overall parasite population size.

One factor facilitating the effect of host body size on N_e may be the low migration rates of permanent parasites. Migration among parasite infrapopulations is expected to increase N_e. However, permanent parasites, such as lice, have minimal dispersal capabilities and thus migration rates are expected to be very low. While host population size has been previously identified as a potential driver of parasite population dynamics (13), the lack of relationship between parasite N_e and host population size might be indicative of these very low migration rates. In this case, N_e is mainly influenced by the inbreeding of infrapopulations and not by the overall size of the total parasite population, because low migration prevents the overall population from approaching panmixis.

Another factor to consider is that smaller-bodied host species also typically have a lower parasite prevalence (*i.e.*, proportion of host individuals that are inhabited by the parasite) (9). This pattern might be due to smaller infrapopulations being more susceptible to local extinction because of environmental and demographic stochasticity, a known factor shaping N_e (4, 13). Therefore, host body size could influence local extinction probability and thus play a role in determining N_e of permanent parasites.

Considerations of effective population size also have implications for conservation. Parasites are among the earth's most diverse, threatened, and under-protected animals (14). Under the global parasite conservation plan, risk assessment, along with applying conservation genomics to parasites, were identified as two of the major goals for parasite conservation over the next decade (15). Our result that host body size, but not host population size, is a good predictor of parasite N_e can easily translate into parasite conservation practices, drawing attention to conservation of smaller bodied hosts as a practice to conserve parasites.

Overall, our study shows that host body size plays a major role in shaping parasite population genomics and provides evidence for the essential role that individual hosts play as habitat for permanent parasites with very limited transmission abilities.

Materials and Methods

We sampled 89 specimens representing 71 different species of *Columbicola* (Table S1) and performed genomic sequencing on these individuals. We assembled 2,395 nuclear single-copy orthologue protein-coding genes for each sample, as well as the mitochondrial COI gene. Using these assembled genes, we ran species delimitation analyses, phylogenetic and cophylogenetic analyses, and obtained a time-calibrated phylogenetic tree. We called whole-genome-based SNPs and used these data to estimate θ, a metric related to N_e. We compiled host body and population size data and performed phylogenetic comparative analyses. Full methods are available in the SI Appendix.

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Figures
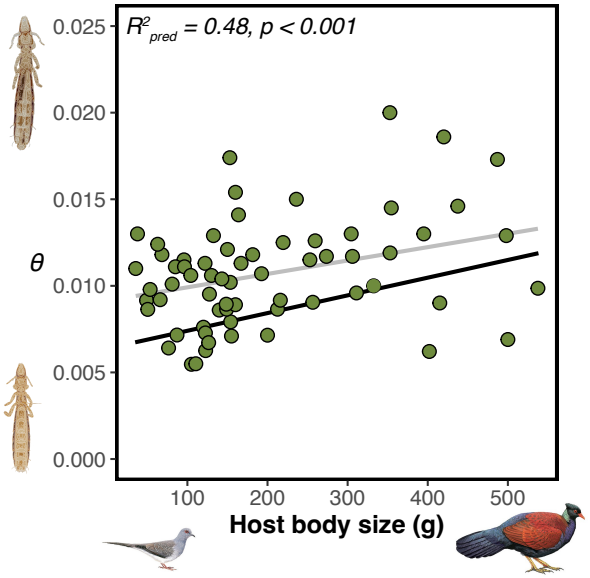
Figure 1. Relationship between a genome-wide measure (θ) of effective population size and host body size. The black regression line corresponds to the PGLS model and the gray regression line to the same GLS model without accounting for phylogenetic non-independence. Credit: louse photos on the left: Stephany Virrueta-Herrera; bird illustrations on the bottom, ©Lynx Edicions.