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The evolution of monogamy is associated with reversals from male to female bias in the survival cost of parasitism

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The extent to which parasites reduce host survival should depend upon how hosts balance trade-offs between reproduction and survival. For example, parasites are predicted to impose greater survival costs under polygynous or promiscuous mating systems in which competition for mates favours increased reproductive investment, particularly in males. We provide, to our knowledge, the first comparative test of the hypothesis that the mating system of the host is an important determinant of (i) the extent to which parasites reduce survival, and (ii) the extent to which males and females differ in the survival cost of parasitism. Using meta-analysis of 85 published estimates of the survival cost of parasitism from 72 studies of 64 species representing diverse animal lineages, we show that parasites impose a mean 3.5-fold increase in the odds of mortality on their hosts. Although this survival cost does not differ significantly across monogamous, polygynous and promiscuous mating systems, females incur a greater survival cost than males in monogamous species, whereas males incur a greater survival cost than females in polygynous and promiscuous species. Our results support the idea that mating systems shape the relative extent to which males and females invest in reproduction at the expense of defence against parasites.

1. Introduction

By definition, parasites reduce host fitness, and they can do so through a variety of mechanisms, such as lowering feeding rate, decreasing fat stores, triggering costly immune responses and inducing behavioural changes that may lead to increased predation [1–4]. Collectively, the deleterious effects of parasites can substantially impact the survival of their hosts [5]. The magnitude of the survival cost of parasitism, as frequently inferred from the relative survival rates of infected versus non-infected hosts, is highly variable across host taxa [5]. This variation is partially explained by differences in the parasites themselves (e.g. parasites with complex life cycles have greater effects on host survival) as well as extrinsic environmental factors (e.g. the risk of host mortality associated with parasitism decreases as latitude increases) [5]. However, concepts from sexual selection and life-history theory suggest that the magnitude of the survival cost of parasitism may often depend upon how hosts balance the trade-off between survival (including resistance, the ability to limit or reduce parasite load, and tolerance, the ability to reduce the costs of a given parasite load) and reproduction (mate acquisition and offspring production) [6–11]. Moreover, the trade-off between reproduction and survival is often expected to differ as a function of sex [12–17] and mating system [12,18–24]. Therefore, host sex and mating system may be important determinants of the extent to which hosts differ in the survival cost of parasitism. Here, we provide, to our knowledge, the first comparative test of the hypothesis that host mating system influences the extent to which parasites reduce host survival, as well as the extent to which males and females differ in this fitness cost of parasitism.

Survival and reproduction are the two primary components of Darwinian fitness. Owing to various constraints limiting maximal investment in both

processes, organisms are often forced to trade current reproduction against survival and future reproduction [8,25–29]. Because mating systems can structure the opportunity for sexual selection and fecundity selection, they can also influence the optimal levels of investment in current reproduction versus survival for one or both sexes [20,22,30–34]. Given that the immune system is intimately related to survival [35,36] and energetically expensive to develop, maintain and use [37–39], and that variation in immune function explains variation in survival [40–43], the immune system is likely to be one of a number of factors mediating the trade-off between reproduction and survival. For example, in a variety of insect species, selection lines evolved under experimentally enforced monogamy have improved survival [30,44–46] and increased immune function [47–49] relative to lines evolved under promiscuity. More broadly, mating system and reproductive investment are correlated with and known to causally affect longevity, survival and immune function [30,44,50–56]. Through this mechanism of immune function, variation in sexual selection and reproductive investment is hypothesized to explain variation in the survival cost of parasitism [6]. Given that polygynous and promiscuous mating systems lead to increased sexual selection relative to monogamy, we expect the survival cost of parasitism to be greater in those systems. However, in some systems and circumstances, sexual selection may reinforce natural selection [57,58], and thus has the potential to drive evolutionary increase in host resistance and tolerance to parasites. Moreover, if mating carries an increased risk of infection, polygynous and promiscuous systems may favour increased immune function over monogamous systems [59].

