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Predicting the response of disease vectors to global change: The importance of allometric scaling

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Abstract

The distribution of disease vectors such as mosquitoes is changing. Climate change, invasions and vector control strategies all alter the distribution and abundance of mosquitoes. When disease vectors undergo a range shift, so do disease burdens. Predicting such shifts is a priority to adequately prepare for disease control. Accurate predictions of distributional changes depend on how factors such as temperature and competition affect mosquito life-history traits, particularly body size and reproduction. Direct estimates of both body size and reproduction in mosquitoes are logistically challenging and time-consuming, so the field has long relied upon linear (isometric) conversions between wing length (a convenient proxy of size) and reproductive output. These linear transformations underlie most models projecting species' distributions and competitive interactions between native and invasive disease vectors. Using a series of meta-analyses, we show that the relationship between wing length and fecundity are nonlinear (hyperallometric) for most mosquito species. We show that whilst most models ignore reproductive hyperallometry (with respect to wing length), doing so introduces systematic biases into estimates of population growth. In particular, failing to account for reproductive hyperallometry overestimates the effects of temperature and underestimates the effects of competition. Assuming isometry also increases the potential to misestimate the efficacy of vector control strategies by underestimating the contribution of larger females in population replenishment. Finally, failing to account for reproductive hyperallometry and variation in body size can lead to qualitative errors via the counter-intuitive effects of Jensen's inequality. For example, if mean sizes decrease, but variance increases, then reproductive outputs may actually increase. We suggest that future disease vector models incorporate hyperallometric relationships to more accurately predict changes in mosquito distribution in response to global change.

KEYWORDS
allometric scaling, arbovirus, disease transmission, hyperallometry, isometry, mosquito vectors, population growth

1 | INTRODUCTION

The distribution of vector-borne diseases is likely to change with future climates. For example, mosquitoes and ticks are responding to warmer temperatures and changed ecological conditions, expanding their ranges and invading new habitats (Benedict et al., 2007; Hales et al., 2002). Understanding how and where these disease vectors will spread is a major goal of present disease ecology (Li et al., 2019; Mordecai et al., 2020; Ryan et al., 2020; Shocket et al., 2020). Accordingly, investigations of how changes in temperature are likely to affect the distribution of the main vector mosquito species (and their diseases) have expanded during the past decade (Kraemer et al., 2019; Mordecai et al., 2020; Rogers & Randolph, 2006; Ryan et al., 2020; Shocket et al., 2020). The majority of thermal models predict an increase in the extent of habitat suitable for mosquitoes, potentially allowing for a broader geographical distribution of vector species (Benedict et al., 2007). Whether changes in vector distribution lead to increased disease occurrence (and severity), depends on a number of factors including transmission dynamics, blood-feeding and thermal optima of both the host and their diseases (Cohen et al., 2020; Mordecai et al., 2013; Ryan et al., 2020; Shocket et al., 2020; Shragai et al., 2017).

Predicting range expansion and invasion of disease vectors is not a trivial exercise—it requires an understanding of how climatic and ecological factors interact to shape species' distributions now, and in the future. Predictions also require comprehensive estimates of a number of ecological and demographic variables that can be challenging to obtain in natural settings. Population viability in mosquitoes is traditionally estimated by calculating the per capita rate of population change (r; or an 'operational estimate of per capita rate of change' (r') when it is impractical to estimate r directly) in a mosquito cohort (Livdahl & Sugihara, 1984). This index is based on the measurements of key life-history parameters such as development time, survival, body size, and fecundity (see also Livdahl, 1982, 1984). Since its inception, this index has been applied in a variety of models addressing, for example, the competitive interactions between native and invasive mosquitoes (Alto et al., 2008; Armistead et al., 2008; Reiskind & Lounibos, 2009), or responses to nutritional, thermal or density manipulations (Ciota et al., 2014; Leisnham et al., 2019; Leonard & Juliano, 1995; Murrell & Juliano, 2008; Parker et al., 2019).

A critical component of r' is fecundity and its relationship with body size. Mosquito fecundity is difficult to estimate, particularly under field conditions. Similarly, weighing individual mosquitoes is challenging, and weight can vary substantially with feeding history (see Christophers, 1960; Colless & Chellapah, 1960). Consequently, the use of wing length (a relatively easier trait to measure, and more stable throughout adult life) has become the dominant proxy for both maternal size and a convenient predictor of fecundity (see Livdahl & Sugihara, 1984).

Given its use as a linear estimator of body mass, how does wing length covary with mass in mosquitoes? From a simple geometric perspective, linear dimensions of size should generally scale hyperallometrically with volume, that is, size should scale hyperallometrically with mass with exponents around 3 (i.e. a cubic relationship). Accordingly, across a wide range of other groups (e.g. fish) measures of body length tend to show a strong cubic relationship with mass. Foundational studies on mosquitoes seem to confirm this general pattern (Christophers, 1960; Hawley, 1985a; Nasci, 1990) but despite these early studies, almost all contemporary studies fit or assume an isometric (linear) relationship between wing length and mass (e.g. Lounibos et al., 2002; Reiskind & Zarrabi, 2012, but see also Tables S.1 and S.2). Thus, the theoretical underpinning of models of vector invasion and disease spread predominantly assumes a linear relationship between wing length and mass—and it is here that problems may emerge.

