



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

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

4  
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19

20 **ABSTRACT**

21 The intensity of biotic interactions varies around the world, in such a way that mortality risk  
22 imposed by natural enemies is usually higher in the tropics. A major role of offspring  
23 attendance is protection against natural enemies, so the benefits of this behaviour should be  
24 higher in tropical regions. We tested this macroecological prediction with a meta-regression

25 of field experiments in which the mortality of guarded and unguarded broods was compared  
 26 in arthropods. Mortality of unguarded broods was higher, and parental care was more  
 27 beneficial, in warmer, less-seasonal environments. Moreover, in these same environments,  
 28 additional lines of defence further reduced offspring mortality, implying that offspring  
 29 attendance alone is not enough to deter natural enemies in tropical regions. These results help  
 30 to explain the high frequency of parental care among tropical species and how biotic  
 31 interactions influence the occurrence of parental care over large geographic scales. Finally,  
 32 our findings reveal that additional lines of defences – an oftentimes neglected component of  
 33 parental care – have an important effect on the covariation between the benefits of parental  
 34 care and the climate-mediated mortality risk imposed by natural enemies.

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

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## 56 I. INTRODUCTION

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

73 In several species, however, active parental protection is not sufficient to deter all  
74 natural enemies that may attack the offspring (e.g. Eberhard, 1975; Kudo & Ishibashi, 1996;  
75 Kudo, 1996; Miller, Rudolph, & Zink, 2011; Consolmagno *et al.*, 2016). Additionally,  
76 stressful abiotic conditions may constrain egg attendance to only some periods of the day,  
77 exposing the offspring to long periods of parental absence (Machado *et al.*, 2004; Chelini &  
78 Machado, 2012; Consolmagno *et al.*, 2016). In some arthropod species, additional lines of  
79 defence may protect the offspring by either hampering brood detection by predators and  
80 parasitoids or by decreasing consumption rates during periods of temporary parental

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2  
3 81 abandonment. Examples of additional defences include: nest building in earwigs and spiders  
4  
5 82 (e.g. Lamb, 1976; Evans, 1998; Kölliker & Vancassel, 2007; Fig. 1); deposition of silk layers  
6  
7 83 around the eggs in spiders and mites (e.g. Mori, Saito & Sakagami, 1999; Vieira & Romero,  
8  
9 84 2008; Gonzaga & Leiner, 2013; Fig. 1); egg coating with mucus in harvestmen (e.g. Requena  
10  
11 85 *et al.*, 2009; Chelini & Machado, 2014; Fig. 1); egg covering with debris and silk in  
12  
13 86 webspinners (e.g. Edgerly, 1987); egg coating with offensive chemicals or hard protective  
14  
15 87 membranes in leaf beetles (e.g. Chaboo, 2011); and defensive mutualism with ants in tree  
16  
17 88 hoppers (Del-Claro & Oliveira, 2000; Billick, Weidmann & Reithel, 2001; Fig. 1). In most  
18  
19 89 studies mentioned above, additional defences have been experimentally demonstrated to  
20  
21 90 improve offspring protection, decreasing mortality rates even in the absence of the parents.  
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24  
25 91 Wilson (1975) postulated that intense predation on eggs by conspecifics and ants, as  
26  
27 92 well as the high risk of fungal infection in tropical rainforests, might have been major forces  
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29 93 selecting for the evolution of parental care in arthropods. Although this hypothesis does not  
30  
31 94 explain why offspring attendance has evolved in some species and not in others, it brings  
32  
33 95 some insights into how the benefits of offspring attendance vary across broad geographic  
34  
35 96 scales. Wilson's (1975) hypothesis is based on the assumption that the intensity of predation  
36  
37 97 and fungal infection is higher in tropical than in extra-tropical areas. Indeed, theoretical  
38  
39 98 studies based on mathematical modelling suggest that an increase in temperature and  
40  
41 99 humidity promotes higher movement rates, resulting in more frequent and diverse biotic  
42  
43 100 interactions (Moya-Laraño, 2010). Moreover, experimental evidence shows that activity and  
44  
45 101 metabolic rates of several predatory arthropods increase with temperature, promoting an  
46  
47 102 increase in encounter and consumption rates (Huey & Kingsolver, 1989; Gilbert & Raworth,  
48  
49 103 1996; Mohaghegh, De Clercq & Tirry, 2001; Kruse, Toft & Sunderland, 2008), which  
50  
51 104 suggests that predation pressure may be more intense in warm climates. Finally, Schemske *et*  
52  
53 105 *al.* (2009) reviewed the existence of latitudinal gradients in the importance of biotic  
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3 106 interactions and showed that insect predation by ants and crop diseases caused by fungi and  
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5 107 viruses are more frequent at lower latitudes.

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7 108         Considering that temperature and rainfall have an important role in modulating the  
8  
9 109 intensity of predation and parasitism, one macroecological prediction arising from Wilson's  
10  
11 110 (1975) hypothesis is that the benefits of offspring attendance should be higher in warm and  
12  
13 111 humid than in cold and dry climates, because in the former the offspring are under more  
14  
15 112 intense threat from natural enemies. Our goal was to test this prediction using a powerful  
16  
17 113 statistical approach, a phylogenetic meta-regression. Specifically, we only used studies of  
18  
19 114 experimental removal of parental individuals (males or females) from their broods, conducted  
20  
21 115 under natural field conditions, for arthropod species exhibiting uniparental offspring  
22  
23 116 attendance. We classified the species into two groups according to an oftentimes neglected  
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25 117 component of parental care: the presence or absence of additional lines of offspring  
26  
27 118 protection. Given that these additional defences are known to attenuate offspring mortality,  
28  
29 119 we predict that the total benefits of parental care (i.e. attendance + additional defences) should  
30  
31 120 be higher in species in which offspring are protected by physical barriers, chemical deterrents,  
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33 121 or defensive mutualisms. Moreover, this pattern should be more pronounced in warm and  
34  
35 122 humid than in cold and dry climates.