Males and females often use different life-history strategies, with females favoured to balance current reproductive success against survival and future reproduction, whereas males are often favoured to maximize current mating success at the expense of survival [10,12,60–66]. Sex differences in allocation to reproduction versus survival may be mediated in part through differential investment in immune function, leading to sex differences in the fitness costs associated with parasitism [67,68]. For example, in broiler chickens (*Gallus gallus domesticus*) descended from promiscuous jungle fowl, males have weaker antibody responses and greater hatchling mortality than females, and also suffer greater mortality than females when challenged with pathogenic bacteria [69]. By contrast, the reproductive interests of males should largely overlap those of females under monogamy, and selection on patterns of allocation between mating success and survival should generally be more similar between the sexes under monogamy than under polygyny or promiscuity. Therefore, any sex differences in the survival cost of parasitism in monogamous species should be shaped primarily by sex differences in aspects of reproductive investment other than mating, such as egg and offspring provisioning, which should reduce male bias in the survival cost of parasitism and could even lead to greater survival costs in females [70].

While there is no general pattern of male- or female-biased parasitism across all animals, it is common for one sex or the other to exhibit a higher parasite burden in any given lineage or species [71–74]. Often, such evidence of sex-biased parasitism has been implicitly assumed to translate into a sex bias in the cost of parasitism. However, males and females may also differ in their tolerance of

parasites [75,76], such that a sex bias in parasite burden does not necessarily correspond to a sex difference in the fitness costs of parasitism. Although previous meta-analyses have shown that sex biases in parasitism are common in many taxa [71,72,74] and that parasites generally impose a substantial fitness cost in terms of host survival [5], it is presently unknown whether there is an overall trend towards male or female bias in the survival cost of parasitism, or whether host characteristics such as mating system influence the magnitude and direction of sex bias in this cost. Here, we address these questions using a meta-analysis of experimental and descriptive studies in which survival is reported separately for individuals that are either parasitized or not. In addition to estimating the overall extent to which parasites reduce host survival, we also test (i) whether the magnitude of the survival cost of parasitism differs as a function of host mating system, (ii) whether male and female hosts differ in the survival cost of parasitism, and (iii) whether the magnitude and direction of sex bias in the survival cost of parasitism differs as a function of host mating system. Relative to monogamous species, we predict that polygynous and promiscuous species will (i) suffer a greater survival cost of parasitism and (ii) exhibit a relatively larger male bias in the survival cost of parasitism.

2. Methods

(a) Data acquisition

We conducted a systematic literature search for studies investigating the effects of parasitism on survival using Web of Science and including any studies published before July 2020. We searched using logical combinations of the following keywords: parasit*, pathogen, virus, viral, protist, gregarine, fluke, trematode, cestode, mite, tick, nematode, acanthocephal*, botfly, ectoparasite, flea, louse, surviv*, mortality, virulen*, longevity, removal, treatment, infect*, experiment, medicine, medication, anthelmintic, anti, fumigation, exposure, inject*, male bias, female bias and sex bias. We included studies that quantified the survival of parasitized versus unparasitized individuals using experimental infection with parasites, experimental removal of parasites or natural variation in the presence or absence of parasites. We excluded studies that did not provide information on costs of parasitism separately for each sex. We included all animal taxa with distinct male and female sexes except for domesticated animals. We included only those studies that reported a measure of variance associated with survival, and induced a significant change in the parasite load with experimental infection or removal. A PRISMA flow diagram depicting the filtering of the studies is provided in the electronic supplementary material, figure S1. When infection studies used more than one dose of parasites, we took the weighted average across parasite doses, with each dose class weighted by its respective variance [77].