If wing length actually relates to mass nonlinearly, then assuming otherwise introduces systematic errors into subsequent projections of fecundity or r', with the potential for profound misestimations. For example, mosquitoes developing at higher larval densities tend to grow less (Agnew et al., 2009, but see also Table S.5). If only wing length is measured and assumed to relate linearly with body mass, then any slight effect of density on wing length will be interpreted as a slight effect on body mass. On the other hand, if wing length actually scales nonlinearly with body mass, then a slight effect of density on wing length translates into a large effect on body mass (see Figure 1d for an illustrative example). Thus, we could be systematically misestimating the effects of, for example, temperature and larval density on body mass. If we are to predict changes in the distribution of mosquito-borne diseases, we need an accurate estimate of how wing length relates to body mass in mosquitoes and an understanding of how assumptions that deviate from this scaling estimate affect model projections. Here, we use a meta-analytic approach to compile available estimates of the critical relationship between wing length and body mass for major disease vectors. Before we explore how these estimates affect model projection, however, we must also consider the relationship between body mass and fecundity, and between wing length and fecundity.

Most models, whether they be general models of growth, or specifically relating to mosquitoes, tend to assume a linear relationship between estimates of size and reproductive output—often referred to as reproductive isometry. Assuming reproductive isometry greatly simplifies the modelling of size effects and is hardwired into many physiological models of growth. Further, models of agricultural pests (e.g., fruit flies; Chua, 1992), invasive species (e.g. lionfish; Morris et al., 2011) and endangered species management (e.g. axolotls; Zambrano et al., 2007) all make strong (typically linear) assumptions about how size affects reproduction. Increasingly, this assumption seems unjustified. A global meta-analysis of marine fish reproduction, for example, revealed that reproductive isometry rarely occurs. Instead, heavier fish tend to produce disproportionately more offspring than lighter fish, a pattern known as reproductive hyperallometry (Barneche et al., 2018). Since then, reproductive hyperallometry has been noted in some invertebrate species, including insects (Marshall & White, 2019b), suggesting that similar relationships could occur in mosquitoes.

Assuming reproductive isometry where in fact reproductive hyperallometry occurs, compounds the systematic errors of assuming a linear relationship between wing length and body size (Figure 1). Recent studies in marine protected areas, for example, show that

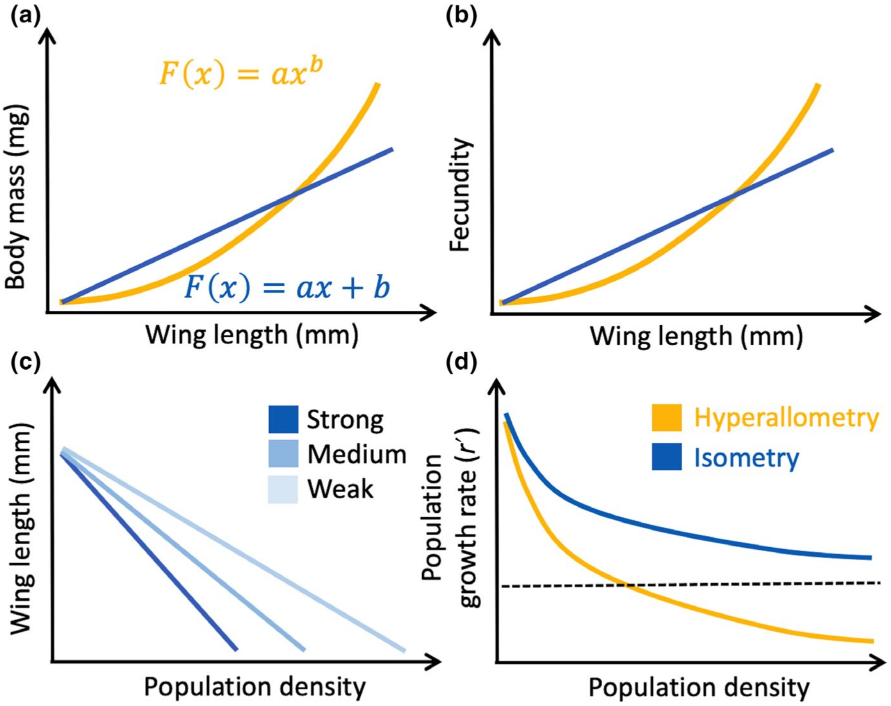

FIGURE 1 Hypothetical relationship between mosquito life-history traits, tested in subsequent analyses. Depicted is the hypothetical difference in estimates of mosquito life-history traits using either isometric (blue) or hyperallometric (orange) scaling relationship between (a) body mass~wing length and (b) fecundity~wing length. (c) Different strengths of density-dependence on mosquito wing length (weak, medium and strong density-dependence) and (d) per capita rate of change r' with increasing population density, under the assumption of isometric (blue) or hyperallometric (orange) scaling between wing length and fecundity

projections of population replenishment are systematically biased if reproductive hyperallometry is not considered (Marshall et al., 2019) and the benefits of management interventions are, therefore, underestimated. Meanwhile, other models assume size independence in projections, under the assumption that external factors such as rainfall, temperature or predation are the primary drivers of population dynamics (Marini et al., 2020; Nance et al., 2018; Tran et al., 2020). We argue that both external factors and size-dependent fecundity are important elements in robust projections of population dynamics.

The relationship between mass (and wing length) versus reproductive output remains unclear in mosquitoes. Again, we use a meta-analytic approach to resolve this uncertainty. By reviewing the literature, we compiled a comprehensive database to quantify the scaling of intraspecific relationships between wing length, mass and fecundity in mosquitoes (Figure 1b). We next explored how the underlying scaling between body size (measured as mass or wing length) and fecundity impacts projections of population growth and r' at various population densities and with different strengths of density-dependence on the size of emerging females (Figure 1c,d). We discuss the importance of incorporating reproductive hyperallometry into models of mosquito invasion and response to climate change.