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40 123         High offspring mortality in the absence of care is one of the main ecological conditions  
41  
42 124 for parental care to evolve from an ancestral state of no care (Klug *et al.*, 2012). As far as we  
43  
44 125 are aware, however, no previous study has formally investigated how such ecological  
45  
46 126 conditions affect the benefits of offspring attendance on a broad geographic scale. Thus, the  
47  
48 127 results presented here provide insights into why offspring attendance is comparatively more  
49  
50 128 frequent among tropical arthropods, as already noted by Wilson (1975). Moreover, by  
51  
52 129 emphasizing the role of additional lines of offspring defence, we enhance our understanding  
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3 130 of how ecological conditions may affect the occurrence of different forms of parental care on  
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5 131 large geographic scales.  
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## 9 133 **II. METHODS**

### 11 134 **(1) Data collection and inclusion criteria**

13  
14 135 Our literature search was based on Preferred Reporting Items for Systematic reviews  
15  
16 136 and Meta-Analyses as far as possible (<http://www.prisma-statement.org/>). We searched the  
17  
18 137 literature on *Web of Science*, *Scopus*, and *Google Scholar* using all available years up to and  
19  
20 138 including March 2016, and a combination of the following key words: ‘parental care’ AND  
21  
22 139 ‘protection’ AND ‘experiment’ OR ‘benefit\*’ OR ‘Arthropod\*’ OR ‘insect\*’ OR ‘arachnid\*’.  
23  
24 140 We also searched review papers and their reference sections (Eickwort, 1981; Hinton, 1981;  
25  
26 141 Tallamy, 1999; Wong, Meunier & Kölliker, 2013), and all taxonomic chapters of *The Other*  
27  
28 142 *Insect Societies* (Costa, 2006). Finally, we included studies that were presented at conferences  
29  
30 143 that some of us attended (see online Supporting Information, Dataset S1). From the resultant  
31  
32 144 list of documents, we used their titles to identify studies of interest, and scanned their  
33  
34 145 abstracts searching for information on parental removal experiments conducted in the wild.  
35  
36 146 When this information was found, or indicated that the data might be of use, we consulted the  
37  
38 147 main text. When a study was selected, we searched their references (backward search) and  
39  
40 148 citation record (forward search) for other studies that could provide additional data.  
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45 149 When available, information on estimates of mean offspring number, their S.D. (or  
46  
47 150 S.E.), and sample sizes (numbers of eggs, young, and broods included in the study) was  
48  
49 151 extracted from each publication. If a publication from the final list lacked some of this  
50  
51 152 information, or if the published information indicated that data of interest were collected but  
52  
53 153 not published, we contacted the corresponding author. In some cases, we obtained data from  
54  
55 154 figures using *GraphClick* (Arizona Software). If descriptive statistics were not available, we  
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3 155 extracted information from inferential statistics (i.e. *t*-values and their associated degrees of  
4  
5 156 freedom) associated with the difference between (i) number of broods that survived, and (ii)  
6  
7 157 number of offspring that survived per experimental group (see Section II.2). From each paper,  
8  
9 158 we also recorded all sources of offspring loss.

11 We had to exclude some studies, even though they contained potentially relevant  
12  
13 160 information (Fig. S1). In order to be included in our analyses, the study had to have: (i)  
14  
15 161 experimentally manipulated the presence of the parent (either male or female), thus creating a  
16  
17 162 *control group* in which the parent was left protecting the brood, and a *removal group* in which  
18  
19 163 the parent was removed, leaving the brood unprotected; (ii) been conducted on a species that  
20  
21 164 exhibits uniparental care by either the male or the female parent; and (iii) been conducted  
22  
23 165 under natural field conditions, so that we eliminated from our sample any study that  
24  
25 166 artificially increased offspring mortality risk (e.g. Filippi-Tsakamoto *et al.*, 1995; Punzo,  
26  
27 167 1998). Excluded studies and the reasons for their exclusion are summarized in Table S1.

29 For each paper included in the analyses, we used relevant locality information to obtain  
30  
31 168 global positioning system (GPS) coordinates, when these were not explicitly provided. Based  
32  
33 169 on these locality data, we gathered two types of environmental variable. The first was the  
34  
35 170 actual evapotranspiration (AET), which is a measure of primary productivity (Hawkins *et al.*,  
36  
37 171 2003). Although there is no universally accepted proxy for biotic interactions in the  
38  
39 172 macroecological literature, there is meta-analytical evidence showing that primary  
40  
41 173 productivity is positively related to species richness in many taxa (Field *et al.*, 2009) and also  
42  
43 174 to the abundance of ants (Kaspari, O'Donnell & Kercher, 2000; Monkkonen, Forsman &  
44  
45 175 Bokma, 2006), which are the most important group of offspring predator in our dataset (see  
46  
47 176 Section III). The second climatic variable was a principal component analysis (PCA)  
48  
49 177 component that synthesized the relationships between temperature, precipitation, and  
50  
51 178 seasonality (see Appendix S1). Positive values of the first axis (RC1) of this PCA were  
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3 180 associated with high annual mean temperature, high annual precipitation, and weak  
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5 181 temperature seasonality – conditions typically found in tropical climates (Peel, Finlayson &  
6  
7 182 McMahon, 2007). On the other hand, negative values of RC1 were associated with low  
8  
9 183 annual mean temperature, low annual precipitation, and strong temperature seasonality –  
10  
11 184 conditions typically found in temperate climates (Peel *et al.*, 2007).