We quantified the effect size for each study as the natural log of the odds ratio for mortality (LOR), which is calculated by classifying each individual as either parasitized (P) or unparasitized (U) at the beginning of an interval, recording each individual as either dead (D) or alive (A) at the end of that interval, using these count data to calculate the odds of mortality for parasitized and unparasitized groups, and then calculating their ratio as

$$\ln(\text{odds ratio}) = \ln\left(\frac{P_D/P_A}{U_D/U_A}\right) = \ln\left(\frac{P_D U_A}{U_D P_A}\right) = \text{LOR}.$$

The sampling variance in the LOR is calculated as the sum of the inverse of each cell (P_D, P_A, U_D, U_A) [78]. If any of these four

cells contained a value of five or less, we used Jewell's small sample size correction to calculate the LOR and its associated sampling variance [79]. If count data were not presented in a study, we calculated them using data on the proportion of alive or dead individuals in each category and their respective sample sizes. When data were unavailable to calculate the odds ratio directly, we used the `compute.es` package in R v. 4.0 to calculate another effect size and convert it to LOR [80].

We classified host mating system as monogamous, polygynous or promiscuous. We defined monogamous systems as those in which both males and females tend to have a single mate throughout a reproductive season. Because many 'socially monogamous' species may actually produce a high percentage of extrapair offspring [81], we also collected genetic data on extrapair paternity whenever possible for all putatively monogamous species. With one exception, all putatively monogamous species for which we obtained genetic parentage data produce fewer than 11% of their clutches with multiple sires (mean = 7.4%, range 4–10% extrapair paternity), so we considered them effectively monogamous [81]. We defined polygynous systems as those in which males tend to have multiple mates whereas females tend to have a single mate. This classification includes species with diverse mating tactics, ranging from the gelada baboon (*Theropithecus gelada*) in which males hold a harem of females to the housefly (*Musca domestica*) in which females are only receptive to a single mating. We defined promiscuous systems as those in which males and females both tend to have multiple mates. We initially included an additional category for polyandrous species, defined as those in which females have multiple mates whereas males tend to have a single mate, but our final dataset did not include any species that fit this criterion. Information on host mating system was gathered from the references listed in the electronic supplementary material, table S1. For each study, we also recorded the following measures as potential confounding sources of variation in the survival cost of parasitism: parasite type (ectoparasite, bacteria, fungus, helminth, protist or virus), study method (parasite removal, parasite infection or natural variation in parasitism), host taxon (arthropod, bird, fish or mammal) and host age (adult, juvenile). The full dataset is presented in the electronic supplementary material, table S1, and is also available online as a spreadsheet (see the Data accessibility statement).

(b) Data analysis

For analysis, we weighted effect sizes (LORs) from each study by the inverse of their respective sampling variances. For the overall cost of parasitism, we used the weighted average of the LOR of males and females from each study with the sampling variance for the average calculated as the inverse of the sum of the male and female weights (inverse of their respective sampling variances) [77]. To assess sex-specific effects of parasitism, we calculated the sex difference for each study (male LOR – female LOR), and calculated the associated sampling variance of this difference as the sum of male and female sampling variances minus the covariance between male and female LOR [77]. The correlation between male LOR and female LOR across the dataset was $r = 0.76$. Study and species were included as random factors in all models. We used profile plots of random-effect estimates to test for over-parametrization. We give estimates of heterogeneity as their raw values (τ^2 or σ^2) as well as their per cent contribution to the total variance (I^2), and for statistical tests of heterogeneity, we used Cochran's Q statistic. We tested for publication bias using a regression of the residuals from our meta-analytic models on the inverse of their respective standard errors (a measure of precision) and performed a trim-and-fill analysis to estimate the number of missing studies and model their potential impact [82,83]. We used the R_0 estimator for the trim-and-fill

analysis [82]. We detected significant publication bias for the average cost of parasitism (intercept = 0.55, s.e. = 0.18, $p = 0.003$), and trim-and-fill analysis indicated funnel plot asymmetry and missing studies (7, s.e. = 4, $p = 0.004$, electronic supplementary material, figure S2). We did not find any indications of publication bias for the sex difference in the LOR (intercept = 0.20 ± 0.15 s.e., $p = 0.18$), nor did trim-and-fill analysis indicate funnel plot asymmetry or missing studies (1, s.e. = 2, $p = 0.25$; electronic supplementary material, figure S3).