2 | MATERIALS AND METHODS

2.1 | Meta-analysis of size and fecundity relationships

We systematically reviewed the literature following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2009), using the online databases Google Scholar and Web of Science (April, 2020). Our search pertained to peer-reviewed research papers on the relationship between mosquito mass, wing length and fecundity. We restricted our search to the most commonly studied mosquito genera; *Aedes*, *Anopheles* and *Culex* (*Ae*., *An*., and *Cx*., onwards). Search terms included '*the genus* & wing length OR mass OR body size AND reproductive output OR fecundity OR clutch size OR number of eggs' and '*the genus* AND competition OR density OR interspecific interactions AND wing length OR body size OR fecundity', and we included any relevant references cited within research papers identified with the above-mentioned search terms. We also compiled literature pertaining to the relationship between population density and mosquito survival, development time and wing length (see below). Raw data were extracted from the published literature using the free online tool, Web Plot Digitizer, 2018.

Data used to fit the wing length-fecundity, wing length-mass and mass-fecundity relationships are listed in Tables S.1–S.4, and only datasets with more than 30 data points were included in the statistical analysis (see Figure S.1 for PRISMA flow diagram). We included both field and laboratory studies. When studies involved multiple treatments, we extracted data from control treatments only, or pooled treatments to obtain sufficient data points. In this way, the studies we include span several temperatures, but since too few studies formally tested temperature effects on scaling relationships, we were unable to test this effect on the scaling between wing length, mass and fecundity. All statistical analyses were performed in R (v. 3.3.3; R Development Core Team). Using the 'brms' package we estimated all scaling relationships in a Bayesian framework by fitting a linear model with study ID as a random effect to the raw scale data (isometry), as well as a linear model to the log10-transformed data (hyperallometric;

$\log(y) = b^*\log(x) + \log(a)$, where x = mass and fecundity and y = wing length). We used 20,000 iterations, 5000 warmup iterations, a thinning of 5, and specified delta to 0.99 and a maximum tree depth of 17. Priors were derived using the function ‘get_prior’ in the ‘brms’ package, which assumes a flat distribution for the fixed effects (wing length) and a student distribution for the random effects (study ID) when more than one study per species is modelled. Using a Wald-test we determined whether the best fitting hyperallometric scaling exponent was significantly different from isometry (linear, slope/exponent of 1). In cases where we obtained scaling exponents for two out of the three relationships, we imputed the third, missing scaling exponent. In this way, for species where we derived scaling exponents for both fecundity~wing length and fecundity~mass, but no data existed on the mass~wing length relationship, we then calculated the latter relationship, by dividing the exponent derived from the fecundity~wing length, by the exponent derived for the fecundity~mass relationship.

Regressions between wing length and body size were performed on measurements of either adult dry weight or pupal wet weight. Measures of fecundity were limited to egg number, egg production and total fecundity, whereas studies that measured parous rate, follicle number or number of eggs per raft were excluded in this analysis.

2.2 | Density-dependence of life-history traits

We collected empirical estimates of density-dependence on wing length, development time and survival (see Table S.5). We fitted linear regressions between population density and the three traits (wing length, development time and survival) using informative priors (using the function ‘get_prior’ in the ‘brms’ package, as described above), 15,000 iterations, 5000 warmup, thinning = 3, delta = 0.99, maximum tree depth = 17, and we included study ID as a random effect when applicable. All density treatments were transformed to the same unit (individuals ml^{-1}) prior to analysis.

2.3 | Estimating per capita rate of change, *r′*

The operational estimate of per capita rate of change (r') was estimated for a mosquito cohort following Livdahl and Sugihara (1984), under the assumptions of reproductive isometry and reproductive hyperallometry. r' comprises information about a number of ecological variables, including development time, survival and the size of newly emerging females and represents a robust estimate for the rate of population change (see Livdahl & Sugihara, 1984).

$$r' = \frac{\ln\left(\frac{1}{N_0}\sum_x A_x f(w_x)\right)}{D + \frac{\sum_x x A_x f(w_x)}{\sum_x A_x f(w_x)}}, \tag{1}$$

where x is a given day of adult emergence, w_x is the average size of females emerging on day x. A_x is the number of adult females emerging on day x, N_0 is the initial number of female larvae in the cohort (set to 50% of the initial population density), $f(w_x)$ is a function that converts female size (using either wing length or mass) into the predicted per capita number of offspring and D is a constant determined by the delay between adult emergence and oviposition.

In this study, we estimated r' across a gradient of ecologically relevant population densities (1–5000 females) using empirically collected data for each trait relationship (as described above), for eight of the most frequently studied mosquito species (*Ae. aegypti*, *Ae. albopictus*, *Ae. geniculatus*, *Ae. triseriatus*, *An. arabiensis*, *An. gambiae*, *Cx. pipiens* and *Cx. quinquefasciatus*). We should note that population densities above 3000 individuals per litre are relatively common in laboratory studies, although they are unlikely to be common in real-world conditions. Nevertheless, these experimental manipulations represent the range of values used to estimate density dependence, and so we feel obliged to present the full range of values that have been explored empirically. We suspect that such high densities are used in laboratory studies because the conditions in the laboratory are more benign (high food, low predation, constant physical environment) relative to natural conditions. As such, laboratory studies probably overestimate natural densities but underestimate the strength of density dependence. Thus, whilst we provide modelling outcomes for a range of densities and density-dependencies (which reflect values from the literature), we would argue that the scenarios where population density is relatively low (e.g. 500 individuals per litre) and density-dependence is high (medium or strong), are most relevant to real-world conditions.

