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Macroecology of parental care in arthropods: higher mortality risk leads to higher benefits of offspring protection in tropical climates

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ABSTRACT

The intensity of biotic interactions varies around the world, in such a way that mortality risk imposed by natural enemies is usually higher in the tropics. A major role of offspring attendance is protection against natural enemies, so the benefits of this behaviour should be higher in tropical regions. We tested this macroecological prediction with a meta-regression of field experiments in which the mortality of guarded and unguarded broods was compared in arthropods. Mortality of unguarded broods was higher, and parental care was more beneficial, in warmer, less-seasonal environments. Moreover, in these same environments, additional lines of defence further reduced offspring mortality, implying that offspring attendance alone is not enough to deter natural enemies in tropical regions. These results help to explain the high frequency of parental care among tropical species and how biotic interactions influence the occurrence of parental care over large geographic scales. Finally, our findings reveal that additional lines of defences – an oftentimes neglected component of parental care – have an important effect on the covariation between the benefits of parental care and the climate-mediated mortality risk imposed by natural enemies.

Key words: abiotic factors, biotic interactions, evapotranspiration, egg attendance, egg coating, meta-regression, nest, parasitism, parental removal, predation.

CONTENTS

I. INTRODUCTION

Forms of post-ovipositional parental care are incredibly diverse in animals, ranging from egg attendance to extended care after nutritional independence of the offspring (Smiseth, Kölliker & Royle, 2012). Among ectotherms, the most widespread form of post-ovipositional care is offspring attendance (Crump, 1995; Trumbo, 2012), which occurs when one or both parents remain with their offspring after hatching at a fixed location or escort the young as they move around (Smiseth *et al.*, 2012). As with any other form of parental care, offspring attendance is favoured when the fitness benefits to the parents outweigh the costs associated with care in terms of parental survival and future residual reproduction (Trivers, 1972; Klug, Alonzo & Bonsall, 2012; Klug & Bonsall, 2014). Empirical studies show that offspring attendance is indeed beneficial when it improves offspring survival due to reduced risk of dehydration (e.g. arthropods: Smith, 1997; Gilbert, 2014; frogs: Delia, Ramírez-Bautista & Summers, 2013; Poo & Bickford, 2013) or increased egg oxygenation (e.g. arthropods: Munguía-Steyer, Favila & Macías-Ordóñez, 2008; fish: Green, 2004). Moreover, extensive experimental evidence indicates that the absence of the parent condemns the offspring to death, mostly due to predator and parasitoid attacks as well as fungal infection (see examples in Clutton-Brock, 1991; Royle, Smiseth & Kölliker, 2012).

In several species, however, active parental protection is not sufficient to deter all natural enemies that may attack the offspring (e.g. Eberhard, 1975; Kudo & Ishibashi, 1996; Kudo, 1996; Miller, Rudolph, & Zink, 2011; Consolmagno *et al.*, 2016). Additionally, stressful abiotic conditions may constrain egg attendance to only some periods of the day, exposing the offspring to long periods of parental absence (Machado *et al.*, 2004; Chelini & Machado, 2012; Consolmagno *et al.*, 2016). In some arthropod species, additional lines of defence may protect the offspring by either hampering brood detection by predators and parasitoids or by decreasing consumption rates during periods of temporary parental abandonment. Examples of additional defences include: nest building in earwigs and spiders (e.g. Lamb, 1976; Evans, 1998; Kölliker & Vancassel, 2007; Fig. 1); deposition of silk layers around the eggs in spiders and mites (e.g. Mori, Saito & Sakagami, 1999; Vieira & Romero, 2008; Gonzaga & Leiner, 2013; Fig. 1); egg coating with mucus in harvestmen (e.g. Requena *et al.*, 2009; Chelini & Machado, 2014; Fig. 1); egg covering with debris and silk in webspinners (e.g. Edgerly, 1987); egg coating with offensive chemicals or hard protective membranes in leaf beetles (e.g. Chaboo, 2011); and defensive mutualism with ants in tree hoppers (Del-Claro & Oliveira, 2000; Billick, Weidmann & Reithel, 2001; Fig. 1). In most studies mentioned above, additional defences have been experimentally demonstrated to improve offspring protection, decreasing mortality rates even in the absence of the parents.

Wilson (1975) postulated that intense predation on eggs by conspecifics and ants, as well as the high risk of fungal infection in tropical rainforests, might have been major forces selecting for the evolution of parental care in arthropods. Although this hypothesis does not explain why offspring attendance has evolved in some species and not in others, it brings some insights into how the benefits of offspring attendance vary across broad geographic scales. Wilson's (1975) hypothesis is based on the assumption that the intensity of predation and fungal infection is higher in tropical than in extra-tropical areas. Indeed, theoretical studies based on mathematical modelling suggest that an increase in temperature and humidity promotes higher movement rates, resulting in more frequent and diverse biotic interactions (Moya-Laraño, 2010). Moreover, experimental evidence shows that activity and metabolic rates of several predatory arthropods increase with temperature, promoting an increase in encounter and consumption rates (Huey & Kingsolver, 1989; Gilbert & Raworth, 1996; Mohaghegh, De Clercq & Tirry, 2001; Kruse, Toft & Sunderland, 2008), which suggests that predation pressure may be more intense in warm climates. Finally, Schemske *et al*. (2009) reviewed the existence of latitudinal gradients in the importance of biotic interactions and showed that insect predation by ants and crop diseases caused by fungi and viruses are more frequent at lower latitudes.

Considering that temperature and rainfall have an important role in modulating the intensity of predation and parasitism, one macroecological prediction arising from Wilson's (1975) hypothesis is that the benefits of offspring attendance should be higher in warm and humid than in cold and dry climates, because in the former the offspring are under more intense threat from natural enemies. Our goal was to test this prediction using a powerful statistical approach, a phylogenetic meta-regression. Specifically, we only used studies of experimental removal of parental individuals (males or females) from their broods, conducted under natural field conditions, for arthropod species exhibiting uniparental offspring attendance. We classified the species into two groups according to an oftentimes neglected component of parental care: the presence or absence of additional lines of offspring protection. Given that these additional defences are known to attenuate offspring mortality, we predict that the total benefits of parental care (i.e. attendance + additional defences) should be higher in species in which offspring are protected by physical barriers, chemical deterrents, or defensive mutualisms. Moreover, this pattern should be more pronounced in warm and humid than in cold and dry climates.

High offspring mortality in the absence of care is one of the main ecological conditions for parental care to evolve from an ancestral state of no care (Klug *et al*., 2012). As far as we are aware, however, no previous study has formally investigated how such ecological conditions affect the benefits of offspring attendance on a broad geographic scale. Thus, the results presented here provide insights into why offspring attendance is comparatively more frequent among tropical arthropods, as already noted by Wilson (1975). Moreover, by emphasizing the role of additional lines of offspring defence, we enhance our understanding of how ecological conditions may affect the occurrence of different forms of parental care on large geographic scales.

II. METHODS

(1) Data collection and inclusion criteria

Our literature search was based on Preferred Reporting Items for Systematic reviews and Meta-Analyses as far as possible (http://www.prisma-statement.org/). We searched the literature on *Web of Science*, *Scopus,* and *Google Scholar* using all available years up to and including March 2016, and a combination of the following key words: ‘parental care’ AND ‘protection’ AND ‘experiment’ OR ‘benefit*’ OR ‘Arthropod*’ OR ‘insect*’ OR ‘arachnid*’. We also searched review papers and their reference sections (Eickwort, 1981; Hinton, 1981; Tallamy, 1999; Wong, Meunier & Kölliker, 2013), and all taxonomic chapters of *The Other Insect Societies* (Costa, 2006). Finally, we included studies that were presented at conferences that some of us attended (see online Supporting Information, Dataset S1). From the resultant list of documents, we used their titles to identify studies of interest, and scanned their abstracts searching for information on parental removal experiments conducted in the wild. When this information was found, or indicated that the data might be of use, we consulted the main text. When a study was selected, we searched their references (backward search) and citation record (forward search) for other studies that could provide additional data.

When available, information on estimates of mean offspring number, their S.D. (or S.E.), and sample sizes (numbers of eggs, young, and broods included in the study) was extracted from each publication. If a publication from the final list lacked some of this information, or if the published information indicated that data of interest were collected but not published, we contacted the corresponding author. In some cases, we obtained data from figures using *GraphClick* (Arizona Software). If descriptive statistics were not available, we extracted information from inferential statistics (i.e. *t*-values and their associated degrees of freedom) associated with the difference between (*i*) number of broods that survived, and (*ii*) number of offspring that survived per experimental group (see Section II.2). From each paper, we also recorded all sources of offspring loss.

We had to exclude some studies, even though they contained potentially relevant information (Fig. S1). In order to be included in our analyses, the study had to have: (*i*) experimentally manipulated the presence of the parent (either male or female), thus creating a *control group* in which the parent was left protecting the brood, and a *removal group* in which the parent was removed, leaving the brood unprotected; (*ii*) been conducted on a species that exhibits uniparental care by either the male or the female parent; and (*iii*) been conducted under natural field conditions, so that we eliminated from our sample any study that artificially increased offspring mortality risk (e.g. Filippi-Tsukamoto *et al.*, 1995; Punzo, 1998). Excluded studies and the reasons for their exclusion are summarized in Table S1.

For each paper included in the analyses, we used relevant locality information to obtain global positioning system (GPS) coordinates, when these were not explicitly provided. Based on these locality data, we gathered two types of environmental variable. The first was the actual evapotranspiration (AET), which is a measure of primary productivity (Hawkins *et al.*, 2003). Although there is no universally accepted proxy for biotic interactions in the macroecological literature, there is meta-analytical evidence showing that primary productivity is positively related to species richness in many taxa (Field *et al.*, 2009) and also to the abundance of ants (Kaspari, O'Donnell & Kercher, 2000; Monkkonen, Forsman & Bokma, 2006), which are the most important group of offspring predator in our dataset (see Section III). The second climatic variable was a principal component analysis (PCA) component that synthesized the relationships between temperature, precipitation, and seasonality (see Appendix S1). Positive values of the first axis (RC1) of this PCA were associated with high annual mean temperature, high annual precipitation, and weak temperature seasonality – conditions typically found in tropical climates (Peel, Finlayson & McMahon, 2007). On the other hand, negative values of RC1 were associated with low annual mean temperature, low annual precipitation, and strong temperature seasonality – conditions typically found in temperate climates (Peel *et al*., 2007).