First, to test the hypothesis that parasites impose a survival cost on their hosts, we used the `metafor` package for R v. 4.0 [84,85] to perform a random-effects meta-analysis and test whether the grand mean effect size (LOR) describing the survival cost of parasitism differs significantly from zero across our entire dataset ($k = 85$ from 64 species and 72 studies; figure 1*b*; electronic supplementary material, table S1). Second, to test the hypothesis that the survival cost of parasitism is influenced by host mating system, and to account for any potential influence of the additional moderator variables (host taxon, parasite type, study method and host age), we built mixed-effect meta-analytic models containing all additive combinations of all moderator variables using the `multcomp` package for R v. 4.0 [86] ($k = 84$ from 63 species; figure 1*b*). We compared these models using the small sample size-corrected Akaike information criterion (AICc) and retained the top supported model. The top 10 models, with their associated AICc values, are provided in the electronic supplementary material, table S2. Additionally, for each moderator, we calculated an importance value as the sum of the weights of all models containing that moderator (electronic supplementary material, table S3). Third, we tested whether the overall sex difference in the survival cost of parasitism differed from zero using a random-effects meta-analysis ($k = 85$ from 64 species; figure 1*c*; electronic supplementary material, table S1). Fourth, we used the same model building and comparison approach described above to test whether the sex difference in the survival cost of parasitism is influenced by host mating system while accounting for the suite of other potential moderator variables ($k = 84$ from 63 species; figure 1*c*). The top 10 supported models, with their associated AICc values, are provided in the electronic supplementary material, table S4, while the moderators and their importance values are provided in the electronic supplementary material, table S5.

For models investigating the average cost of parasitism, visual analysis of qqplots indicated minor departures of residuals from normality, while qqplots for the sex bias in the cost of parasitism indicated normality (electronic supplementary material, figures S4 and S5). Although non-normality is not a major concern in mixed-effects models and does not bias estimates of fixed effects, it may impact estimates of their standard errors [87]. We, therefore, used smoothed-cases bootstrapping to generate standard errors and confidence intervals (CIs) for the model coefficients from models investigating the average cost of parasitism [88–91]. Details of the bootstrapping procedure are provided in the electronic supplementary material p. S1.

To assess the need for phylogenetic control when estimating the overall survival cost of parasitism and when testing our *a priori* hypotheses about host mating system, we first tested for phylogenetic signal in the survival cost of parasitism (LOR) and in the residuals of the regression of the survival cost of parasitism on the potential moderator variables [92]. We used this same procedure to investigate phylogenetic signal in the sex difference in the survival cost of parasitism. We created a phylogeny (figure 1*a*) using the TimeTree database [93], which uses time since divergence to calculate branch lengths. Twenty-three of the species in our dataset were not represented in the TimeTree database, so we placed them on the phylogeny using the closest related lineage available (electronic supplementary material, table S6). We tested for phylogenetic signal using Pagel's λ with the `phylosig` function in the R package `phytools`