We estimated r' under the assumption of reproductive isometry and hyperallometry and varied the strength of negative density-dependence (weak, medium and strong) imposed on wing length (“medium” represents species-specific observed density-dependencies, whereas weak and strong represent a 50% decrease or increase in density-dependencies, respectively). Briefly, this modification of the strength of density-dependence is mathematically described following a linear regression: $\text{WL} = a^*\text{density} + \text{b}$, where a and b are constants derived from the literature. In this way, three levels of density-dependence is enforced as follows: low: $\text{WL} = (0.5^*a)^*\text{density} + \text{b}$, medium: $\text{WL} = a^*\text{density} + \text{b}$, and high: $\text{WL} = (1.5^*a)^*\text{density} + b$. We used a random draw of 1000 posterior samples from regressions of density-dependence on mosquito wing length, development time and survival (Section 2.2), and a random draw of 3000 posterior samples from regressions between wing length and fecundity (Section 2.1). Finally, we regressed the full domain of emergence days across the gradient of population densities, allowing for differences in emergence time within any population density.

2.4 | Mapping the use of reproductive scaling in estimates of *r′*

We assessed the general use of reproductive scaling in research papers included in the meta-analysis and additional peer-reviewed papers citing the foundational paper developing r' (Livdahl & Sugihara, 1984).

3 | RESULTS

3.1 | Allometric scaling in mosquitoes

We found 53 datasets that related wing length, body mass and/or fecundity, which spanned the most common mosquito species (Tables S.1–S.4). On average, wing length scaled hyperallometrically with fecundity and with body size, with exponents of around 3. For the few ($n = 5$) studies that estimated scaling between mass and fecundity, relationships varied between ~0.6 and ~1.7 (Table 1).

3.1.1 | Wing length and fecundity

We found that the relationship between wing length and fecundity was almost always hyperallometric with scaling exponents ranging between 0.55 and 5.6 (Table S.2). Two of four studies with exponent ≤1 was performed on field-collected *Ae. albopictus* and the data were relatively noisy. Exclusion of these led to a global average scaling exponent of 3, compared to 1.41 when included (Table 1). The use of isometry thereby frequently underestimated fecundity at the edges of the observed size distribution, both in the laboratory and in the field (Figure 2). Despite hyperallometry being the rule, all the original studies used linear (isometric) relationships between wing length and fecundity

3.1.2 | Wing length and body mass

Hyperallometric scaling provided the best fit in 13 out of 14 studies (see Table S.3; Figure S.2), with an average hyperallometric scaling exponent of 3.41 (Table 1). In contrast, 85% of the original studies used isometric fits to describe this relationship (studies on *Ae. aegypti* were the notable exception; Table S.3).

3.1.3 | Body mass and fecundity

Isometric scaling provided the best fit in six out of eight studies (see Table S.4), with an average hypoallometric scaling exponent of 0.85. One species (*Ae. geniculatus*) had a notably low scaling exponent (~0.63) and exclusion of this species led to an average hyperallometric exponent of 1.12 (Table 1). Among the original studies, 90% used linear regressions to describe the relationship between mass and fecundity.

3.2 | Consequences of using isometry for demographic projections

3.2.1 | Reproductive output

The use of isometric scaling relationships between wing length and fecundity (or mass) leads to repeated underestimates of reproductive output for high-density populations (see Figure S.3 for models used to estimate density-dependence on mosquito wing length), and this bias increases with strong density-dependence (Figures S.4 and S.5). Despite some species-specific variation in the relationship between hyperallometry versus isometry, the use of isometry led to lower estimates of fecundity (ratio > 1, Hyper>Iso) at any density above ~500 individuals per litre, and this effect was further exacerbated with strong density-dependence (Figure 3).

3.2.2 | Population growth

The use of isometric scaling overestimates the population growth rates of high-density populations and systematically underestimates the negative density-dependence of r' in all studied species. Here, we present estimates of r' for two of the species in our analyses; *Ae. aegypti* and *Ae. triseriatus* (Figure 4, see Figure S.6 for estimates of r' for all studied species). This bias is worsened with increasing density-dependence in wing length, whereby isometry almost always leads to notably higher estimates of carrying capacity, particularly when density-dependence is strong (Figure 4).

3.3 | The use of allometric scaling in modelling studies

The majority of studies that model r', assume an isometric relationship between wing length and fecundity (or body mass). Two approaches to calculating fecundity were employed: 87 studies used a direct conversion of wing length to fecundity whilst 31 used body mass as the predictor for fecundity. Amongst the studies that used wing length directly, only 30% fitted nonlinear relationships (Table S.6). For the studies that used body mass in their calculation of fecundity, all but one study assumed a scaling exponent of equal to or less than 1 (Table S.7). Importantly, even if an isometric relationship exists between body mass and fecundity, 16 studies converted wing lengths to mass via isometric regressions prior to calculating fecundity and thereby introduced repeated underestimates of reproductive output.

3.4 | Do assumptions about reproductive scaling matter?

Female size (in terms of wing length) may decline by up to 15% in response to a 5°C increase in temperature (Ciota et al., 2014). The use of standard assumptions of isometry between wing length, mass and fecundity then lead to a prediction of zero (often negative) fecundity in emerging females. In contrast, using the appropriate hyperallometric scaling relationship, the same model predicts positive, albeit reduced, fertility in these smaller females. In other words, using isometry results in a twofold overestimate of the negative impacts of increasing temperature, and leads to a

TABLE 1 Overview of estimated scaling exponents derived from regressions on extracted data from the literature and imputed scaling exponents of missing regressions (Imputed) for each species. For each species, multiple references may have been used (References) and *N* represents the total sample size in each analysis. In this way, the estimated scaling exponents and associated estimated error (Exp. ± Est. error) for each relationship is based on the variable number of datasets, and thus reported with the associated estimated SE