We obtained global climatic data with 1 km^2 spatial resolution (www.worldclim.org; Hijmans *et al.*, 2005), and extracted the climate data for each study locality by creating a 0.5° buffer zone around the centre of the locality. We computed the average value for each variable within this buffer zone. To obtain evapotranspiration data for each locality, we used the geographic coordinate of the experimental site to extract its associated AET. We used MODIS generated evapotranspiration data (mm/year) averaged between 2000 and 2012 (http://ntsg.umt.edu/project/mod16; Mu, Zhao & Running, 2011).

(2) Data coding and effect size calculation

We coded the type of additional lines of offspring defence for each species (either present or absent) for each effect size (Dataset S1), because we predicted that this form of parental care would interact with the climatic covariate. This prediction is based on the fact that additional defences attenuate offspring mortality even in the absence of parents. Thus, in warm–humid climates, additional defences should provide more benefits than in cold–dry climates. We included the presence or absence of additional defences in each species (Dataset S1) as a fixed term in our meta-regression models. Moreover, we included the climatic variable (AET or the RC1) as covariates in the models. The climatic variables were centred and scaled to improve the interpretation of model coefficients (Gelman, 2008; Schielzeth, 2010). We modelled the interaction between the presence of additional defences and the climatic covariate because we predict that unguarded offspring of species that lack additional defences would suffer greater mortality in warm–humid climates than in cold–dry climates (i.e. at greater values of AET and RC1). On the other hand, we predict that unguarded offspring of species that have additional defences would be able to cope better with the increased natural enemy pressure in warm–humid climates. Therefore, we expect that the mortality in this experimental group would be low and similar along the climatic covariate axis.

Our main meta-analytic database contained two types of results from the original experimental papers, which led us to calculate two different effect sizes. The first type of result, called *survival data*, were presented in the original papers as the initial number of broods included in each experimental group (control or removal), and the subsequent number of broods that survived (with at least one egg) until the end of the experimental period. For these results, we used the odds ratio (OR) as our standardized effect size. The OR effect sizes estimate the ratio between brood mortality in the parental removal group (numerator) and in the control group (denominator). An OR = 1 means that there is no difference in survival between the two groups, an OR > 1 means that the probability of brood survival in the control group is higher than in the removal group, and an OR < 1 means the opposite (Fleiss & Berlin, 2009). Thus, OR is a measure of the benefit of providing parental care in terms of increasing the probability of brood survival. Greater values of OR mean that parental care results in large benefits (higher probability of brood survival) when compared to no parental care. All statistical analyses were conducted on the logarithm of OR, and its measurement error. We used standard equations to calculate OR and its variance (Nakagawa & Cuthill, 2007; Fleiss & Berlin, 2009).

The second type of result, called *intensity of mortality*, was presented in the original studies as the mean offspring number, its S.D., and sample size per experimental group at the beginning and at the end of the experimental period. From these results, we calculated *Zr*

(Fisher's transformation of the correlation coefficient) as our standardized effect size (Nakagawa & Cuthill, 2007). We estimated *Zr* from the descriptive data reported for the end of the experimental period, as this represented the maximum predicted difference between the two experimental groups. High values of *Zr* represent large differences in the number of surviving offspring between control and removal groups (i.e. many more surviving offspring in control). *Zr* effect sizes were calculated from standard formulae provided in Lipsey & Wilson (2001) and Nakagawa & Cuthill (2007). We adopted *Zr*, instead of a more popular standardized mean difference effect size (e.g. Hedges' *d*), because of the nature of our data set. As some experiments had complete mortality in one experimental group and no mortality in the other group, estimating a standardized mean difference from these data would lead to extreme values of effect size. However, by using *Zr* we avoided such issues and the distribution of effect sizes was not affected by extreme cases. We note that the use of *Zr* when assessing mean differences is common in biological studies (Nakagawa & Santos, 2012), and in our case, this effect size represents a measure of the intensity of offspring mortality, and thus a direct estimate of the benefits of offspring protection.

Our database includes 76 effect sizes from 45 studies, covering 45 arthropod species belonging to nine orders of the classes Arachnida, Crustacea, and Hexapoda (Dataset S1). Of these 45 species, 23 (51%) do not possess additional defences, whereas 22 (49%) have some sort of additional defences (Dataset S1). These species are distributed in all continents (except Antarctica), encompassing great climatic diversity, ranging from arid regions to pluvial forests (Fig. 1).

(3) Statistical analysis

An assumption of our study is that evapotranspiration represents the intensity of biotic interactions in a given place, so that higher evapotranspiration is associated with more attacks by natural enemies. We took advantage of the experimental design of the studies included in the analysis and tested whether the intensity of mortality was positively associated with AET. We regarded broods with no additional offspring defences from the removal group as analogous to baits set out by a researcher to estimate the intensity of natural enemy activity. Complete destruction of unguarded broods would be evidence of intense natural enemy activity, whereas little to no destruction would indicate negligible activity. This effect size represents a standardized mean difference in the number of offspring between the end and the beginning of each experiment. Thus, greater negative values mean that more offspring were lost during the experimental period (note that this effect size is opposite from others presented in the main results, where effect size represents the benefit of parental care, such that greater *positive* values mean more offspring were lost during the experimental period in removal groups relative to control groups). We found a significant negative association between the effect size of offspring mortality of non-guarded broods and AET (linear model: $\beta_{\mathrm{AET}} = -0.295$, $t = -2.413$, $P = 0.036$, $r^2 = 0.305$; Fig. S2), which suggests that our assumption is valid.

We then used one model to estimate the effect size of the probability of brood survival [log(OR) as the response variable] in guarded *versus* unguarded broods, and a separate model to estimate the effect size of the intensity of mortality (*Zr* as the response variable) in guarded *versus* unguarded broods. We built phylogenetic meta-analytic models (Hadfield & Nakagawa, 2010; Nakagawa & Santos, 2012) with restricted maximum likelihood fitted using the R package *metafor* (Viechtbauer, 2010). For details regarding the phylogeny we used, see Fig. S3 and Appendix S1.

We quantified heterogeneity (i.e. the proportion of variance between effect sizes that cannot be attributed to sampling errors) using a modified version of I^2 for phylogenetic meta-analysis, which assesses the consistency of effects across studies (Higgins *et al.*, 2003; Nakagawa & Santos, 2012). I^2 is calculated as the residual variance plus the variance components for the random effects divided by the sum of these two components (random effect variance and residual variance) and the within-study variance (see equation 22 in Nakagawa & Santos, 2012). We checked for potential publication bias in our data set using Egger's regression, which is calculated by fitting a linear regression to the residuals and the precision associated with each effect size as a predictor in the model (Egger *et al.*, 1997). If the intercept of Egger's regression is not significantly different from zero, one can conclude that there is little evidence for publication bias. Finally, we conducted a 'soft' retrospective power analysis to assess the validity of our findings (see Appendix S1 for details). All analyses were conducted in R version 3.0.2 (R Core Team, 2014).

III. RESULTS

(1) Environmental effect on overall probability of brood survival

The mean log(*OR*) estimates were positive, indicating that removing parents from broods with or without additional defences increased the probability that these broods would not survive [without additional defences: mean meta-analytic log(*OR*) = 3.906, 95% C.I. = 1.292 to 6.521; with additional defences: mean meta-analytic log(*OR*) = 2.727, 95% C.I. = 0.219 to 5.235]. Overall, AET did not significantly predict the magnitude of the probability of brood survival; nor did the effect of AET differ between broods with and without additional defences (interaction term: $\beta_{\text{[Additional defence:AET]}} = -0.292$, 95% C.I. = –1.354 to 0.770; Fig. 2). Nevertheless, we noted a slight positive effect of AET on the log(*OR*) of broods without additional defences (meta-regression: $\beta_{\text{[AET]}} = 0.438$, 95% C.I. = –0.443 to 1.319; Fig. 2). RC1 had a qualitatively similar effect as AET on the estimates of *Zr* for broods with and without additional defences (Fig. 2).

Total statistical heterogeneity was high ($I^2 = 79.15\%$; Table 1), which is consistent with the idea that our data on the probability of brood survival is modulated by covariates. In the

AET model, heterogeneity at the level of the species was 29.62%, and at the level of the phylogeny 30.10%.

(2) Environmental effect on intensity of brood mortality

The mean *Zr* estimates were positive, which indicates that removing parents from broods with or without additional defences increased the intensity of mortality (without additional defences: mean meta-analytic *Zr* = 1.392, 95% C.I. = –1.432 to 4.216; with additional defences: mean meta-analytic *Zr* = 0.950, 95% C.I. = –1.870 to 3.772). The effect of AET upon the benefit of parental care was significantly different in broods with and without additional defences (interaction term: $\beta_{\text{[Additional defence:AET]}}$ = –0.617, 95% C.I. = –1.163 to –0.070, Fig. 3). For broods without additional defences, AET had a significant positive effect on the magnitude of brood mortality (meta-regression: $\beta_{\text{[AET]}}$ = 0.422, 95% C.I. = 0.092 to 0.751). The effect of AET in broods with additional defences, however, was not different from zero (slope: $\beta_{\text{[Additional defence:AET]}}$ –0.087, 95% C.I. = –0.643 to 0.469; Fig. 3). RC1 had a qualitatively similar effect as AET on the estimates of *Zr* for broods with and without additional defences (Fig. 3).

Total statistical heterogeneity was high (I^2 = 98.53%; Table 1), which is consistent with the idea that our data on the probability of brood survival is modulated by covariates. In the AET model, heterogeneity at the level of the species was 29.46%, and at the level of the phylogeny 56.17%.

(3) Sources of offspring mortality

To quantify the sources of offspring mortality, we used 48 papers – 45 from our main data set plus three papers that could not be used in the meta-regression (Tallamy & Denno, 1981; Edgerly, 1987; Crespi, 1990). Of the total, 41 papers provided information on the sources of offspring mortality. Predators and parasitoids were the main source of offspring loss. Ants were the most frequent predators, being reported in 23 studies (56.1%), usually as the main source of offspring mortality. Cannibalism and parasitoid wasps were recorded in 16 studies each (39%). Spiders (N = 14 studies; 34.1%), hemipterans (N = 9 studies; 22%), predatory wasps (N = 5 studies; 12.2%), and other arthropods (N = 25 studies; 61%) were also reported consuming offspring. Fungal infection was reported as a source of offspring loss in 11 studies (26.8%). Abiotic factors were recorded as a minor source of offspring loss in only six studies (14.6%); in three studies eggs dehydrated and in three they were destroyed by heavy rain. These sources of mortality affected both guarded and non-guarded broods, indicating that parents are unable to cope with abiotic-driven offspring loss.