12  
13  
14 185 We obtained global climatic data with 1 km<sup>2</sup> spatial resolution (www.worldclim.org;  
15  
16 186 Hijmans *et al.*, 2005), and extracted the climate data for each study locality by creating a 0.5°  
17  
18 187 buffer zone around the centre of the locality. We computed the average value for each  
19  
20 188 variable within this buffer zone. To obtain evapotranspiration data for each locality, we used  
21  
22 189 the geographic coordinate of the experimental site to extract its associated AET. We used  
23  
24 190 MODIS generated evapotranspiration data (mm/year) averaged between 2000 and 2012  
25  
26 191 (<http://ntsg.umd.edu/project/mod16>; Mu, Zhao & Running, 2011).  
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## 32 (2) Data coding and effect size calculation

33  
34 194 We coded the type of additional lines of offspring defence for each species (either  
35  
36 195 present or absent) for each effect size (Dataset S1), because we predicted that this form of  
37  
38 196 parental care would interact with the climatic covariate. This prediction is based on the fact  
39  
40 197 that additional defences attenuate offspring mortality even in the absence of parents. Thus, in  
41  
42 198 warm–humid climates, additional defences should provide more benefits than in cold–dry  
43  
44 199 climates. We included the presence or absence of additional defences in each species (Dataset  
45  
46 200 S1) as a fixed term in our meta-regression models. Moreover, we included the climatic  
47  
48 201 variable (AET or the RC1) as covariates in the models. The climatic variables were centred  
49  
50 202 and scaled to improve the interpretation of model coefficients (Gelman, 2008; Schielzeth,  
51  
52 203 2010). We modelled the interaction between the presence of additional defences and the  
53  
54 204 climatic covariate because we predict that unguarded offspring of species that lack additional  
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3 205 defences would suffer greater mortality in warm–humid climates than in cold–dry climates  
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5 206 (i.e. at greater values of AET and RC1). On the other hand, we predict that unguarded  
6  
7 207 offspring of species that have additional defences would be able to cope better with the  
8  
9 208 increased natural enemy pressure in warm–humid climates. Therefore, we expect that the  
10  
11 209 mortality in this experimental group would be low and similar along the climatic covariate  
12  
13 210 axis.

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15  
16 211 Our main meta-analytic database contained two types of results from the original  
17  
18 212 experimental papers, which led us to calculate two different effect sizes. The first type of  
19  
20 213 result, called *survival data*, were presented in the original papers as the initial number of  
21  
22 214 broods included in each experimental group (control or removal), and the subsequent number  
23  
24 215 of broods that survived (with at least one egg) until the end of the experimental period. For  
25  
26 216 these results, we used the odds ratio (OR) as our standardized effect size. The OR effect sizes  
27  
28 217 estimate the ratio between brood mortality in the parental removal group (numerator) and in  
29  
30 218 the control group (denominator). An OR = 1 means that there is no difference in survival  
31  
32 219 between the two groups, an OR > 1 means that the probability of brood survival in the control  
33  
34 220 group is higher than in the removal group, and an OR < 1 means the opposite (Fleiss &  
35  
36 221 Berlin, 2009). Thus, OR is a measure of the benefit of providing parental care in terms of  
37  
38 222 increasing the probability of brood survival. Greater values of OR mean that parental care  
39  
40 223 results in large benefits (higher probability of brood survival) when compared to no parental  
41  
42 224 care. All statistical analyses were conducted on the logarithm of OR, and its measurement  
43  
44 225 error. We used standard equations to calculate OR and its variance (Nakagawa & Cuthill,  
45  
46 226 2007; Fleiss & Berlin, 2009).

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50  
51 227 The second type of result, called *intensity of mortality*, was presented in the original  
52  
53 228 studies as the mean offspring number, its S.D., and sample size per experimental group at the  
54  
55 229 beginning and at the end of the experimental period. From these results, we calculated  $Z_r$   
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3 230 (Fisher's transformation of the correlation coefficient) as our standardized effect size  
4  
5 231 (Nakagawa & Cuthill, 2007). We estimated  $Z_r$  from the descriptive data reported for the end  
6  
7 232 of the experimental period, as this represented the maximum predicted difference between the  
8  
9 233 two experimental groups. High values of  $Z_r$  represent large differences in the number of  
10  
11 234 surviving offspring between control and removal groups (i.e. many more surviving offspring  
12  
13 235 in control).  $Z_r$  effect sizes were calculated from standard formulae provided in Lipsey &  
14  
15 236 Wilson (2001) and Nakagawa & Cuthill (2007). We adopted  $Z_r$ , instead of a more popular  
16  
17 237 standardized mean difference effect size (e.g. Hedges'  $d$ ), because of the nature of our data  
18  
19 238 set. As some experiments had complete mortality in one experimental group and no mortality  
20  
21 239 in the other group, estimating a standardized mean difference from these data would lead to  
22  
23 240 extreme values of effect size. However, by using  $Z_r$  we avoided such issues and the  
24  
25 241 distribution of effect sizes was not affected by extreme cases. We note that the use of  $Z_r$  when  
26  
27 242 assessing mean differences is common in biological studies (Nakagawa & Santos, 2012), and  
28  
29 243 in our case, this effect size represents a measure of the intensity of offspring mortality, and  
30  
31 244 thus a direct estimate of the benefits of offspring protection.  
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35  
36 245 Our database includes 76 effect sizes from 45 studies, covering 45 arthropod species  
37  
38 246 belonging to nine orders of the classes Arachnida, Crustacea, and Hexapoda (Dataset S1). Of  
39  
40 247 these 45 species, 23 (51%) do not possess additional defences, whereas 22 (49%) have some  
41  
42 248 sort of additional defences (Dataset S1). These species are distributed in all continents (except  
43  
44 249 Antarctica), encompassing great climatic diversity, ranging from arid regions to pluvial  
45  
46 250 forests (Fig. 1).  
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49 251