	Mass~Wing length			**Fecundity~Wing length**			**Fecundity~Body mass**		
Species	**References**	***N***	**Exp. (±Est. error)**	**References**	***N***	**Exp. (±Est. error)**	**References**	***N***	**Exp. (±Est. error)**
Ae. aegypti	Christophers (1960), Koenraadt (2008)	176	2.94 (±0.10)	Farjana and Tuno (2012), Leisnham and Juliano (2010)	505	2.76 (±0.10)	Colless and Chellapah (1960), Steinwasher (1984)	98	0.93 (±0.10)
Ae. albopictus	Blackmore and Lord (2000), Lounibos et al. (2002), Reiskind and Zarrabi (2012)	332	3.79 (±0.12)	Armbruster and Hutchinson (2002), Blackmore and Lord (2000), Briegel and Timmermann (2001), Costanzo et al. (2018), Farjana and Tuno (2012), Leisnham et al. (2009), Lounibos et al. (2002), Nicholson et al. (2015)	952	3.34 (±0.15)	Armbruster and Hutchinson (2002)	56	1.69 (±0.11)
Ae. atropalpus				O'Meara and Krasnick (1970)	60	5.6 (±0.26)			
Ae. cantans				Renshaw et al. (1994)	490	3.21 (±0.23)			
Ae. geniculatus	Imputed		5.47	Armbruster and Hutchinson (2002)	135	3.12 (±0.20)	Armbruster and Hutchinson (2002)	156	0.57 (±0.04)
Ae. notoscriptus				Nicholson et al. (2015)	57	6.51 (±0.47)			
Ae. punctor	Takken et al. (1998)	100	2.87 (±0.26)	Packer and Corbet (1989)	63	4.11 (±0.18)	Imputed		1.47
Ae. triseriatus	Imputed		3	Livdahl (1984)	50	3.02 (±0.51)	Livdahl (1982)	50	1.01 (±0.18)
Ae. sierrensis	Imputed		3.59	Kesavaraju et al. (2014)	67	4.06 (±0.20)	Hard and Bradshaw (1993), Hawley (1985b)	132	1.13 (±0.05)
An. stephensi	Takken et al. (2013)	50	3.73 (±0.19)						
An. arabiensis				Hogg et al. (1996)	289	2.78 (±0.52)			
An. darlingi	Lounibos et al. (1995)	46	3.55 (±0.31)						
An. dirus				Kitthawee et al. (1992)	38	3.21 (±0.36)			
An. gambiae	Koella and Lyimo (1996), Takken et al. (1998), Takken et al. (2013)	500	3.29 (±0.11)	Hogg et al. (1996),Howard et al. (2011), Lyimo and Takken (1993), Yaro et al. (2006)	840	2.38 (±0.23)	Imputed		0.72
Cx. pipiens	Shin et al. (2012)	62	1.29 (±0.22)	Leisnham et al. (2019), Vinogradova (2008)	141	1.90 (±0.21)	Imputed		1.47
Cx. quinquefasciatus	Petersen et al. (2016)	178	2.67 (±0.18)	Lima et al. (2003), McCann et al. (2009)	224	2.58 (±0.42)	Imputed		0.99
Cx. tritaeniorhynchus	Roy et al. (2016)	36	7.76 (±0.27)						
Cx. restuans				Ower and Juliano (2019)	57	3.47 (±0.85)			

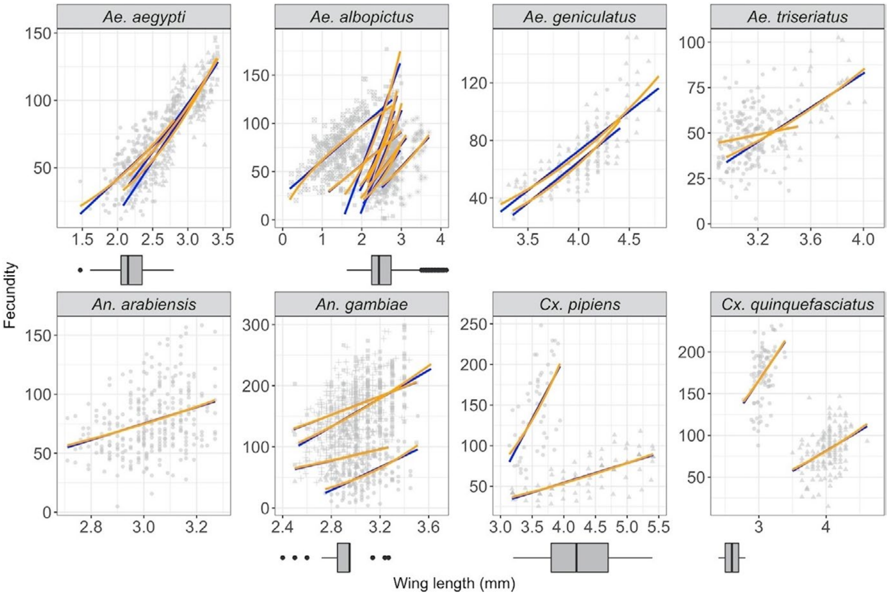

FIGURE 2 The fit of isometric (blue) versus hyperallometric (orange) scaling between wing length and fecundity in the most commonly studied mosquito species. Grey points show raw data extracted from the literature and each set of regressions (isometric and hyperallometric) correspond to an individual datasets for each mosquito species. Grey boxplot under each panel visualise the distribution of wing lengths as observed in the field (note: due to absence of field data, no boxplot is shown for *Ae. triseriatus*, *An. geniculatus* and *An. arabiensis*).