(4) Publication bias

There was little evidence for publication bias in either the log(*OR*) or the *Zr* effect size data sets, as the intercepts of Egger's regressions were not significantly different from zero [log(OR) AET model: (intercept) = –6.172, 95% C.I. = –14.085 to 0.344; *Zr* AET model: (intercept) = 6.498, 95% C.I. = –18.927 to 31.322].

IV. DISCUSSION

In this study, we predicted that the benefits of offspring attendance should be higher in places where eggs and young are under more severe threat from natural enemies. We also predicted that the presence of additional lines of protection should further reduce the total mortality of offspring over and above the effect of attendance. The results of our meta-regression show that unguarded broods without additional lines of defence experienced more intense mortality in places with higher AET, and with a warmer and more humid climate, which were the two proxies we used for the intensity of biotic interactions. Moreover, we found that additional defences play a crucial role in attenuating the intensity of mortality imposed by natural enemies. Offspring mortality was consistently lower in species exhibiting additional defences, and we detected no relationship with our proxies of intensity of biotic interactions. Below, we discuss the implications of these findings, emphasizing how they address some gaps in the current knowledge of parental care, and also possible directions for future studies.

If we are to understand the selective forces associated with the occurrence of parental care at large geographic scales, we need to be specific about the environmental conditions influencing the costs and benefits of this behaviour. By using evapotranspiration and climatic variables as predictors of the intensity of biotic interactions, our findings provide information on the possible drivers of the benefits of offspring attendance. Although latitude has been widely used in the macroecological literature (see Schemske *et al.*, 2009 and references therein), latitude alone represents only a small fraction of the variance of climatic conditions (Macías-Ordóñez, Macedo & Machado, 2013). In fact, the results presented here would not be found using latitude as explanatory variable (see Appendix S1 for the latitude results). Moreover, information on the sources of offspring mortality, coupled with our macroecological meta-regression, allows us to infer that the intensity of biotic interactions is the main factor influencing the benefits of offspring attendance in arthropods. Considering that protection against natural enemies has been regarded as one of the main functions of offspring attendance in several terrestrial ectothermic vertebrates, such as frogs, salamanders, and lizards (Balshine, 2012), we predict that the patterns reported here should also hold for other animal groups.

The fact that parental presence increases offspring survival does not explain how ecological factors may affect the evolution of offspring attendance (but see Pike *et al.*, 2016 for an example of how predation can lead to nest guarding). To understand the evolution of offspring attendance we need a comprehensive understanding of the fitness consequences of attendance not only to the offspring, but also to the parents (Alonso-Alvarez & Velando, 2012). High risk of offspring mortality in warm–humid climates increases the benefits of parental attendance in terms of offspring protection. However, the costs to parents in terms of exposure to natural enemies should also increase due to more frequent encounters with predators or parasitoids while attending the offspring (for instance, see Ghalambor & Martin, 2001). On the other hand, high temperatures accelerate embryonic development of arthropods and ectotherm vertebrates (Willmer, Stone, & Johnston, 2005), thus decreasing the amount of time parents are exposed to natural enemies. Shorter caring periods, in turn, may also attenuate other costs of offspring attendance, such as reduced food intake and increased energy expenditure related to parental activities (Alonso-Alvarez & Velando, 2012). Therefore, a comprehensive view of the evolution of offspring attendance requires information on how the costs paid by the parents vary in response to biotic and abiotic conditions (Requena, Munguía-Steyer & Machado, 2013). Unfortunately, studies about the costs of offspring attendance under natural conditions are limited to only a few arthropod species (Munguía-Steyer & Macías-Ordóñez, 2007; Buzatto *et al.*, 2007; Gilbert, Thomas & Manica, 2010; Requena *et al.*, 2012; Requena & Machado, 2014), so that it is not yet possible to envisage general patterns.

Although widespread among species exhibiting offspring attendance, the functional role of additional lines of defence has been poorly explored. Here we provide compelling evidence that the presence of these additional defences attenuates predation intensity upon the offspring, even when parents are experimentally removed (Fig. 3). Some of these additional defences, such as nests, burrows, and egg covering with debris, may conceal the offspring and decrease the probability of predators finding eggs or early-hatched young (Edgerly, 1987; Machado & Raimundo, 2001). Other lines of defence, such as mutualism with ants and egg coating with silk, mucus, or offensive chemicals, may protect the offspring from the activity of some natural enemies that are able to overcome parental protection (Evans, 1998; Mori *et al.*, 1999; Del-Claro & Oliveira, 2000; Requena *et al.*, 2009). The presence of additional defences may also allow the parents to leave the offspring temporarily unattended so that they can forage or avoid stressful abiotic conditions or adult-specific predators, without condemning eggs or early-hatched young to intense predation (e.g. Zink, 2003; Requena *et al.*, 2009; Chelini & Machado, 2012). Indeed, a recent study on a clade of Neotropical harvestmen has shown a strong correlation between the presence of additional defences (mucus or debris egg coating) with temporary or permanent parental abandonment of eggs (Chelini & Machado, 2014). It would be worthwhile to investigate the order in which these two traits have evolved to test whether additional defences are a cause or a consequence of offspring abandonment.

Most of the studies on the benefits of egg attendance in arthropods – and perhaps other taxa—are concentrated in a few particular regions of the world (see Fig. 1; points are clumped in south-eastern Brazil, Central America, and Japan). There are vast areas for which there are no available data, including large parts of Africa, continental Asia, and Australia. In some of these areas, such as extremely cold or xeric regions (white areas in Fig. 1), arthropod diversity is low and species are usually rare (Chown & Nicolson, 2004). These areas, however, offer the opportunity to investigate whether the benefits of offspring attendance are higher in 'harsh environments', as also proposed by Wilson (1975). Our data set does not allow us to test this hypothesis because the great majority of the species occur in 'benign environments', including temperate and tropical forests. Moreover, with few exceptions, the experiments of parental removal included in our analyses do not report significant offspring mortality due to abiotic factors. We know that several insect species exhibiting post-ovipositional parental care are able to attenuate adverse abiotic conditions (review in Danks, 2002), but quantitative data on the benefits of offspring attendance in these species are unfortunately scarce (Gilbert, 2014). The removal experiments we used as source of information in our meta-regression are easily conducted in the field and, depending on the species, data on offspring protection against biotic and abiotic factors can be obtained in a few days. Thus, we hope our study stimulates researchers to collect information about species living in harsh environments, and also species in which parents may provide benefit to offspring by attenuating adverse abiotic conditions.

Most of the macroecological studies focus on variation in species richness, abundances, distributions, and body sizes (see examples in Gaston & Blackburn, 2000). These studies have reported some global patterns, such as Allen's rule, which posits that endotherms from colder climates have shorter limbs than their relatives from warmer climates, and Bergmann's rule, which posits that species from colder climates are larger than their relatives from warmer climates. In both cases, broad-scale variation in morphology is explained by a decrease in the surface area to volume ratio, which increases heat conservation in cold climates (Gaston & Blackburn, 2000). In contrast to the abundant literature reporting variation in morphological traits, studies investigating how and why reproductive traits vary geographically in response to environmental factors are scarce (Macías-Ordóñez *et al.*, 2013). Exceptions are the studies of clutch size, cooperative breeding, and parental provisioning in birds, which provide evidence of broad-scale variation in reproductive traits in response to environmental conditions such as primary productivity, climatic seasonality, between-year variability in precipitation, and offspring mortality risk (Ricklefs, 2000; Jetz, Sekercioglu & Boehning-Gaese, 2008; Jetz & Rubenstein, 2011; Martin, 2015). Here we show that the benefits of parental care in arthropods on a global geographical scale are also influenced by environmental conditions, so that higher mortality risk leads to higher benefits of offspring protection. This pattern, however, is found only when we consider the presence or absence of additional lines of offspring defence. In the presence of additional defences, offspring mortality is greatly reduced, implying that offspring attendance alone may not be enough to cope with stronger predation/parasitism in tropical climates.

V. CONCLUSIONS

(1) We found meta-analytic evidence that supports the hypothesis that the benefits of egg attendance are higher in tropical climates, where biotic interactions are likely to be more intense. However, support for this hypothesis is only revealed when we take into account an often-neglected component of parental care: the presence of additional lines of offspring defence. This result stresses the key defensive role of physical barriers, chemical deterrents, and defensive mutualisms as additional lines of offspring defences in species already presenting offspring attendance. Moreover, it also provides new insights into how the benefits of parental care change in response to climate-mediated mortality risk imposed by natural enemies.

(2) Our results on the sources of offspring mortality, compiled from the studies included in the meta-regression, clearly indicate that ants are the predators that are the main source of mortality of arthropod broods, with cannibalism and parasitoids also being somewhat important sources of mortality. Our review also reveals that abiotic factors are negligible sources of brood mortality.

(3) We found little evidence of publication bias in our data set, which suggests that our findings are robust. There was, however, substantial heterogeneity in the effect sizes of both our meta-analyses, which was expected for such a wide-ranging data set (both in the phylogenetic and geographical sense). Even after the inclusion of the moderator and inclusion of random factors in the models, the amount of heterogeneity remained substantial,

suggesting that other factors may moderate the effects of the intensity of biotic interactions on the benefits of parental care.

(4) The patterns reported in our meta-regression help to explain the high frequency of parental care among tropical species and how biotic interactions influence the occurrence of parental care over large geographic scales.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Supplemental methods.

Dataset S1. Raw data file: effect sizes included in the meta-analyses.

Fig. S1. PRISMA flow diagram of our literature search and data collection.

Fig. S2. Relationship between actual evapotranspiration (AET; centred and scaled) and the effect size *Zr* of the intensity of brood mortality in non-guarded broods (removal group) with no additional offspring defence.

Fig. S3. Topology used in the phylogenetic meta-analytic models. See **Appendix S1, Section (2)** for detailed explanation of numbering and colours.

Table S1. List of studies excluded from the meta-analysis.

Table S2. Climatic variables, their meanings, factor loadings and eigenvalue of the principal component for the climatic variables used in the PCA.

Table S3. Summary of the correlation matrix of the 19 climatic variables used to calculate the PCA.

Table S4. The statistical power of the *Zr* effect sizes from the meta-analysis of the effect of actual evapotranspiration (AET) on the benefit of parental care in species with and without additional defences.