### 50 252 **(3) Statistical analysis**

51  
52 253 An assumption of our study is that evapotranspiration represents the intensity of biotic  
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54 254 interactions in a given place, so that higher evapotranspiration is associated with more attacks  
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3 255 by natural enemies. We took advantage of the experimental design of the studies included in  
4  
5 256 the analysis and tested whether the intensity of mortality was positively associated with AET.  
6  
7 257 We regarded broods with no additional offspring defences from the removal group as  
8  
9 258 analogous to baits set out by a researcher to estimate the intensity of natural enemy activity.  
10  
11 259 Complete destruction of unguarded broods would be evidence of intense natural enemy  
12  
13 260 activity, whereas little to no destruction would indicate negligible activity. This effect size  
14  
15 261 represents a standardized mean difference in the number of offspring between the end and the  
16  
17 262 beginning of each experiment. Thus, greater negative values mean that more offspring were  
18  
19 263 lost during the experimental period (note that this effect size is opposite from others presented  
20  
21 264 in the main results, where effect size represents the benefit of parental care, such that greater  
22  
23 265 *positive* values mean more offspring were lost during the experimental period in removal  
24  
25 266 groups relative to control groups). We found a significant negative association between the  
26  
27 267 effect size of offspring mortality of non-guarded broods and AET (linear model:  $\beta_{\text{AET}} = -$   
28  
29 268  $0.295$ ,  $t = -2.413$ ,  $P = 0.036$ ,  $r^2 = 0.305$ ; Fig. S2), which suggests that our assumption is valid.  
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34 269 We then used one model to estimate the effect size of the probability of brood survival  
35  
36 270 [ $\log(\text{OR})$  as the response variable] in guarded *versus* unguarded broods, and a separate model  
37  
38 271 to estimate the effect size of the intensity of mortality ( $Z_r$  as the response variable) in guarded  
39  
40 272 *versus* unguarded broods. We built phylogenetic meta-analytic models (Hadfield &  
41  
42 273 Nakagawa, 2010; Nakagawa & Santos, 2012) with restricted maximum likelihood fitted using  
43  
44 274 the R package *metafor* (Viechtbauer, 2010). For details regarding the phylogeny we used, see  
45  
46 275 Fig. S3 and Appendix S1.  
47  
48

49 276 We quantified heterogeneity (i.e. the proportion of variance between effect sizes that  
50  
51 277 cannot be attributed to sampling errors) using a modified version of  $I^2$  for phylogenetic meta-  
52  
53 278 analysis, which assesses the consistency of effects across studies (Higgins *et al.*, 2003;  
54  
55 279 Nakagawa & Santos, 2012).  $I^2$  is calculated as the residual variance plus the variance  
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3 280 components for the random effects divided by the sum of these two components (random  
4  
5 281 effect variance and residual variance) and the within-study variance (see equation 22 in  
6  
7 282 Nakagawa & Santos, 2012). We checked for potential publication bias in our data set using  
8  
9 283 Egger's regression, which is calculated by fitting a linear regression to the residuals and the  
10  
11 284 precision associated with each effect size as a predictor in the model (Egger *et al.*, 1997). If  
12  
13 285 the intercept of Egger's regression is not significantly different from zero, one can conclude  
14  
15 286 that there is little evidence for publication bias. Finally, we conducted a 'soft' retrospective  
16  
17 287 power analysis to assess the validity of our findings (see Appendix S1 for details). All  
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19 288 analyses were conducted in R version 3.0.2 (R Core Team, 2014).  
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### 290 III. RESULTS

#### 291 (1) Environmental effect on overall probability of brood survival

292 The mean  $\log(OR)$  estimates were positive, indicating that removing parents from  
293 broods with or without additional defences increased the probability that these broods would  
294 not survive [without additional defences: mean meta-analytic  $\log(OR) = 3.906$ , 95% C.I. =  
295 1.292 to 6.521; with additional defences: mean meta-analytic  $\log(OR) = 2.727$ , 95% C.I. =  
296 0.219 to 5.235]. Overall, AET did not significantly predict the magnitude of the probability of  
297 brood survival; nor did the effect of AET differ between broods with and without additional  
298 defences (interaction term:  $\beta_{[\text{Additional defence:AET}]} = -0.292$ , 95% C.I. =  $-1.354$  to  $0.770$ ; Fig. 2).  
299 Nevertheless, we noted a slight positive effect of AET on the  $\log(OR)$  of broods without  
300 additional defences (meta-regression:  $\beta_{[\text{AET}]} = 0.438$ , 95% C.I. =  $-0.443$  to  $1.319$ ; Fig. 2).  
301 RC1 had a qualitatively similar effect as AET on the estimates of  $Z_r$  for broods with and  
302 without additional defences (Fig. 2).

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

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3 305 AET model, heterogeneity at the level of the species was 29.62%, and at the level of the  
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5 306 phylogeny 30.10%.

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## 8 9 308 **(2) Environmental effect on intensity of brood mortality**

10  
11 The mean  $Z_r$  estimates were positive, which indicates that removing parents from  
12  
13 310 broods with or without additional defences increased the intensity of mortality (without  
14  
15 311 additional defences: mean meta-analytic  $Z_r = 1.392$ , 95% C.I. =  $-1.432$  to  $4.216$ ; with  
16  
17 312 additional defences: mean meta-analytic  $Z_r = 0.950$ , 95% C.I. =  $-1.870$  to  $3.772$ ). The effect  
18  
19 313 of AET upon the benefit of parental care was significantly different in broods with and  
20  
21 314 without additional defences (interaction term:  $\beta_{[\text{Additional defence:AET}]} = -0.617$ , 95% C.I. =  $-$   
22  
23 315  $1.163$  to  $-0.070$ , Fig. 3). For broods without additional defences, AET had a significant  
24  
25 316 positive effect on the magnitude of brood mortality (meta-regression:  $\beta_{[\text{AET}]} = 0.422$ , 95%  
26  
27 317 C.I. =  $0.092$  to  $0.751$ ). The effect of AET in broods with additional defences, however, was  
28  
29 318 not different from zero (slope:  $\beta_{[\text{Additional defence:AET}]} = -0.087$ , 95% C.I. =  $-0.643$  to  $0.469$ ; Fig.  
30  
31 319 3). RC1 had a qualitatively similar effect as AET on the estimates of  $Z_r$  for broods with and  
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33 320 without additional defences (Fig. 3).