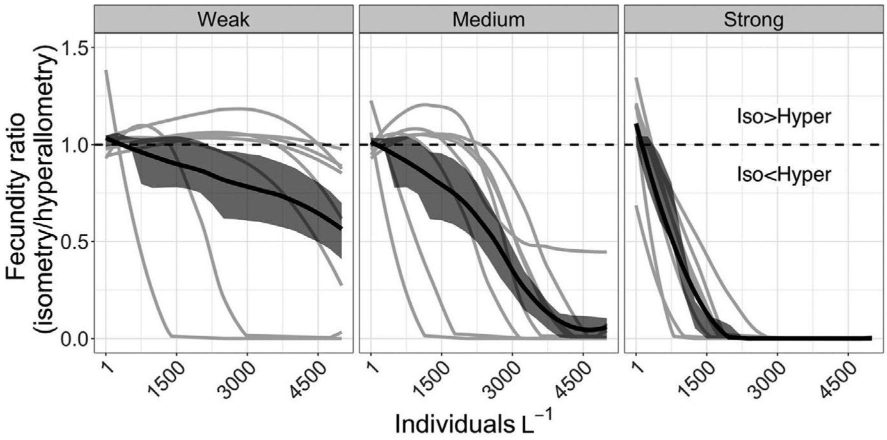

FIGURE 3 Mean ratio of isometry to hyperallometry in predicted reproductive output across a gradient of population densities (individuals per litre). The thick black line represents mean values (±SD), and thin shaded grey lines show values for individual mosquito species. Panels are different strengths of density-dependence in wing length (weak, medium and strong). Black dashed line (ratio = 1) represents identical fecundity predictions by isometry and hyperallometry. Ratios above the black dashed line are instances where isometry overestimate fecundity (Iso>Hyper), and values below the black dashed line represent ratios where isometry underestimate fecundity (Iso<Hyper)

conclusion of complete loss of fertility when in reality, some fertility would be retained in small females. The mis-estimations introduced are further exacerbated due to Jensen's inequality and non-linear averaging (Figure 5a, see Denny, 2017).

Jensen's inequality is a conceptual demonstration of the counterintuitive fact that, for non-linear relationships, the mean of a predictor variable will not predict the mean of the response variable if there is variation in the predictor variable. In other words, mean wing length in a mosquito population will not predict the mean fecundity in that same population when wing lengths are variable. Instead, the larger females produce disproportionally more offspring, and thereby increase mean fecundity beyond what would be predicted by projecting fecundity from the mean wing length alone. The impacts of Jensen's inequality increase with increasing variance in the predictor.

In our case, because wing length relates to fecundity nonlinearly, the average drop in wing length cannot be used to predict the average drop in fecundity in response to climate change (Figure 5b) or changes in population density. Rather, using mean wing length (instead of considering size distributions within a population) leads to a 30% overestimate of the negative effect of climate change on reproductive output. If climate change affects both mean and variance in size (which seems likely, see Chen et al., 2014 for an example), then the impacts of climate are even more counterintuitive. For example, if higher temperatures decrease mean size but increase variance, then reproductive outputs could actually increase under warmer conditions.

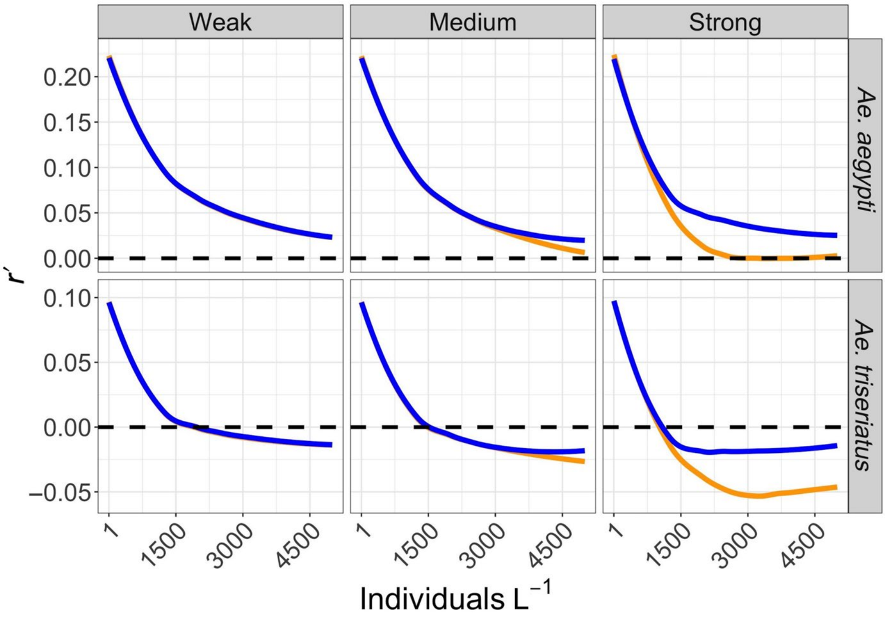

FIGURE 4 Estimates of r' for two of the studied species (*Ae. aegypti* and *Ae. triseriatus*) across a gradient of population densities (individuals per litre), using isometric (blue) or hyperallometric (orange) scaling relationships between wing length and fecundity. The black dashed line ($r' = 0$) represents the point of no increase in population growth (carrying capacity), whereby values below this line represent population declines and values above represent population growth