Figure legends

Fig. 1. Geographic distribution of the species included in the meta-analysis (some points are overlapped). Species with additional lines of offspring defence are shown as triangles, and species without additional lines of offspring defence are shown as circles. The colours on the map represent actual evapotranspiration (AET) in mm/year. The photographs illustrate some of the species included in our data set: (A) female of the Hawaiian spider *Theridion gralator*, whose eggs are additionally protected by a sac of silk (photograph by D. Murawski); (B) two females of the North American tree hopper *Publilia concava* attending eggs, which are additionally protected by mutualistic ants (photograph by G. Pronevitz); (C) female of the European earwig *Forficula auricularia* attending eggs inside a burrow (photograph by J. Meunier); (D) female of the Japanese sawfly *Cephalcia isshikii* attending eggs attached to leaves (photograph by S. Kudo); (E) female of the Costa Rican leaf bug *Platyphora selvae* attending larvae on a leaf (photograph by D.M. Windsor); (F) male of the Brazilian harvestman *Iporangaia pustulosa* attending eggs, which are additionally protected by a thick mucus coat (photograph by S. García); (G) male of the African assassin bug *Rhinocoris tristis* attending eggs and recently hatched nymphs on a branch (photograph by L.K. Thomas); (H) female of the Malaysian butterfly *Hypolimnas anomala* attending eggs under a leaf (photograph by S. Chye).

Fig. 2. (A) Relationship between actual evapotranspiration (AET) and the effect size [log(*OR*)] of the probability of brood survival until the end of the experiment of arthropod parental removal. AET has been centred and scaled. Red circles depict data points from broods that had no additional lines of defence, and blue triangles depict data points from broods with additional lines of defence. Lines represent phylogenetic meta-analysis estimated effects for each category of additional defences (i.e. present *versus* absent). The size of symbols represents their relative precision (larger symbols = more precise). (B)

Phylogenetic meta-regression model estimates for the log(*OR*) effect sizes. For each parameter, the point estimate represents the mean, and the lines span the 95% confidence interval. The intercept represents effect sizes [log(*OR*)] for species that do not present any form of additional brood defence. The $\beta_{\text{[Additional defence:Covariate]}}$ label represents the slope coefficient of AET (or RC1) for species with additional defences, while the $\beta_{\text{[Covariate]}}$ represents the slope of AET (or RC1) for species without additional defences. Grey symbols denote the model in which AET is the covariate, and white circles denote the model in which the rotated component of the PCA (RC1) is the covariate.

Fig. 3. (A) Relationship between actual evapotranspiration (AET) and the effect size *Zr* of the intensity of brood mortality in the experiment of arthropod parental removal. AET has been centred and scaled. Red circles depict data points from broods that had no additional line of defence, and blue triangles depict data points from broods with additional lines of defence. Lines represent phylogenetic meta-analysis estimated effects for each category of additional defences (i.e. present *versus* absent). The size of symbols represents their relative precision (larger symbols = more precise). (B) Phylogenetic meta-regression model estimates for the *Zr* effect sizes. For each parameter, the point estimate represents the mean, and the lines span the 95% confidence interval. The intercept represents effect sizes *Zr* for species that do not present any form of additional brood defence. The $\beta_{\text{[Additional defence:Covariate]}}$ label represents the slope coefficient of AET (or RC1) for species with additional defences, while the $\beta_{\text{[Covariate]}}$ represents the slope of AET (or RC1) for species without additional defences. Grey symbols denote the model in which actual evapotranspiration (AET) is the covariate, and white circles denote the model in which the rotated component of the PCA (RC1) is the covariate.

Fig. 1

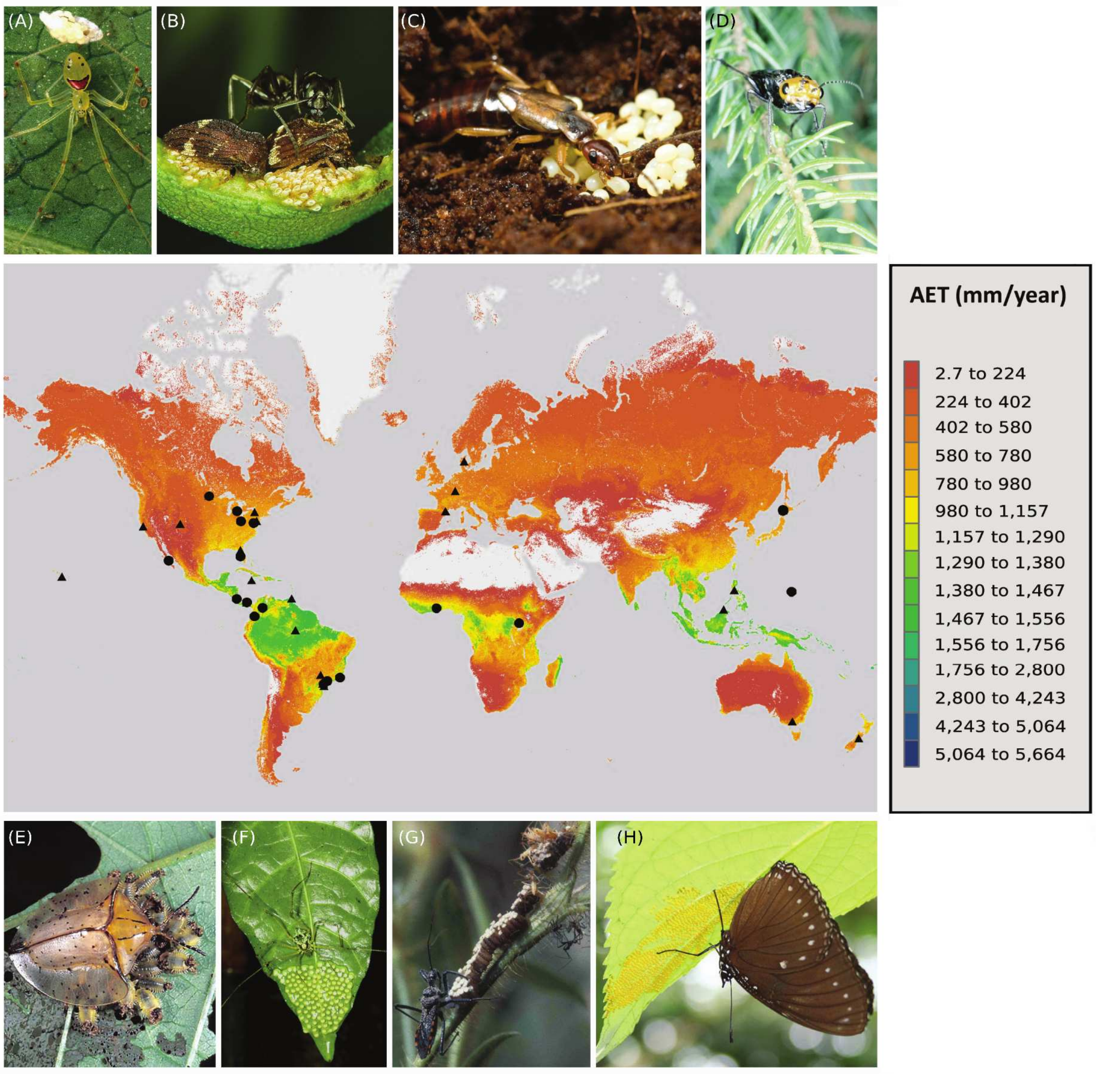

(A)
(B)
(C)
(D)
AET (mm/year)
2.7 to 224
224 to 402
402 to 580
580 to 780
780 to 980
980 to 1,157
1,157 to 1,290
1,290 to 1,380
1,380 to 1,467
1,467 to 1,556
1,556 to 1,756
1,756 to 2,800
2,800 to 4,243
4,243 to 5,064
5,064 to 5,664
(E)
(F)
(G)
(H)

Fig. 2

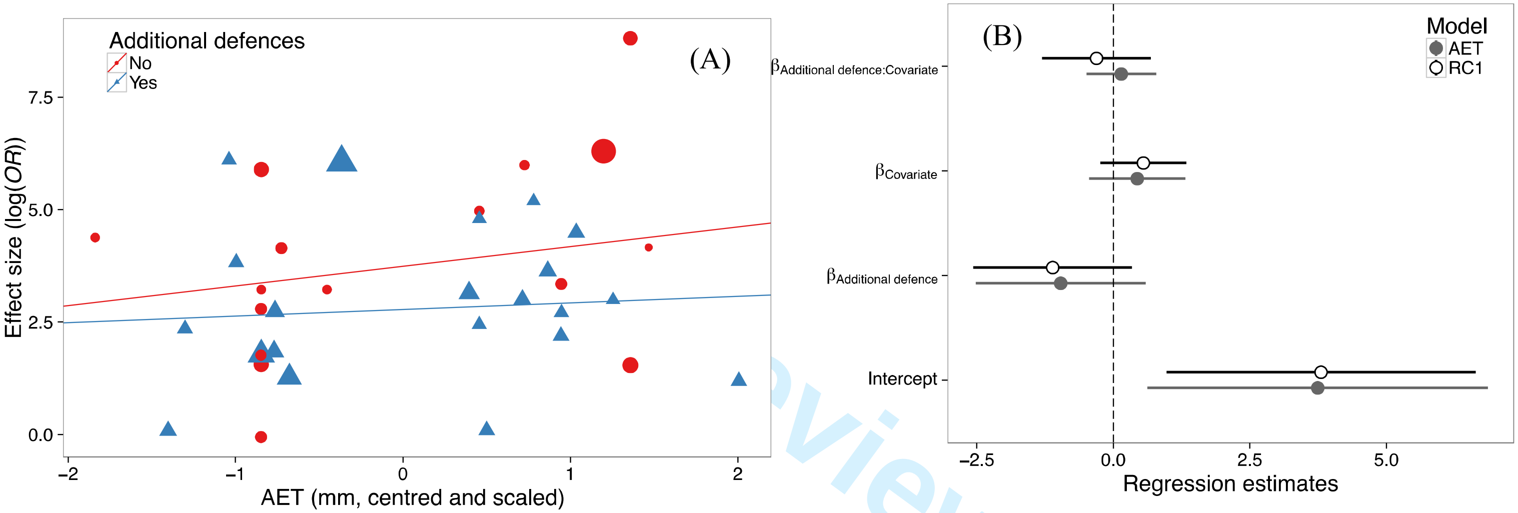

Additional defences
No
Yes
(A)
Effect size (log(OR))
7.5
5.0
2.5
0.0
−2
−1
0
1
2
AET (mm, centred and scaled)
(B)
Model
AET
RC1
$\beta_{\text{Additional defence:Covariate}}$
$\beta_{\text{Covariate}}$
$\beta_{\text{Additional defence}}$
Intercept
−2.5
0.0
2.5
5.0
Regression estimates