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39 321 Total statistical heterogeneity was high ( $I^2 = 98.53\%$ ; Table 1), which is consistent with  
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41 322 the idea that our data on the probability of brood survival is modulated by covariates. In the  
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43 323 AET model, heterogeneity at the level of the species was 29.46%, and at the level of the  
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45 324 phylogeny 56.17%.

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## 48 49 326 **(3) Sources of offspring mortality**

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51 To quantify the sources of offspring mortality, we used 48 papers – 45 from our main  
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53 327 data set plus three papers that could not be used in the meta-regression (Tallamy & Denno,  
54  
55 328 1981; Edgerly, 1987; Crespi, 1990). Of the total, 41 papers provided information on the  
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3 330 sources of offspring mortality. Predators and parasitoids were the main source of offspring  
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5 331 loss. Ants were the most frequent predators, being reported in 23 studies (56.1%), usually as  
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7 332 the main source of offspring mortality. Cannibalism and parasitoid wasps were recorded in 16  
8  
9 333 studies each (39%). Spiders ( $N = 14$  studies; 34.1%), hemipterans ( $N = 9$  studies; 22%),  
10  
11 334 predatory wasps ( $N = 5$  studies; 12.2%), and other arthropods ( $N = 25$  studies; 61%) were also  
12  
13 335 reported consuming offspring. Fungal infection was reported as a source of offspring loss in  
14  
15 336 11 studies (26.8%). Abiotic factors were recorded as a minor source of offspring loss in only  
16  
17 337 six studies (14.6%); in three studies eggs dehydrated and in three they were destroyed by  
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19 338 heavy rain. These sources of mortality affected both guarded and non-guarded broods,  
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21 339 indicating that parents are unable to cope with abiotic-driven offspring loss.  
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#### 341 (4) Publication bias

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

348 In this study, we predicted that the benefits of offspring attendance should be higher in  
349 places where eggs and young are under more severe threat from natural enemies. We also  
350 predicted that the presence of additional lines of protection should further reduce the total  
351 mortality of offspring over and above the effect of attendance. The results of our meta-  
352 regression show that unguarded broods without additional lines of defence experienced more  
353 intense mortality in places with higher AET, and with a warmer and more humid climate,  
354 which were the two proxies we used for the intensity of biotic interactions. Moreover, we  
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3 355 found that additional defences play a crucial role in attenuating the intensity of mortality  
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5 356 imposed by natural enemies. Offspring mortality was consistently lower in species exhibiting  
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7 357 additional defences, and we detected no relationship with our proxies of intensity of biotic  
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9 358 interactions. Below, we discuss the implications of these findings, emphasizing how they  
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11 359 address some gaps in the current knowledge of parental care, and also possible directions for  
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13 360 future studies.

16 361 If we are to understand the selective forces associated with the occurrence of parental  
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18 362 care at large geographic scales, we need to be specific about the environmental conditions  
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20 363 influencing the costs and benefits of this behaviour. By using evapotranspiration and climatic  
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22 364 variables as predictors of the intensity of biotic interactions, our findings provide information  
23  
24 365 on the possible drivers of the benefits of offspring attendance. Although latitude has been  
25  
26 366 widely used in the macroecological literature (see Schemske *et al.*, 2009 and references  
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28 367 therein), latitude alone represents only a small fraction of the variance of climatic conditions  
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30 368 (Macías-Ordóñez, Macedo & Machado, 2013). In fact, the results presented here would not be  
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32 369 found using latitude as explanatory variable (see Appendix S1 for the latitude results).  
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34 370 Moreover, information on the sources of offspring mortality, coupled with our  
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36 371 macroecological meta-regression, allows us to infer that the intensity of biotic interactions is  
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38 372 the main factor influencing the benefits of offspring attendance in arthropods. Considering  
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40 373 that protection against natural enemies has been regarded as one of the main functions of  
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42 374 offspring attendance in several terrestrial ectothermic vertebrates, such as frogs, salamanders,  
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44 375 and lizards (Balshine, 2012), we predict that the patterns reported here should also hold for  
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46 376 other animal groups.

51 377 The fact that parental presence increases offspring survival does not explain how  
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53 378 ecological factors may affect the evolution of offspring attendance (but see Pike *et al.*, 2016  
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55 379 for an example of how predation can lead to nest guarding). To understand the evolution of  
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3 380 offspring attendance we need a comprehensive understanding of the fitness consequences of  
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5 381 attendance not only to the offspring, but also to the parents (Alonso-Alvarez & Velando,  
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7 382 2012). High risk of offspring mortality in warm–humid climates increases the benefits of  
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9 383 parental attendance in terms of offspring protection. However, the costs to parents in terms of  
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11 384 exposure to natural enemies should also increase due to more frequent encounters with  
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13 385 predators or parasitoids while attending the offspring (for instance, see Ghalambor & Martin,  
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15 386 2001). On the other hand, high temperatures accelerate embryonic development of arthropods  
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17 387 and ectotherm vertebrates (Willmer, Stone, & Johnston, 2005), thus decreasing the amount of  
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19 388 time parents are exposed to natural enemies. Shorter caring periods, in turn, may also  
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21 389 attenuate other costs of offspring attendance, such as reduced food intake and increased  
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23 390 energy expenditure related to parental activities (Alonso-Alvarez & Velando, 2012).  
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25 391 Therefore, a comprehensive view of the evolution of offspring attendance requires  
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27 392 information on how the costs paid by the parents vary in response to biotic and abiotic  
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29 393 conditions (Requena, Munguía-Steyer & Machado, 2013). Unfortunately, studies about the  
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31 394 costs of offspring attendance under natural conditions are limited to only a few arthropod  
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33 395 species (Munguía-Steyer & Macías-Ordóñez, 2007; Buzatto *et al.*, 2007; Gilbert, Thomas &  
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35 396 Manica, 2010; Requena *et al.*, 2012; Requena & Machado, 2014), so that it is not yet possible  
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37 397 to envisage general patterns.