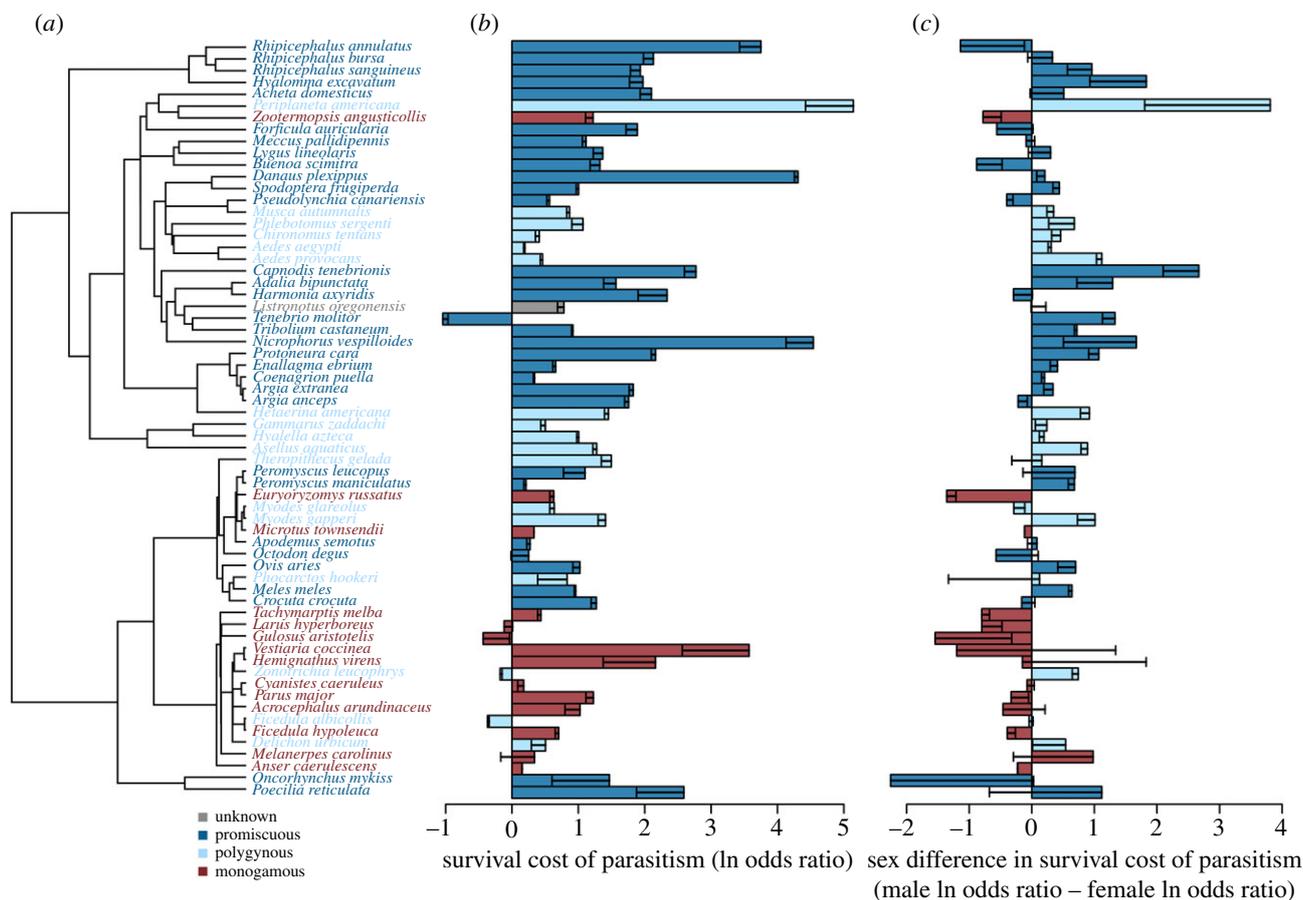


Figure 1. (a) The phylogenetic relationships of the species used; the species are colour coded by mating system. (b) The mean (+ or – the sampling variance) survival cost of parasitism (mean of the ln odds ratio across studies and/or sexes) for each species. (c) The mean (+ or – the sampling variance) difference in the survival cost of parasitism between males and females (sex difference in ln odds ratio across studies). (Online version in colour.)

[94,95]. To account for phylogenetic signal when it was present, we included the λ -transformed phylogenetic correlation matrix as the correlation structure for the random effect of *species* in our meta-analytic models [95,96]. We used the package APE in R v. 4.0 to calculate a distance matrix from the phylogenetic tree using branch lengths and used phytools to λ -transform the phylogenetic variance–covariance matrix, after which we converted it to a correlation matrix [97]. We only found significant phylogenetic signal for the mean survival cost of parasitism ($\lambda = 0.68$, $p = 0.04$) (electronic supplementary material, table S7).