Fig. 3

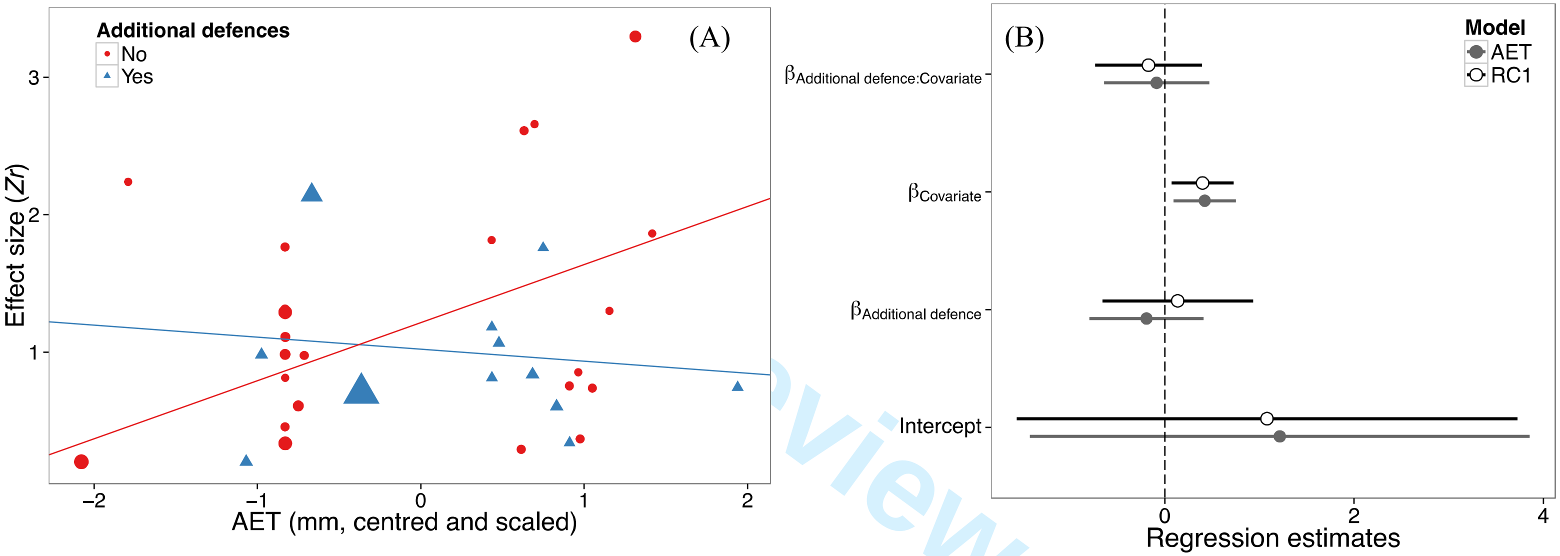
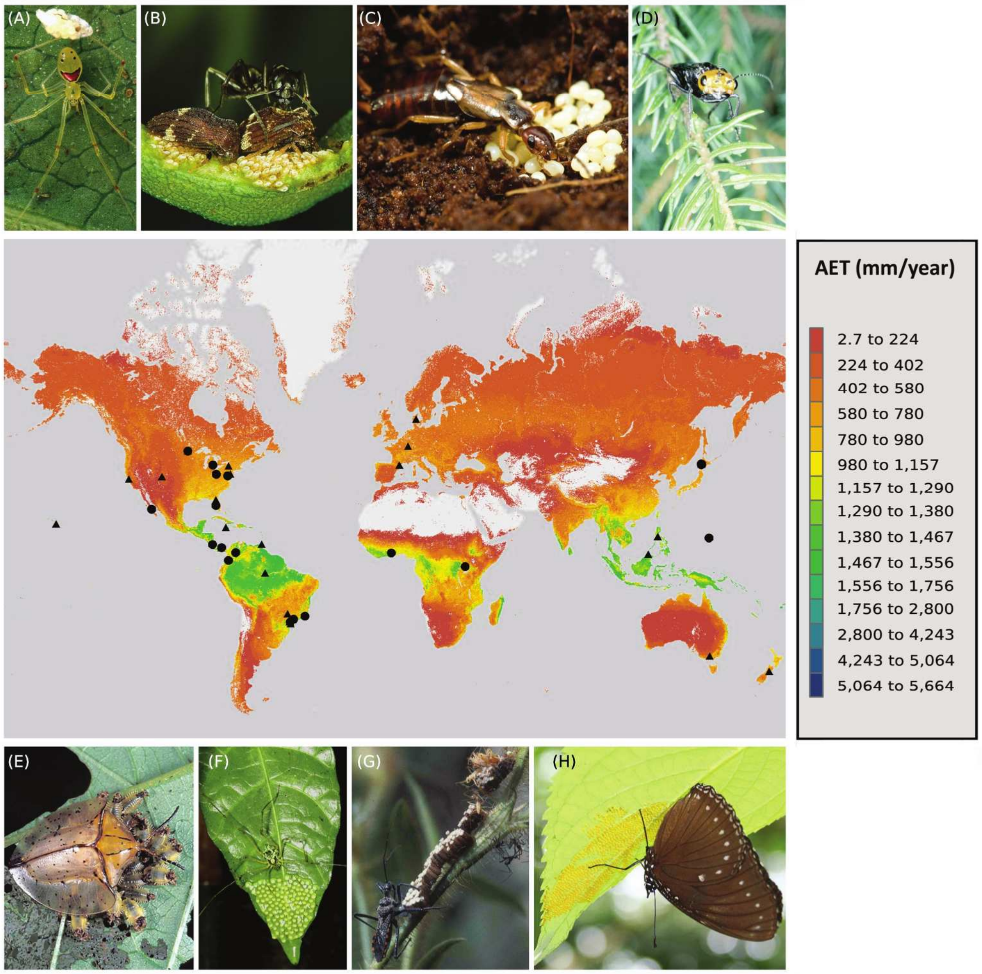
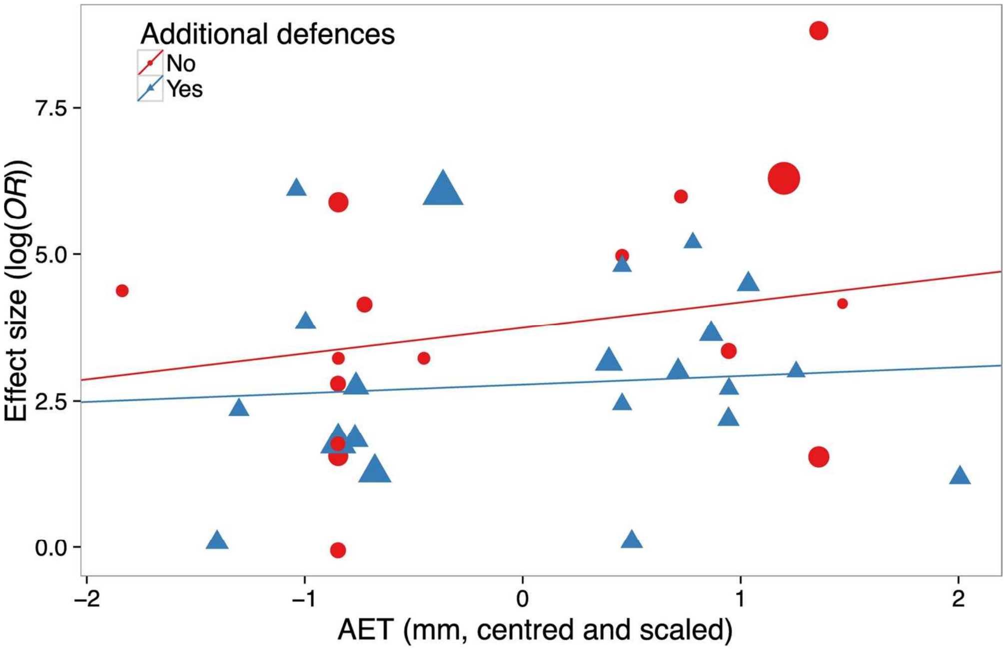

Additional defences
● No
▲ Yes
(A)
Effect size (Zr)
1
2
3
−2
−1
0
1
2
AET (mm, centred and scaled)
(B)
Model
● AET
○ RC1
$\beta_{\text{Additional defence:Covariate}}$
$\beta_{\text{Covariate}}$
$\beta_{\text{Additional defence}}$
Intercept
0
2
4
Regression estimates

Table 1. Univariate-response meta-regression models and their variances, and heterogeneity. Models estimate the effect of actual evapotranspiration (AET) and the presence or absence of additional lines of offspring defence on the log(*OR*) and *Zr* effect sizes. ':' represents an interaction between the covariate (AET) and the categorical variable (additional lines of offspring defence). Heterogeneity (i.e. % variance at a particular level in relation to the total variance) is presented at the level of the species, at the level of the order, and at the level of the phylogeny.

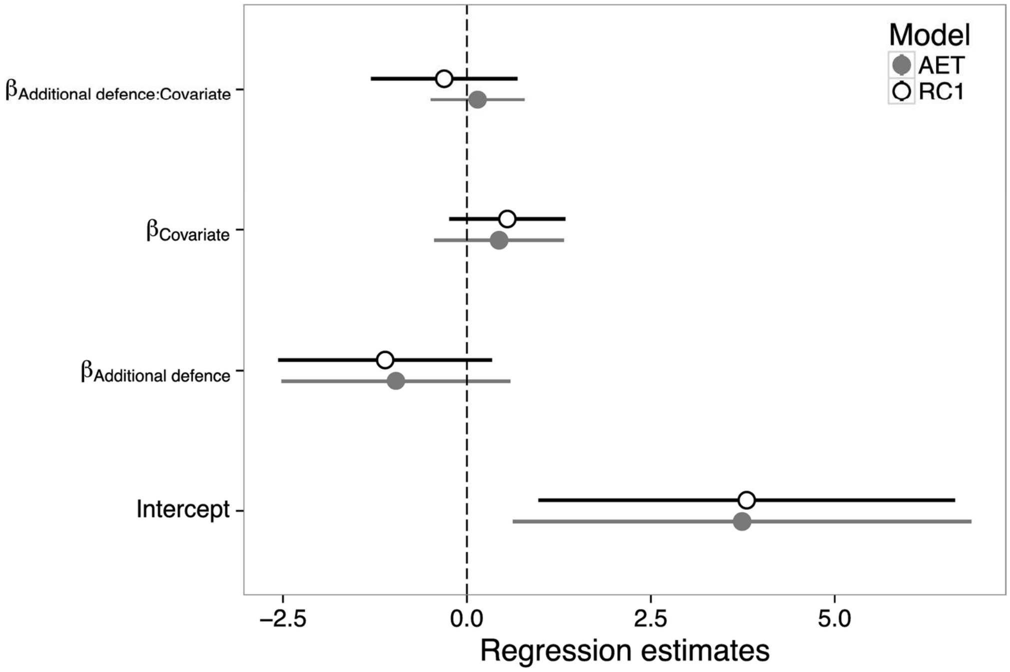
Model	Fixed effects	Random effects	Heterogeneity ($Var_{Species}$) %	Heterogeneity (Var_{Order}) %	Heterogeneity ($Var_{Phylogeny}$) %	Total heterogeneity %
Log(*OR*) models						
Model AET	Additional lines of defences + AET + Additional lines of defences:AET	Species + Order + Phylogeny	29.62	19.42	30.10	79.15
Zr models						
Model AET	Additional lines of defences + AET + Additional lines of defences:AET	Species + Order + Phylogeny	29.46	14.37	56.17	98.53