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42 398 Although widespread among species exhibiting offspring attendance, the functional role  
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44 399 of additional lines of defence has been poorly explored. Here we provide compelling evidence  
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46 400 that the presence of these additional defences attenuates predation intensity upon the  
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48 401 offspring, even when parents are experimentally removed (Fig. 3). Some of these additional  
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50 402 defences, such as nests, burrows, and egg covering with debris, may conceal the offspring and  
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52 403 decrease the probability of predators finding eggs or early-hatched young (Edgerly, 1987;  
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54 404 Machado & Raimundo, 2001). Other lines of defence, such as mutualism with ants and egg  
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3 405 coating with silk, mucus, or offensive chemicals, may protect the offspring from the activity  
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5 406 of some natural enemies that are able to overcome parental protection (Evans, 1998; Mori *et*  
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7 407 *al.*, 1999; Del-Claro & Oliveira, 2000; Requena *et al.*, 2009). The presence of additional  
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9 408 defences may also allow the parents to leave the offspring temporarily unattended so that they  
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11 409 can forage or avoid stressful abiotic conditions or adult-specific predators, without  
12  
13 410 condemning eggs or early-hatched young to intense predation (e.g. Zink, 2003; Requena *et*  
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15 411 *al.*, 2009; Chelini & Machado, 2012). Indeed, a recent study on a clade of Neotropical  
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17 412 harvestmen has shown a strong correlation between the presence of additional defences  
18  
19 413 (mucus or debris egg coating) with temporary or permanent parental abandonment of eggs  
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21 414 (Chelini & Machado, 2014). It would be worthwhile to investigate the order in which these  
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23 415 two traits have evolved to test whether additional defences are a cause or a consequence of  
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25 416 offspring abandonment.

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29 417 Most of the studies on the benefits of egg attendance in arthropods – and perhaps other  
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31 418 taxa—are concentrated in a few particular regions of the world (see Fig. 1; points are clumped  
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33 419 in south-eastern Brazil, Central America, and Japan). There are vast areas for which there are  
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35 420 no available data, including large parts of Africa, continental Asia, and Australia. In some of  
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37 421 these areas, such as extremely cold or xeric regions (white areas in Fig. 1), arthropod diversity  
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39 422 is low and species are usually rare (Chown & Nicolson, 2004). These areas, however, offer  
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41 423 the opportunity to investigate whether the benefits of offspring attendance are higher in ‘harsh  
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43 424 environments’, as also proposed by Wilson (1975). Our data set does not allow us to test this  
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45 425 hypothesis because the great majority of the species occur in ‘benign environments’,  
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47 426 including temperate and tropical forests. Moreover, with few exceptions, the experiments of  
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49 427 parental removal included in our analyses do not report significant offspring mortality due to  
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51 428 abiotic factors. We know that several insect species exhibiting post-ovipositional parental care  
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53 429 are able to attenuate adverse abiotic conditions (review in Danks, 2002), but quantitative data  
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3 430 on the benefits of offspring attendance in these species are unfortunately scarce (Gilbert,  
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5 431 2014). The removal experiments we used as source of information in our meta-regression are  
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7 432 easily conducted in the field and, depending on the species, data on offspring protection  
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9 433 against biotic and abiotic factors can be obtained in a few days. Thus, we hope our study  
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11 434 stimulates researchers to collect information about species living in harsh environments, and  
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13 435 also species in which parents may provide benefit to offspring by attenuating adverse abiotic  
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15 436 conditions.

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18 437 Most of the macroecological studies focus on variation in species richness,  
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20 438 abundances, distributions, and body sizes (see examples in Gaston & Blackburn, 2000). These  
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22 439 studies have reported some global patterns, such as Allen's rule, which posits that endotherms  
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24 440 from colder climates have shorter limbs than their relatives from warmer climates, and  
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26 441 Bergmann's rule, which posits that species from colder climates are larger than their relatives  
27  
28 442 from warmer climates. In both cases, broad-scale variation in morphology is explained by a  
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30 443 decrease in the surface area to volume ratio, which increases heat conservation in cold  
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32 444 climates (Gaston & Blackburn, 2000). In contrast to the abundant literature reporting variation  
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34 445 in morphological traits, studies investigating how and why reproductive traits vary  
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36 446 geographically in response to environmental factors are scarce (Macías-Ordóñez *et al.*, 2013).  
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38 447 Exceptions are the studies of clutch size, cooperative breeding, and parental provisioning in  
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40 448 birds, which provide evidence of broad-scale variation in reproductive traits in response to  
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42 449 environmental conditions such as primary productivity, climatic seasonality, between-year  
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44 450 variability in precipitation, and offspring mortality risk (Ricklefs, 2000; Jetz, Sekercioglu &  
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46 451 Boehning-Gaese, 2008; Jetz & Rubenstein, 2011; Martin, 2015). Here we show that the  
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48 452 benefits of parental care in arthropods on a global geographical scale are also influenced by  
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50 453 environmental conditions, so that higher mortality risk leads to higher benefits of offspring  
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52 454 protection. This pattern, however, is found only when we consider the presence or absence of  
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3 455 additional lines of offspring defence. In the presence of additional defences, offspring  
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5 456 mortality is greatly reduced, implying that offspring attendance alone may not be enough to  
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7 457 cope with stronger predation/parasitism in tropical climates.  
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## 11 459 **V. CONCLUSIONS**