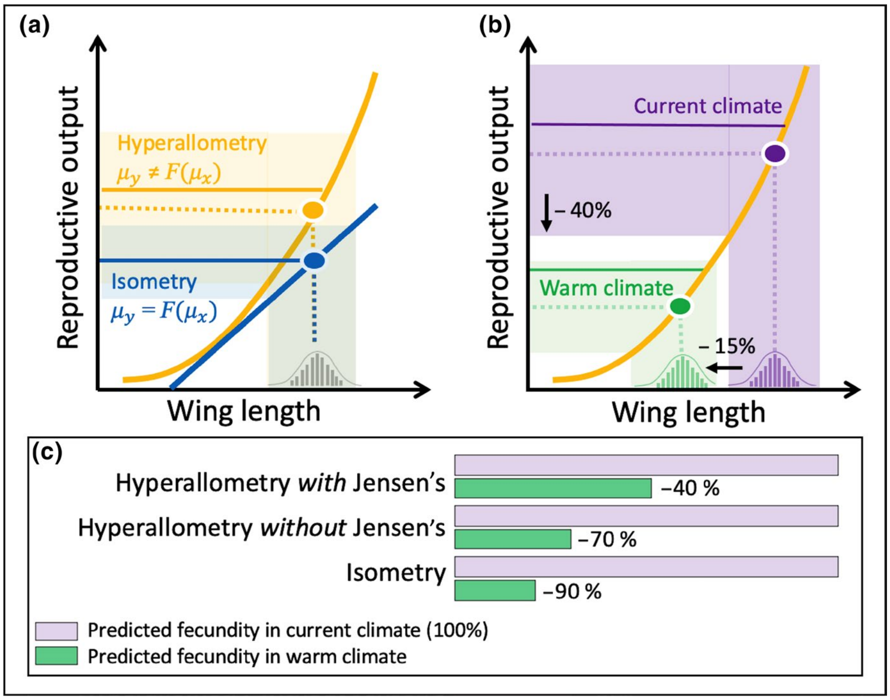

FIGURE 5 The effect of allometric scaling and Jensen's inequality on estimates of reproductive output. (a) Reproductive output as estimated via hyperallometric (orange) and isometric (blue) scaling relationships when accounting for Jensen's inequality (solid line) and population mean (dashed line). (b) Climate change may lead to a 15% reduction in wing length, corresponding to a 40% reduction in reproductive output, which will remain unaccounted for by the use of an isometric scaling relationship. (c) (Mis)estimated reduction in the reproductive output in warmer climates, when considering scaling and Jensen's inequality. In warming climates, the use of isometry may predict a 90% reduction in fecundity, when compared to the reproductive output in the current climate. However, when accounting for the non-linear nature of the relationship between wing length and reproductive output, fecundity in warmer climates might only be expected to drop 70% in future warmer climates. Lastly, when considering both non-linearity and the impact of Jensen's inequality, we may predict that warming climate only reduce fecundity by 40%

4 | DISCUSSION

Accurate estimates of reproductive output and population growth rate are essential in order to make reliable predictions about mosquito distributions and projections of mosquito-borne disease burdens worldwide (Mordecai et al., 2019; Ryan, 2020). Using a meta-analytic approach, we show that most (empirical and modelling) studies use linear relationships between life-history traits in projections of population growth when these relationships are in fact nonlinear. Through worked examples, we show that linear approaches introduce systematic biases into demographic projections used to model the effects of species invasion, climate change and vector control strategies. In summary, we demonstrate how subtle differences in assumptions can have important consequences in projections of population dynamics—nonlinear effects can be highly counterintuitive; seemingly minor differences in model input manifest as major differences in model outputs when summed across the life history of an individual and across a population.

4.1 | Assuming isometry affects predictions

Predicting how disease vectors respond to climate change is essential for anticipating changes in disease dynamics. The common use of isometric scaling assumptions between wing length, mass and fecundity (Table S.1) reduces the accuracy of these predictions. Higher temperatures result in smaller females, but projections based on linear relationships assume that the smallest individuals are completely infertile. However, the reality is different, and these small females do reproduce and thereby contribute to population replenishment. Only when hyperallometry is assumed, this reproductive contribution is considered. As such, the effect of increases in temperature on population replenishment has been systematically overestimated such that temperatures in which populations are predicted to be unviable (due to the emergence of smaller females) will actually persist. These systematic problems introduced by assuming linear isometric relationships between size and fecundity are unlikely to be restricted to mosquitoes.

We focused on disease vectors because they are a relatively well-studied group with important impacts, but we stress that reproductive allometry affects demographic projections for other systems as well (such as in estimates of replenishment of fish populations; Barneche et al., 2018). Across a range of taxa, from flies to axolotls to fish, population models use linear assumptions about body size and reproduction to predict the impacts of invasive species, species recovery efforts and agricultural pest control (Akcakaya & Baker, 1998; Chua, 1992; Zambrano et al., 2007). In each of these instances, the relationship between size and fecundity is actually nonlinear. For example, a demographic model of invasive mussels assumed a linear relationship between shell length and fecundity when it instead scales with an exponent of >4. The role of both larger and smaller females will therefore be systematically mis-estimated. We suggest that future demographic models that include body size and reproduction explicitly consider nonlinear relationships. One key uncertainty that remains, however, is the effect of temperature on reproductive scaling. Whilst we suspect such effects are likely, too few studies have explored this systematically. Thus, we are forced to use the same scaling relationships for current and future temperatures but in reality, these scaling relationships are likely to change.

Changes in the distribution of competing mosquito species are also commonly modelled using isometric scaling (Table S.5). Increasing larval density reduces survival rates, prolongs development time and leads to the emergence of smaller adult mosquitoes (Alto et al., 2008; Armistead et al., 2008; Lounibos et al., 2002). Understanding how the presence of conspecifics and competitors affects individual life-history traits and population growth rate is, therefore, crucial for accurate estimates of invasion probability (Phillips, 2015). We found that models based on isometric scaling are systematically less sensitive to changes in population density and underestimated these negative effects. In turn, since isometric scaling fails to account for fecundity in small females, and underestimates fecundity in large females, these models fail to identify the critical population density at which females experience reduced fecundity, and hence the carrying capacity of a population. Whilst densities of >1000 individuals per litre can occur in the field (see Hancock et al., 2016; Hard et al., 1989; Legros et al., 2009), we suspect they are rare. However, the strength of density-dependence is systematically weaker in laboratory studies due to the more benign conditions (e.g. high food, low predation and constant physical environment) of the laboratory. From this perspective, the 'weak' and 'medium' levels of density-dependence modelled in our study are likely to be gross underestimates of natural density dependencies. When one examines the 'strong' density-dependence condition, the striking effects we observe occur at relatively low (and, therefore, highly representative) population densities (e.g. ~reproductive output drop significantly at densities lower than 1000 individuals per litre, see Figure S.4).