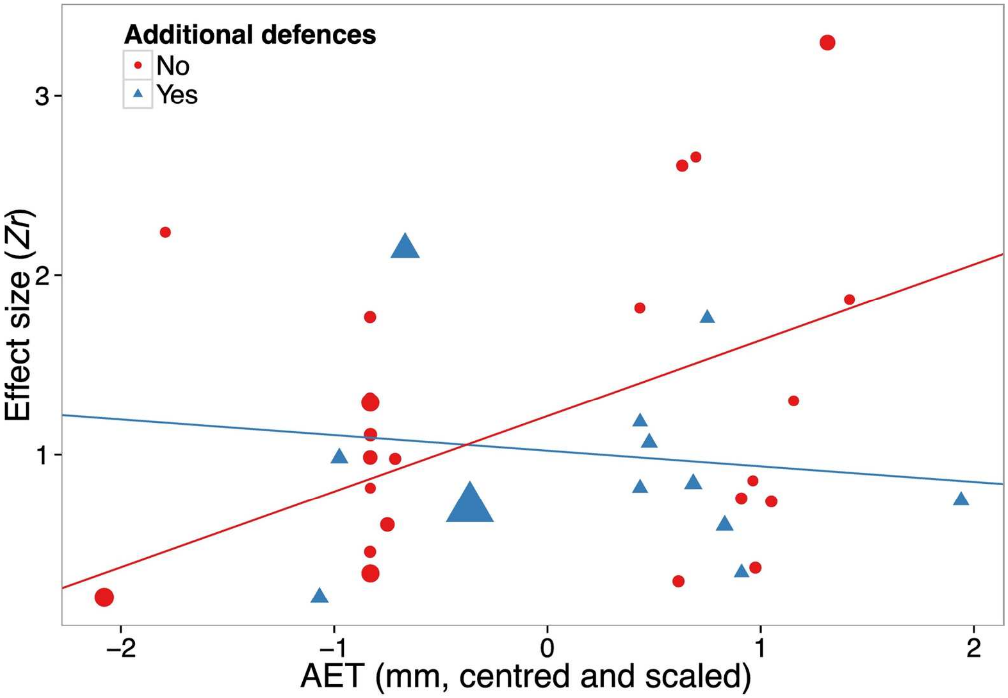
Geographic distribution of the species included in the meta-analysis (some points are overlapped).
Fig. 1
218x215mm (300 x 300 DPI)



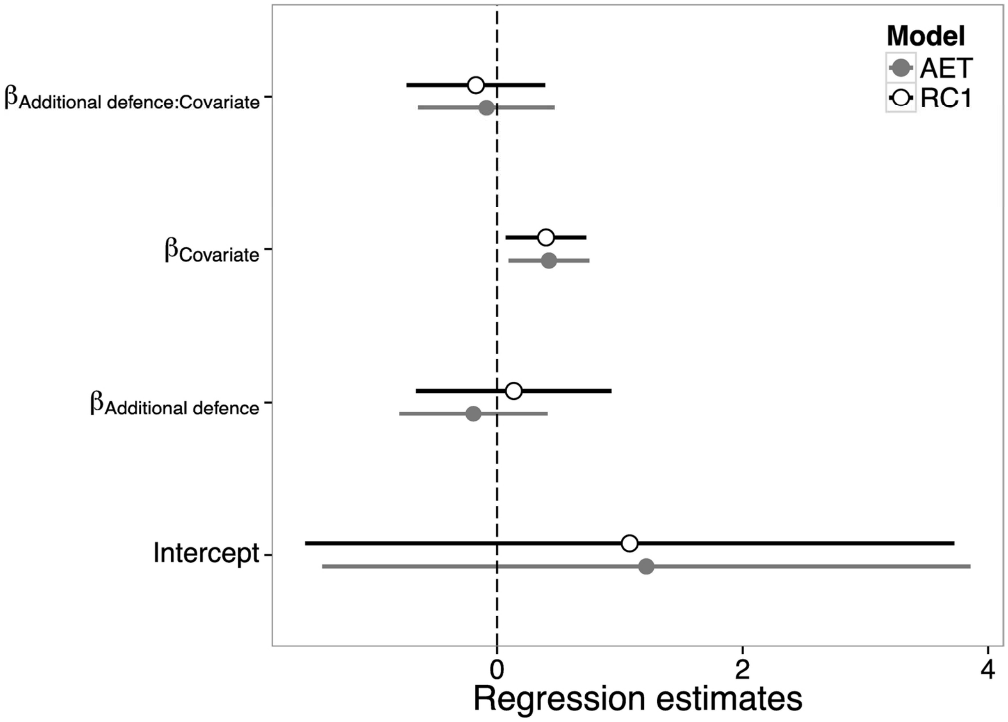
(A) Relationship between actual evapotranspiration (AET) and the effect size [log(OR)] of the probability of brood survival until the end of the experiment of arthropod parental removal.
Fig. 2A
154x99mm (300 x 300 DPI)



(B) Phylogenetic meta-regression model estimates for the log(OR) effect sizes.
Fig. 2B
154x102mm (300 x 300 DPI)



(A) Relationship between actual evapotranspiration (AET) and the effect size Zr of the intensity of brood mortality in the experiment of arthropod parental removal.
Fig. 3A
146x101mm (300 x 300 DPI)



(B) Phylogenetic meta-regression model estimates for the Zr effect sizes.
Fig. 3B
146x104mm (300 x 300 DPI)

Macroecology of parental care in arthropods: higher mortality risk leads to higher benefits of offspring protection in tropical climates

Eduardo S. A. Santos, Pedro P. Bueno, James D. J. Gilbert, Glauco Machado

APPENDIX S1. SUPPLEMENTAL METHODS

(1) PCA to synthesize climatic variables

We used a principal component analysis (PCA) to summarize the 19 climatic variables (see Table S2) into uncorrelated orthogonal axes, and performed the PCA on the correlation matrix of the data, with Varimax factor rotation, using the function *principal* from the *R* package *psych* (*R version 3.0.2;* R Core Team, 2014; Revelle, 2016). The correlation matrix was calculated with a sample size of 42 observations per climatic variable (see Table S3 for more details). As suggested by Budaev (2010), we calculated the Kaiser–Meyer–Olkin (KMO) measure of sampling adequacy of the correlation matrix used in the PCA, which indicated that the matrix was adequate for a PCA (KMO = 0.789). The first rotated principal component (RC1) is a measure of the abiotic conditions at a locality, as explained in Section II.1 of the main text (see Table S2 for factor loadings).

(2) Assembly of phylogenetic tree used in meta-analytic models

Given that no phylogenetic study published so far comprises all species included in our data set (Dataset S1), we assembled different phylogenies in order to obtain the super-tree depicted in Fig. S3. This super-tree includes 45 species belonging to the following arthropod orders: (1) ARACHNIDA: Acari (pink branch), Opiliones (red branches), Araneae (orange branches), (2) CRUSTACEA: Decapoda (grey branch), (3) HEXAPODA: Dermaptera (dark-blue branches), Embioptera (light-blue branch), Hemiptera (green branches), Hymenoptera (light-brown branch), Lepidoptera (purple branch), and Coleoptera (dark-brown branches). The backbone of the super-tree (node 1), i.e. the relationship among arachnids, crustaceans, and hexapods, is based on Regier, Shutlz & Kambic (2005). The relationship among arachnid orders (node 2) is based on Shultz (2007), and the internal phylogeny of the order Opiliones is based on Sharma & Giribet (2011), which provides data on interfamilial relationships (node 3), and Caetano & Machado (2013), which provide data on generic relationships within the family Gonyleptidae (node 4). The phylogeny of the major groups within the order Araneae (node 5) is based on Coddington (2005). The topology of the family Theridiidae is partially based on Agnarsson (2004) (node 6) and Arnedo, Agnarsson & Gillespie (2007) (node 7), according to which *Theridion impressum* should be included in the genus *Phylloneta*, sister group to *Theridion sensu stricto*. The topology of the clade Dionycha (node 8) is based on Bayer & Schoenhofer (2013) and Ramírez (2014). The relationship among insect orders (node 9) is based on Ishiwata *et al.* (2010). Within the order Hemiptera, the topologies of the clades Cimicomorpha (node 10) and Cicadomorpha (node 11) are based on Schuh, Weirauch & Wheeler (2009) and Cryan *et al.* (2004), respectively. Specifically, for the Pentatomoidea (nodes 12 and 13), the generic relationship is based on Grazia, Schuh & Wheeler (2008) and Tsai, Kudo & Yoshizawa (2015). Finally, the generic relationships among genera of the family Chrysomelidae (node 14) are based on Gómez-Zurita, Hunt & Vogler (2008).

(3) Power analysis

The issue of a power analysis in the context of meta-analyses in ecology and evolution has been treated recently by Lajeunesse (2013). Lajeunesse provides guidance as to how and when to employ power analysis to assess the validity of meta-analytic results. One useful piece of information is a simulation that shows (Lajeunesse, 2013, Fig. 22.2B, p. 352) that when the meta-analysis sample size reaches approximately 40 effect sizes, the width of the 95% confidence interval of the effect size stabilizes. It means that increasing the number of effect sizes above this number causes very little improvement in the power of the meta-analysis. On this basis, we argue that our overall sample size ($N = 76$ effect sizes) is almost twice as large as Lajeunesse's simulation suggestion of a reasonable sample size (i.e. a more sensitive study) for a hypothesis-testing meta-analysis. Nevertheless, we calculated the power ('soft' retrospective approach, $\rho^{Z}_{\text{two-tailed}}$) of the analysis of *Zr* effect sizes including the moderators (AET and additional defences). The statistical power of a test allows one to answer the following question "how should one interpret a meta-analysis that fails to reject a null hypothesis?", as the definition of power is the probability of detecting a significant finding when it, in fact, exists (Cohen, 1988). Therefore, in the case of our *Zr* results the interpretation of the following estimates of statistical power would allow readers to evaluate how they view the non-significant result of the effect of AET on broods that have additional defences (see Section III.2 of the main paper). The results from the power analysis (Table S4) suggest that our study had reasonable power to detect nonzero effect sizes using a random-effects model, which could be ultimately interpreted as the observed effects having biological basis that is not due to sampling error.