3. Results

(a) Survival cost of parasitism

Across all species, while accounting for phylogeny, we found that parasitism imposes a significant survival cost (mean LOR = 1.25, CI = 1.03–1.55, $\chi^2_1 = 9.57$, $p = 0.002$), with parasitized individuals facing an average of 3.5 times greater odds of mortality than unparasitized individuals. Accounting for phylogeny leaves a significant amount of residual between-study heterogeneity in the survival cost of parasitism across the dataset ($Q_{84} = 944.38$, $p < 0.0001$; electronic supplementary material, table S8). The best supported model as judged by AICc contains the predictors host mating system, study method and host age (electronic supplementary material, table S2), which together explain a significant amount of variation in the survival cost of parasitism ($\chi^2_3 = 18.65$, $p = 0.002$) while leaving a significant amount of residual between-study heterogeneity ($Q_{78} = 641.97$, $p < 0.0001$; electronic

supplementary material, table S8). Of these three factors, study method is the only individually significant factor in the model (method: $\chi^2_2 = 9.03$, $p = 0.01$; host mating system: $\chi^2_2 = 4.52$, $p = 0.10$, figure 2; host age: $\chi^2_1 = 2.61$, $p = 0.11$). Comparison of levels within study method shows that studies using experimental removal or natural variation have significantly lower estimated costs of parasitism than those using experimental infections (electronic supplementary material, table S9). In model comparisons, study method has the highest importance value of all moderators (0.81), while host age (0.53) and host mating system (0.47) are less important and host taxon (0.19) and parasite type (0.01) appear in few well-supported models (electronic supplementary material, table S3 and figure S6).

(b) Sex differences in the survival cost of parasitism

We found a significant overall male bias in the survival cost of parasitism (mean sex difference in LOR = 0.24, CI = 0.07–0.40, $\chi^2_1 = 7.77$, $p = 0.005$) and significant between-study heterogeneity in this estimate of sex bias ($Q_{84} = 195.30$, $p < 0.0001$; electronic supplementary material, table S10). The best supported model as judged by AICc contains the single moderator of mating system (electronic supplementary material, table S4). Mating system explains a significant amount of variation in the sex difference in the survival cost of parasitism ($\chi^2_2 = 27.79$, $p < 0.0001$) while leaving significant residual between-study heterogeneity ($Q_{81} = 125.22$, $p = 0.001$; electronic supplementary material, table S10). Both polygynous and promiscuous species have significantly more

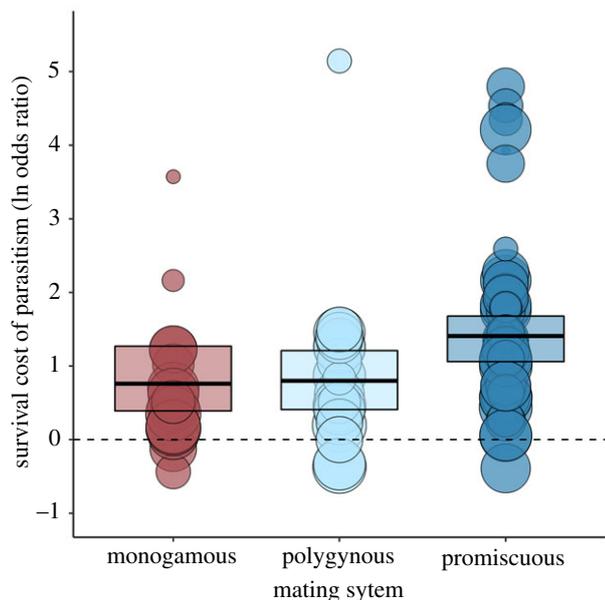


Figure 2. Estimates of the survival cost of parasitism grouped by host mating system. Means from the meta-analytic model are given by the centre line in each box, and the upper and lower edges are the 95% confidence intervals. Points represent means of each individual dataset, with size proportional to the inverse of the variance in the ln odds ratio. The mean survival cost of parasitism does not differ as a function of host mating system. (Online version in colour.)

male-biased costs of parasitism than monogamous species (polygynous–monogamous = 0.90, CI = 0.53–1.26, $p < 0.0001$; promiscuous–monogamous = 0.79, CI = 0.46–1.13, $p < 0.0001$), whereas sex bias does not differ between promiscuous and polygynous species (promiscuous–polygynous = -0.10 , CI = -0.41 to 0.21). Further, promiscuous and polygynous species have significantly male-biased costs while monogamous species have significantly female-biased costs (figure 3). The next best supported model contained the terms mating system and age (electronic supplementary material, table S4), and investigation of this model revealed significant differences between the levels of mating system (as in the case of the best model), but no differences among the levels of age at any level of mating system (mating system: $\chi^2 = 29.19$, $p < 0.0001$; age: $\chi^2 = 0.48$, $p = 0.48$). Further, mating system had the maximum importance value of 1, while age had a substantially smaller importance value of 0.28 (electronic supplementary material, figure S7).