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14 460 (1) We found meta-analytic evidence that supports the hypothesis that the benefits of egg  
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16 461 attendance are higher in tropical climates, where biotic interactions are likely to be more  
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18 462 intense. However, support for this hypothesis is only revealed when we take into account an  
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20 463 often-neglected component of parental care: the presence of additional lines of offspring  
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22 464 defence. This result stresses the key defensive role of physical barriers, chemical deterrents,  
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24 465 and defensive mutualisms as additional lines of offspring defences in species already  
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26 466 presenting offspring attendance. Moreover, it also provides new insights into how the benefits  
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28 467 of parental care change in response to climate-mediated mortality risk imposed by natural  
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30 468 enemies.  
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34 469 (2) Our results on the sources of offspring mortality, compiled from the studies included in  
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36 470 the meta-regression, clearly indicate that ants are the predators that are the main source of  
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38 471 mortality of arthropod broods, with cannibalism and parasitoids also being somewhat  
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40 472 important sources of mortality. Our review also reveals that abiotic factors are negligible  
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42 473 sources of brood mortality.  
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45 474 (3) We found little evidence of publication bias in our data set, which suggests that our  
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47 475 findings are robust. There was, however, substantial heterogeneity in the effect sizes of both  
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49 476 our meta-analyses, which was expected for such a wide-ranging data set (both in the  
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51 477 phylogenetic and geographical sense). Even after the inclusion of the moderator and inclusion  
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53 478 of random factors in the models, the amount of heterogeneity remained substantial,  
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3 479 suggesting that other factors may moderate the effects of the intensity of biotic interactions on  
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5 480 the benefits of parental care.  
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7 481 (4) The patterns reported in our meta-regression help to explain the high frequency of parental  
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9 482 care among tropical species and how biotic interactions influence the occurrence of parental  
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11 483 care over large geographic scales.  
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23 929 treehopper *Publilia concava*. *Behavioral Ecology and Sociobiology* **54**, 406–415.  
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## 932 VIII. SUPPORTING INFORMATION

- 933 Additional supporting information may be found in the online version of this article.  
934 **Appendix S1.** Supplemental methods.  
935 **Dataset S1.** Raw data file: effect sizes included in the meta-analyses.  
936 **Fig. S1.** PRISMA flow diagram of our literature search and data collection.  
937 **Fig. S2.** Relationship between actual evapotranspiration (AET; centred and scaled) and the  
938 effect size  $Z_r$  of the intensity of brood mortality in non-guarded broods (removal group) with  
939 no additional offspring defence.  
940 **Fig. S3.** Topology used in the phylogenetic meta-analytic models. See **Appendix S1, Section**  
941 **(2)** for detailed explanation of numbering and colours.  
942 **Table S1.** List of studies excluded from the meta-analysis.  
943 **Table S2.** Climatic variables, their meanings, factor loadings and eigenvalue of the principal  
944 component for the climatic variables used in the PCA.

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3 945 **Table S3.** Summary of the correlation matrix of the 19 climatic variables used to calculate the  
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5 946 PCA.

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7 947 **Table S4.** The statistical power of the  $Zr$  effect sizes from the meta-analysis of the effect of  
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9 948 actual evapotranspiration (AET) on the benefit of parental care in species with and without  
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11 949 additional defences.