(4) Supplementary results using latitude as a predictor variable

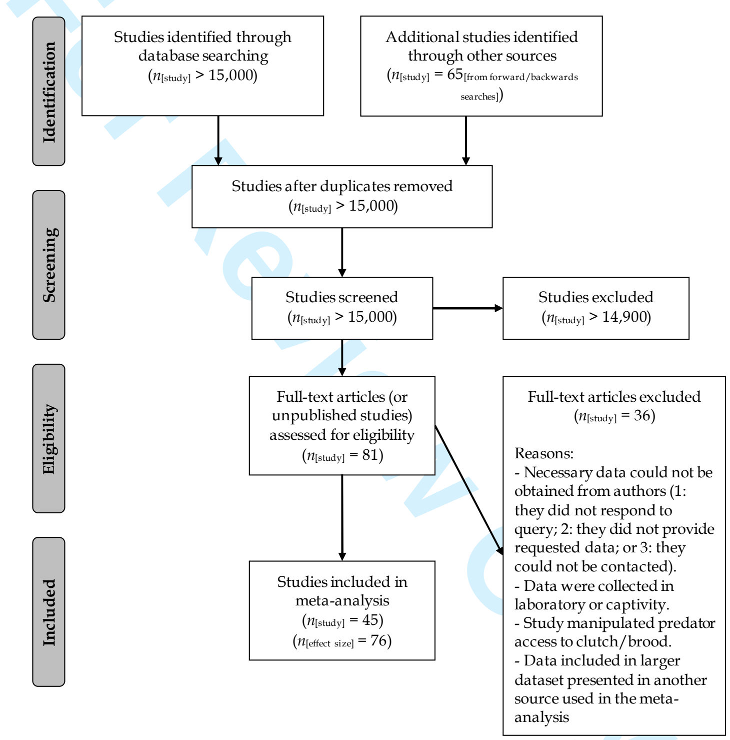
For continuity with the macroecological literature, we also conducted a meta-regression with latitude as a predictor variable of the log(*OR*) and *Zr* effect sizes of the benefits of offspring attendance. Latitude was originally coded in decimal degrees, in such a way that southern latitudes presented negative values and northern latitudes positive values. These data were centred and scaled prior to inclusion in the meta-analytic model, which followed exactly the same protocol as the analyses reported in the main text.

We found no significant effect of the latitude on the magnitude of the log(*OR*) effect size of the probability of brood survival (meta-regression slopes: $\beta_{\text{[No additional defence:latitude]}}$ = –0.321, 95% C.I. = –1.556 to 0.913; $\beta_{\text{[Additional defence:latitude]}}$ = –0.246, 95% C.I. = –0.740 to 0.247; interaction term: $\beta_{\text{[Additional defence:latitude]}}$ = 0.074, 95% C.I. = –1.197 to 1.346). When investigating the interaction between latitude and the presence of additional lines of offspring defence, we found that in the absence of additional defences, there was a negative effect of latitude on the magnitude of the intensity of brood mortality (*Zr*; meta-regression slope: $\beta_{\text{[No additional defence:latitude]}}$ = –0.457, 95% C.I. = –0.939 to 0.024). However, the effect was not statistically significant. In the presence of additional defences, the effect of the latitude covariate was positive, but again non-significant (*Zr*; meta-regression slope: $\beta_{\text{[Additional defence:latitude]}}$ = 0.179, 95% C.I. = –0.554 to 0.912; interaction term: $\beta_{\text{[Additional defence:latitude]}}$ = 0.636, 95% C.I. = –0.135 to 1.408).

In conclusion, the results of the analyses using latitude as predictor variable were all non-significant – both for species with and without additional lines of offspring defence. These findings contrast with those presented in the main text, in which the intensity of brood mortality was influenced by our proxies of biotic interactions. We interpret this discrepancy as evidence that the causal link between environmental conditions and the benefits of parental care is captured better using actual evapotranspiration and climatic variables than latitude *per se*.

Supplementary figures

Fig. S1. PRISMA flow diagram of our literature search and data collection.



From: Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009). *P*referred *R*eporting *I*tems for *S*ystematic Reviews and *M*eta-*A*nalyses: The PRISMA Statement. PLoS Med 6(6): e1000097. doi:10.1371/journal.pmed1000097

For more information, visit www.prisma-statement.org.

Fig. S2. Relationship between actual evapotranspiration (AET; centred and scaled) and the effect size *Zr* of the intensity of brood mortality in non-guarded broods (removal group) with no additional offspring defence.

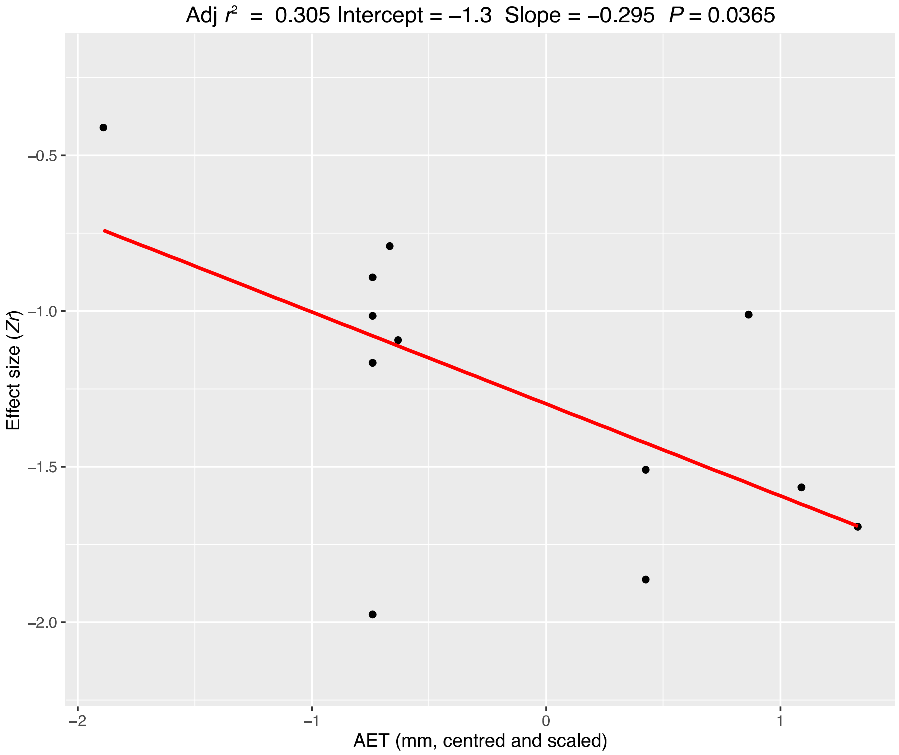
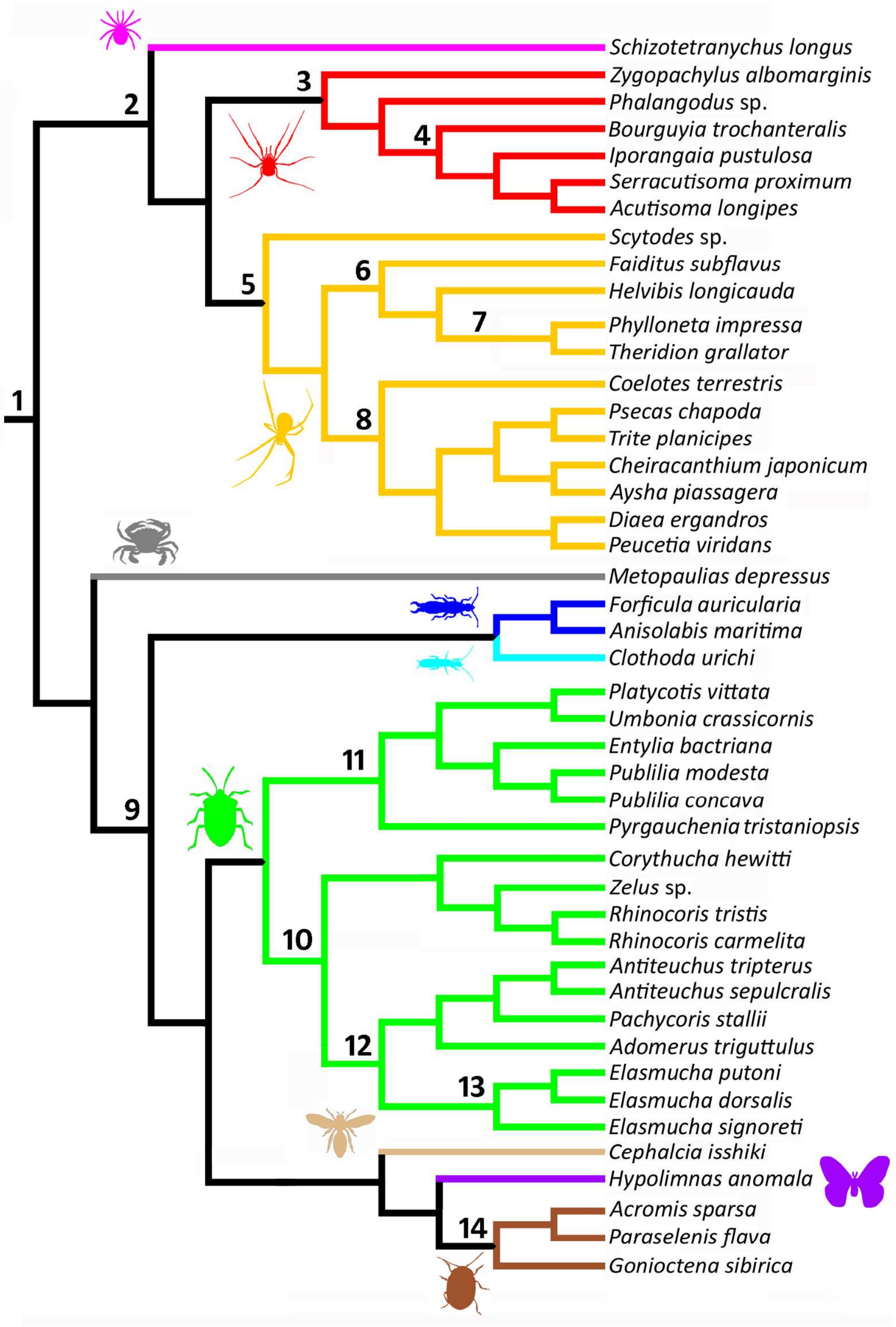


Fig. S3. Topology used in the phylogenetic meta-analytic models. See Appendix S1, Section (2) for detailed explanation of numbering and colours.