4. Discussion

On average across diverse animal lineages, we found that parasitized individuals have 3.5 times greater odds of mortality compared to unparasitized individuals. This result strengthens the findings of a previous meta-analysis on a smaller dataset [6] by confirming that parasites typically impose severe survival costs on host populations. Importantly, we extend this work by providing, to our knowledge, the first evidence that mating system is also a significant predictor of sex bias in the survival cost of parasitism. Specifically, we show that females experience greater survival costs of parasitism than males in monogamous species, whereas males tend to experience greater survival costs of parasitism in non-monogamous species. This is in line with

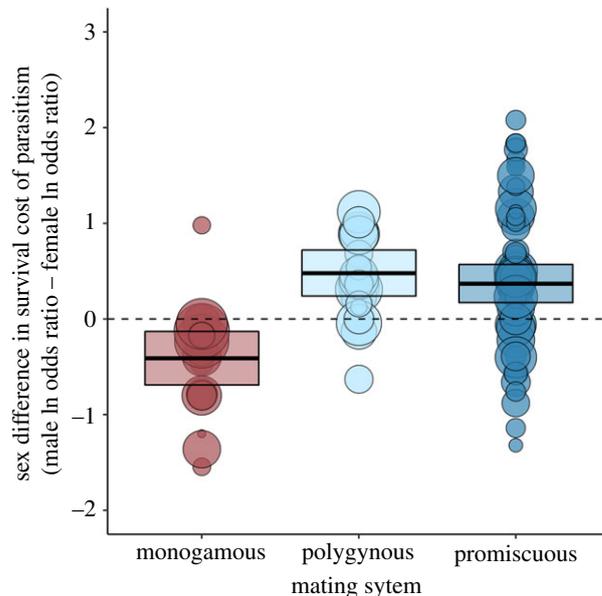


Figure 3. Sex differences in the survival cost of parasitism for species in which males and females were paired within a study, grouped by host mating system. Mean differences are given by the centre line in each box, and the upper and lower edges are the 95% confidence intervals. Points are the sex difference in male and female means for each dataset, with their size proportional to the inverse of the variance in the difference. The mean sex difference in the survival cost of parasitism differs significantly across host mating systems. (Online version in colour.)

previous work showing that male bias in parasite burden is associated with shifts from monogamy to polygyny in mammals [74]. The importance of host mating system and the underlying dynamics of sexual selection and life history may also help explain previous work suggesting that there is no general pattern of male- or female-biased parasitism across animals, despite pronounced sex bias in many lineages and species [71–74]. Collectively, our results are consistent with the idea that different mating systems may predispose males and females to different immune strategies for parasite resistance and/or tolerance while also shaping the relative extent to which males and females invest in reproduction at the expense of defence against parasites.

Increased survival costs of parasitism in males of polygynous and promiscuous species may potentially be explained by the negative relationship between mating rate and survival [98], which may be mediated through immune function. For example, male Indian meal moths (*Plodia interpunctella*) in populations with higher mating rates evolved lower levels of phenoloxidase, an immune defence that correlates with parasite resistance in insects, relative to males in populations with lower male mating rates [49]. This interpretation is supported by our finding that polygynous and promiscuous species exhibit a stronger male bias in the survival cost of parasitism than do monogamous species. However, we also note that many non-monogamous species exhibit a female bias in the survival cost of parasitism, and that the overall survival cost of parasitism is not significantly elevated in promiscuous species, which presumably have the highest mating rates. In monogamous systems where the mating rate is presumably reduced, costs of reproduction other than mating may become more important in structuring the survival cost of parasitism, potentially also driving the evolution of female-biased survival costs [18].