Assuming isometric scaling also introduces systematic misestimates of the effect of vector control strategies such as the release of laboratory-reared *Wolbachia*-infected mosquitoes (McGraw & O'Neill, 2013). Because laboratory-reared mosquitoes are generally larger (and in good nutritional condition), the disproportionally higher reproductive output in these larger females is systematically underestimated when isometry is assumed. A large *Wolbachia*-infected *Ae. albopictus* female, may, for example, be predicted to release 150 eggs if isometry is assumed, but in reality, this female releases 33% more eggs (~200 eggs). In this way, appropriate interpolation from wing length to fecundity is important in designing and predicting the effect of vector release programs because laboratory-reared females are larger than those that emerge in the field.

Our study suggests that in the absence of specific data, simple hyperallometric 'rules of thumb' (i.e. that fecundity scales with wing length with exponents at ~3) would improve the accuracy of mosquito vector models. Even if the difference between isometric and hyperallometric scaling appear subtle at the level of individuals, we demonstrate a major population-level effect of scaling on projections of population demographics. It is important to note that data does not exist for a number of vector species, and for those species that have been studied, the relationship between size and fecundity may be context-dependent (Table 1). We suggest that more studies of the relationship between mosquito size and fecundity are necessary and that future studies also explore how variation in environmental conditions may modify these relationships. Further, in accordance with the Bayesian modelling approach employed in this study, we emphasize that estimates of scaling exponents around 3 are associated with notable credible intervals (see Table S.8 for species-specific estimates and associated 95% credible intervals).

The role of Jensen's inequality tends to be underestimated across a myriad of biological applications (Bernhardt et al., 2018; Denny, 2017; Marshall et al., 2019). Here, we show that a focus on mean sizes leads to systematic misestimates of population responses to competition, temperature and vector control strategies. Whilst traditionally there has been a strong emphasis on how mean size changes among treatments (e.g. competition or temperature) if the variance in size also changes, then Jensen's inequality, coupled with appropriate hyperallometric reproductive scaling will have equally important consequences for population projections. For example, a temperature increase that causes a 5% reduction in size, but also a 10% increase in size variation could (counter-intuitively) increase fecundity despite a decrease in the mean size of mosquitoes. We argue that a better understanding of how climate change affects both mean and variances in life-history traits is crucial for reliable model projections.

The relationship between body mass and fecundity is unclear in mosquitoes. Whilst reproductive hyperallometry is the rule in most marine fish, and examples from other taxa exist (Barneche et al., 2018; Marshall & White, 2019a), we found that the exponents varied enormously from study to study and species to species within mosquitoes. This variation may be a product of limited sample sizes—surprisingly few studies have estimated this pivotal relationship in mosquitoes (see Table S.3). In *Ae. albopictus*, for example, fecundity scaled steeply with body size with an exponent of 1.69, but *Ae. geniculatus* showed an unusual hypoallometric relationship (~0.6). Given that mass-fecundity scaling will drive population dynamics, we suggest that more studies examining this critical relationship are necessary. Furthermore, given body size and offspring size often covary, and can have consequences for population dynamics, future studies should also examine how egg size covaries with body size (see Lim et al., 2014; Marshall et al., 2018).

Several factors may affect our general findings. Scaling relationships may vary between field and laboratory-reared populations, due to differences in nutritional status, environmental conditions such as temperature and water access, or predation pressure. Other factors such as genetics, population divergence and plasticity in scaling likewise remain relatively unexplored and warrant further studies. Such caveats may result in idiosyncratic deviations from our overall findings but with the data available at present remains clear that including non-linear scaling relationships increases the precision of projections of population dynamics. An important next step is to improve our understanding of the drivers of variation in allometry and the extent hereof. Whilst size is often used as a linear predictor of fecundity in many species' demographic projections, several models also assume size independence in estimates of fecundity. In mosquitoes, for example, some models assume that external factors such as rainfall or temperature primarily drive population dynamics (Marini et al., 2020; Nance et al., 2018; Tran et al., 2020). We focused on models that are explicitly interested in, and incorporate, how body size mediates reproductive output. These two approaches, however, are not mutually exclusive and should be considered in combination.

4.2 | Overall, our work identifies four key issues in the study of disease vector life histories

1. Most studies assume or fit a linear relationship between wing length and reproductive output in mosquitoes where, in reality, this relationship is nonlinear and scales hyperallometrically with exponents of around 3 (±0.4).
2. Using linear reproductive relationships systematically misestimates the contribution of different size classes to population replenishment.
3. This misestimate leads to systematic and significant biases in projections of the impacts of climate change, changes in species' distributions and vector control strategies.
4. Better estimates of the relationships between wing length, size and reproductive output (both fecundity and egg size) for disease vectors are necessary, along with assessments of how both temperature and population density affect both the mean and variance in body size.

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CONFLICT OF INTEREST

Authors have no competing interests.

AUTHOR CONTRIBUTION

Louise S. Nørgaard, Elizabeth McGraw, Craig R. White and Dustin J. Marshall conceived the study. Louise S. Nørgaard and Dustin J. Marshall compiled the data. Louise S. Nørgaard, Dustin J. Marshall and Mariana Álvarez-Noriega analysed the data and modelled *r*′. Louise S. Nørgaard wrote the first draft of the manuscript and all authors contributed substantially to revisions and have given final approval of the submitted manuscript.

DATA AVAILABILITY STATEMENT

Data presented in this study can be found in the online repository Figshare via https://doi.org/10.6084/m9.figshare.16788274.

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