Supplementary tables

Table S1. List of studies excluded from the meta-analysis. The corresponding author, and in case of a few studies also co-authors, of the majority of these studies have been contacted. In all these cases, contacted authors either did not respond (marked *) or for various reasons were unable to provide requested information.

Number	**Study**	**Reason for exclusion**	**Species name**
1	Eberhard (1987)	Study was not manipulative experiment	*Apollophanes punctipes*
2	Eberhard (1974)	Study was not manipulative experiment	*Lyssomanes jemineus*
3	West & Alexander (1963)	Study was not manipulative experiment	*Anurogryllus muticus*
4	Filippi *et al.* (2001)	Study was not manipulative experiment	*Parastrachia japonensis*
5	Thiel (1999)	Experiment conducted in marine environment	*Leptocheirus pinguis*, *Casco bigelowi*, *Dyopedos monacanthus*
6	Wyatt (1986)	Insufficient information to calculate effect size	*Bledius spectabilis*
7	Suzuki (2001)	Experiment not conducted in the wild	*Nicrophorus quadripunctatus*
8	Satou *et al.* (2009)	Experiment not conducted in the wild	*Nicrophorus quadripunctatus*
9	Gundermann *et al.* (1997)	Experiment not conducted in the wild	*Coelotes terrestris*
10	Tsukamoto & Tojo (1992)	Experiment not conducted in the wild	*Parastrachia japonensis*
11	Halffter et al. (1996)	Experiment not conducted in the wild	*Copris incertus*
12*	Edgerly (1987)	Insufficient information to calculate effect size	*Clothoda urichi*
13*	Tallamy & Denno (1981)	Insufficient information to calculate effect size	*Gargaphia solani*
14*	Crespi (1990)	Insufficient information to	*Elaphrothrips tuberculatus*

		calculate effect size	
15	Favila (1993)	Experiment not conducted in the wild	*Canthon cyanellus*
16	Honbo & Nakamura (1985)	Insufficient information to calculate effect size	*Elasmucha putoni*
17	Filippi *et al.* (2000)	Predation level manipulated	*Parastrachia japonensis*
18	Aoki (1997)	Experiment conducted in marine environment	*Caprella* sp.
19	Eggert *et al.* (1998)	Experiment not conducted in the wild	*Nicrophorus vespilloides*
20	Filippi-Tsukamoto *et al.* (1995)	Predation level manipulated	*Parastrachia japonensis*
21	Halffter & Matthews (1966)	Could not locate source material	*Copris fricator*
22	Klostermeyer (1942)	Insufficient information to calculate effect size	*Euborellia annulipes*
23*	Kudo (1990)	Insufficient information to calculate effect size	*Elasmucha putoni*
24	Maschwitz & Gutmann (1979)	Study was not manipulative experiment	*Elasmucha fieberi*
25	Melber & Schmidt (1975*a*)	Study was not manipulative experiment	*Elasmucha* sp.
26	Melber & Schmidt (1975*b*)	Study was not manipulative experiment	*Elasmucha* sp.
27	Melber *et al.* (1980)	Could not locate source material	*Elasmucha grisea*
28	Neiswander (1944)	Could not locate source material	*Forficula auricularia*
29	Pukowski (1933)	Insufficient information to calculate effect size	*Nicrophorus* sp.
30	Thiele (1977)	Study was not manipulative experiment	Tribe Pterostichini (14 species)
31	Trumbo (1991)	Experiment not conducted in the wild	*Necrophorus orbicollis*
32	Tyndale-Biscoe (1984)	Experiment not conducted in the wild	*Copris diversus*

33	Weyrauch (1929)	Insufficient information to calculate effect size	*Forficula auricularia*
34	Edwards (1988)	Study was not manipulative experiment	*Kheper nigroaeneus*
35	Punzo (1998)	Predation level manipulated	*Eremobates marathoni*
36	Ruttan (1990)	Predation level manipulated	*Theridion pictum*

Table S2. Climatic variables, their meanings, factor loadings and eigenvalue of the principal component for the climatic variables used in the PCA. Interpretable factor loadings are in bold.

Variable	**Meaning**	**RC1**
BIO1	Annual mean temperature	**0.796**
BIO2	Mean diurnal range [mean of monthly (max temp – min temp)]	**–0.421**
BIO3	Isothermality (BIO2/BIO7) (* 100)	**0.863**
BIO4	Temperature seasonality (standard deviation *100)	**–0.95**
BIO5	Maximum temperature of warmest month	0.239
BIO6	Minimum temperature of coldest month	**0.891**
BIO7	Temperature annual range (BIO5–BIO6)	**–0.942**
BIO8	Mean temperature of wettest quarter	0.268
BIO9	Mean temperature of driest quarter	**0.915**
BIO10	Mean temperature of warmest quarter	**0.435**
BIO11	Mean temperature of coldest quarter	**0.879**
BIO12	Annual precipitation	**0.549**
BIO13	Precipitation of wettest month	**0.636**
BIO14	Precipitation of driest month	–0.060
BIO15	Precipitation seasonality (coefficient of variation)	**0.449**
BIO16	Precipitation of wettest quarter	**0.611**
BIO17	Precipitation of driest quarter	0.113
BIO18	Precipitation of warmest quarter	0.197
BIO19	Precipitation of coldest quarter	**0.503**
Eigenvalue		11.37
Variance explained (%)		40.3

Table S3. Summary of the correlation matrix of the 19 climatic variables used to calculate the PCA. The sample size for each variable used to compute the correlations was $N = 42$ observations.

	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO8	BIO9	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19
BIO1	–0.34	0.88	–0.90	0.72	0.97	–0.89	0.77	0.92	0.87	0.98	0.70	0.78	0.18	0.49	0.77	0.27	0.52	0.48
BIO2	–	–0.25	0.39	0.09	–0.46	0.55	–0.11	–0.34	–0.21	–0.37	–0.57	–0.51	–0.45	0.16	–0.51	–0.46	–0.27	–0.46
BIO3		–	–0.93	0.47	0.91	–0.89	0.55	0.88	0.60	0.92	0.70	0.75	0.23	0.42	0.73	0.33	0.39	0.58
BIO4			–	–0.38	–0.97	0.98	–0.47	–0.96	–0.58	–0.96	–0.65	–0.72	–0.19	–0.39	–0.70	–0.29	–0.41	–0.51
BIO5				–	0.56	–0.34	0.88	0.51	0.94	0.60	0.39	0.46	0.00	0.47	0.47	0.06	0.33	0.22
BIO6					–	–0.97	0.63	0.96	0.75	0.99	0.72	0.78	0.23	0.40	0.76	0.33	0.46	0.54
BIO7						–	–0.45	–0.94	–0.58	–0.95	–0.70	–0.74	–0.26	–0.32	–0.73	–0.36	–0.42	–0.55
BIO8							–	0.50	0.92	0.66	0.55	0.62	0.14	0.43	0.62	0.21	0.62	0.24
BIO9								–	0.67	0.96	0.64	0.70	0.17	0.43	0.69	0.26	0.36	0.52
BIO10									–	0.77	0.58	0.65	0.13	0.48	0.65	0.20	0.49	0.35
BIO11										–	0.70	0.77	0.19	0.46	0.76	0.29	0.48	0.51
BIO12											–	0.96	0.58	0.12	0.96	0.66	0.61	0.82
BIO13												–	0.36	0.36	1.00	0.46	0.66	0.73
BIO14													–	–0.56	0.38	0.98	0.34	0.53
BIO15														–	0.35	–0.49	0.23	–0.01
BIO16															–	0.47	0.69	0.70
BIO17																–	0.39	0.61
BIO18																	–	0.16
BIO19																		–

Table S4. The statistical power of the *Zr* effect sizes ($\bar{\mu}$) from the meta-analysis of the effect of actual evapotranspiration (AET**)** on the benefit of parental care in species with and without additional defences (grouping). All tests had sufficient power based on published conventions (e.g. $\rho^{Z}{}_{\text{two-tailed}} > 0.75$).

Grouping	*K*	Effect size			Statistical power ($\rho^{Z}{}_{\text{two-tailed}}$)		
					Small	Medium	Large
		$\bar{\mu}$	95% C.I.	$\sigma^2(\bar{\mu})$	$\bar{\mu} = 0.2$	$\bar{\mu} = 0.5$	$\bar{\mu} = 0.8$
No additional defence	23	0.422	0.092 to 0.751	0.0422	0.997	1	1
Additional defence	14	–0.087	–0.643 to 0.469	0.0275	0.999	1	1

reference.id	authors	year
ref2	Horel & Gundermann	1992
ref3	Zanatta	2013
ref4	Toyama	1999
ref7	Requena	2007
ref8	Gonzaga & Leiner	2013
ref9	Fink	1986
ref10	Vieira & Romero	2008
ref11	Li *et al.*	1999
ref12	Soerensen	2007
ref13	Gillespie	1990
ref15	Taylor	1997
ref16	Machado & Oliveira	1998
ref17	Machado & Oliveira	2002
ref18	Requena *et al.*	2009
ref19	García & Machado	2014
ref20	Buzatto *et al.*	2007
ref21	Mora	1990
ref22	Diesel	1989
ref24	Choe	1989
ref25	Kudo *et al.*	1995
ref28	Miller & Zink	2012
ref29	Kölliker & Vancassel	2007
ref31	Eberhard	1975
ref32	Santos & Albuquerque	2001
ref33	Kudo *et al.*	1989
ref34	Kudo	2002
ref36	Kudo & Nakahira	1993
ref38	Williams *et al.*	2005
ref40	Zink	2003
ref41	Stegmann & Linsenmair	2002
ref42	Gilbert *et al.*	2010
ref43	Nakahira & Kudo	2008
ref44	Kudo *et al.*	1992
ref45	Nafus & Schreiner	1988
ref47	Billick *et al.*	2001
ref48	Evans	1998
ref49	Faeth	1989
ref50	Kudo & Ishibashi	1996
ref51	Mori *et al.*	1999
ref52	Olmstead & Wood	1990
ref53	Ralston	1977
ref54	Windsor	1987
ref55	Wood	1976
ref56	Wood	1976
ref57	Rossi *et al.*	2013

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