Male bias in the survival cost of parasitism has been proposed as a consequence of divergence in mating and life-history strategies between males and females, with females generally benefiting more than males from investment in survival and future reproduction [6]. In monogamous species, selection on males for investment in current mating success may be reduced in favour of investment in survival and future reproduction, producing a life history more similar to that of females [18,33,99]. In these situations, offspring production, deposition and maternal care, which can be costly in terms of energy, nutrients and immune defence [25,100–102], may lead to relatively higher parasite-mediated mortality in females. Thus, in many monogamous species (and potentially some polygynous and polyandrous species), female reproductive investment may impose a cost of parasite-associated mortality that is equal to or greater than that arising from male investment in courtship and competition for mates. Across mammals, parasitism and overall mortality tend to be sexually equivalent or female-biased in monogamous mating systems, but male-biased in polygynous systems [18,74]. Our findings provide support for the idea that parasitism contributes to overall patterns of sex-biased mortality [18,103], thereby shaping sex-specific patterns of life history and longevity.

The measurement of the survival cost of parasitism used here is directly interpretable as the log of the ratio of the opportunity for survival selection in parasitized populations relative to that in unparasitized populations. Thus, parasites on average cause a 3.5-fold increase in the opportunity for survival selection. By shaping the opportunity for selection, parasites may be key determinants of the strength of selection on a variety of phenotypes. Further, males tend to experience a greater opportunity for parasite-mediated survival selection than females in promiscuous and polygynous species, whereas the opposite occurs in monogamous species. Thus, parasites may also be important in shaping sex-specific patterns of selection via survival and potentially driving sexual conflict. Parasites may also increase the variance in reproductive fitness in a sex-specific manner. For example, in *Drosophila nigrospiracula*, mite parasitism increases the variance in mating success, with males experiencing a greater increase than females [104]. Likewise, in *Drosophila melanogaster*, parasite infection increases the fitness costs of mutations to a greater extent in males than in females, driving sex-specific selection [105]. Therefore, sex differences in the fitness costs of parasitism have the potential to influence a variety of important evolutionary dynamics.

One caveat to our correlative study is that we cannot tease apart whether host mating system causally influences the

survival cost of parasitism, or vice versa. Processes related to reproductive success in both males (increased growth rate, rapid development) and females (fecundity, offspring provisioning) are known to trade off with immune function and survival upon immune challenge [1]. However, parasites may also select for these traits in their hosts, and can potentially cue plastic adjustments of phenotypes [106]. For example, both sexes of the freshwater snail, *Potamopyrgus antipodarum*, had an increased mating rate and a greater number of mating partners when exposed to a parasitic trematode [107].

Our dataset comprises a relatively small number of species (64 total), with the majority of studies (97%) conducted on arthropods, mammals or birds, which may temper the generality of our findings across other lineages. Moreover, our dataset contains relatively few monogamous species (14 total), with only three major lineages (arthropods, mammals and birds) representing clearly independent evolutionary transitions to monogamy. Nonetheless, nearly all of these monogamous species (13 of 14) exhibit a female bias in the survival cost of parasitism, which differs from the strong general trend towards male bias in non-monogamous species. Therefore, we consider our results suggestive, though not conclusive, of an evolutionary association between host mating system and sex differences in the extent to which parasites reduce survival. How and why mating system influences the survival cost of parasitism are open questions, and could prove fruitful directions for future research. To allow for a more informative synthesis, future studies should aim to quantify the sex-specific costs of parasitism using both survival and reproduction as measures of fitness.

Data accessibility. All data used in the analysis are available in the electronic supplementary material and can be downloaded as a spreadsheet from the Open Science Framework at the following link <https://osf.io/z62br>, doi:10.17605/OSF.IO/Z62BR. The data are provided in the electronic supplementary material.

Authors' contributions. T.N.W.: conceptualization, data curation, formal analysis, methodology, visualization, writing—original draft, writing—review and editing; R.M.C.: conceptualization, resources, supervision, visualization, writing—review and editing. Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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