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951 **Figure legends**

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

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

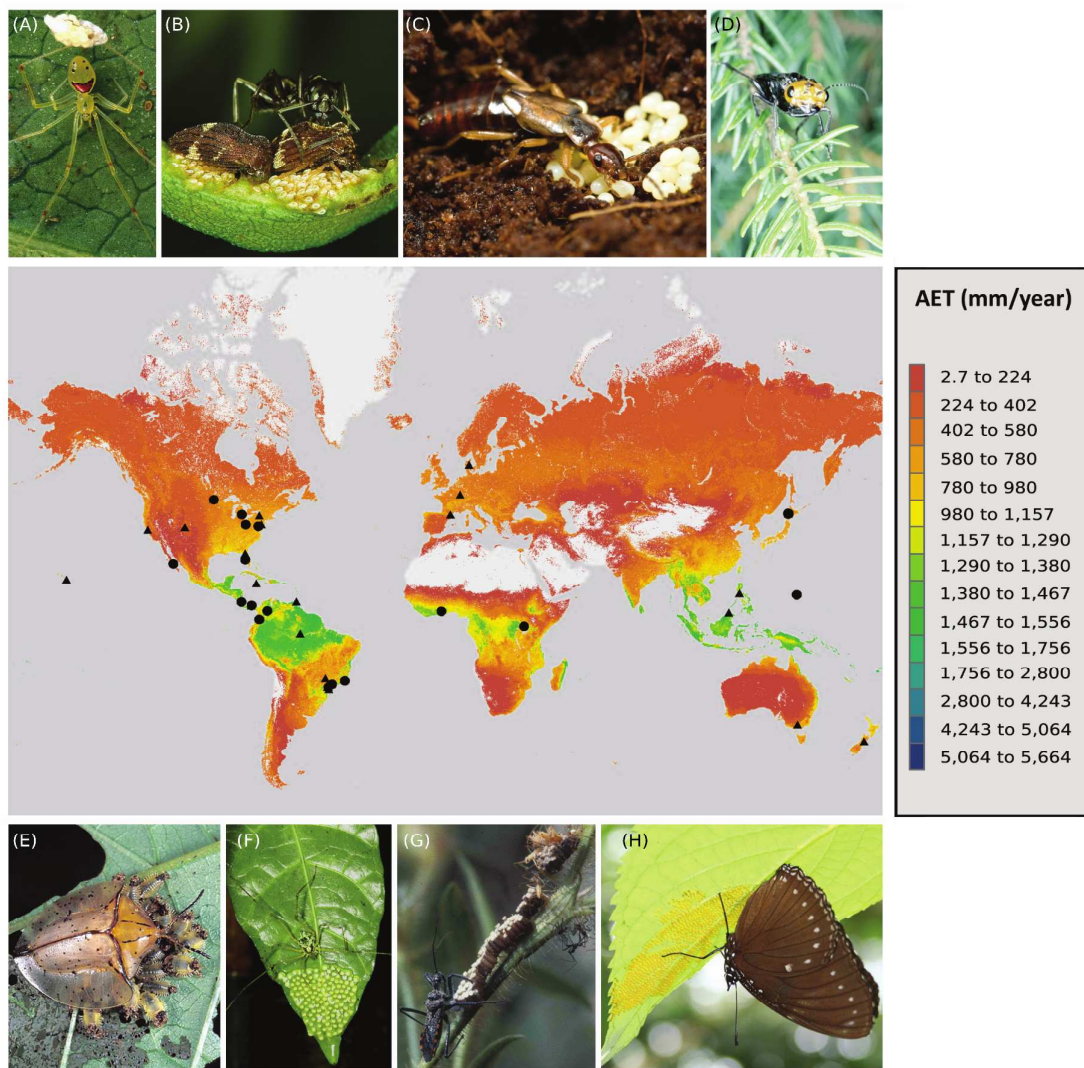


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3 977 Phylogenetic meta-regression model estimates for the  $\log(OR)$  effect sizes. For each  
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5 978 parameter, the point estimate represents the mean, and the lines span the 95% confidence  
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7 979 interval. The intercept represents effect sizes [ $\log(OR)$ ] for species that do not present any  
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9 980 form of additional brood defence. The  $\beta_{[\text{Additional defence:Covariate}]}$  label represents the slope  
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11 981 coefficient of AET (or RC1) for species with additional defences, while the  $\beta_{[\text{Covariate}]}$   
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13 982 represents the slope of AET (or RC1) for species without additional defences. Grey symbols  
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15 983 denote the model in which AET is the covariate, and white circles denote the model in which  
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17 984 the rotated component of the PCA (RC1) is the covariate.  
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23 986 Fig. 3. (A) Relationship between actual evapotranspiration (AET) and the effect size  $Z_r$  of the  
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25 987 intensity of brood mortality in the experiment of arthropod parental removal. AET has been  
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27 988 centred and scaled. Red circles depict data points from broods that had no additional line of  
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29 989 defence, and blue triangles depict data points from broods with additional lines of defence.  
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31 990 Lines represent phylogenetic meta-analysis estimated effects for each category of additional  
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33 991 defences (i.e. present *versus* absent). The size of symbols represents their relative precision  
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35 992 (larger symbols = more precise). (B) Phylogenetic meta-regression model estimates for the  $Z_r$   
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37 993 effect sizes. For each parameter, the point estimate represents the mean, and the lines span  
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39 994 the 95% confidence interval. The intercept represents effect sizes  $Z_r$  for species that do not  
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41 995 present any form of additional brood defence. The  $\beta_{[\text{Additional defence:Covariate}]}$  label represents the  
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43 996 slope coefficient of AET (or RC1) for species with additional defences, while the  $\beta_{[\text{Covariate}]}$   
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45 997 represents the slope of AET (or RC1) for species without additional defences. Grey symbols  
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47 998 denote the model in which actual evapotranspiration (AET) is the covariate, and white  
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49 999 circles denote the model in which the rotated component of the PCA (RC1) is the covariate.  
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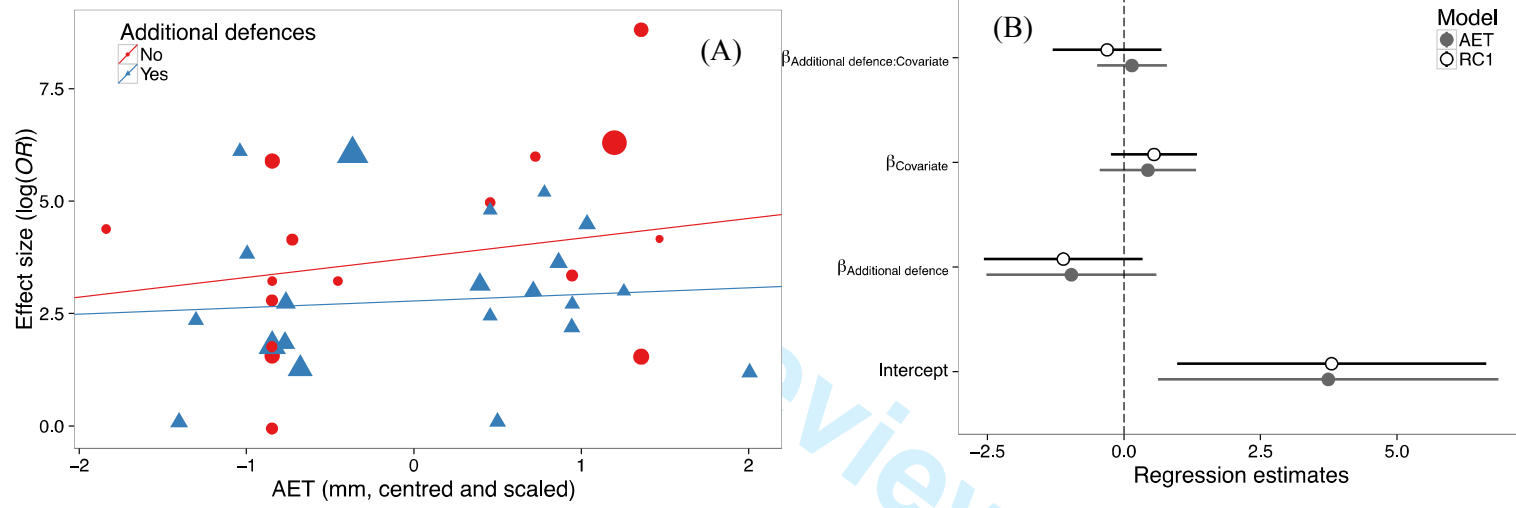
1001 Fig. 1



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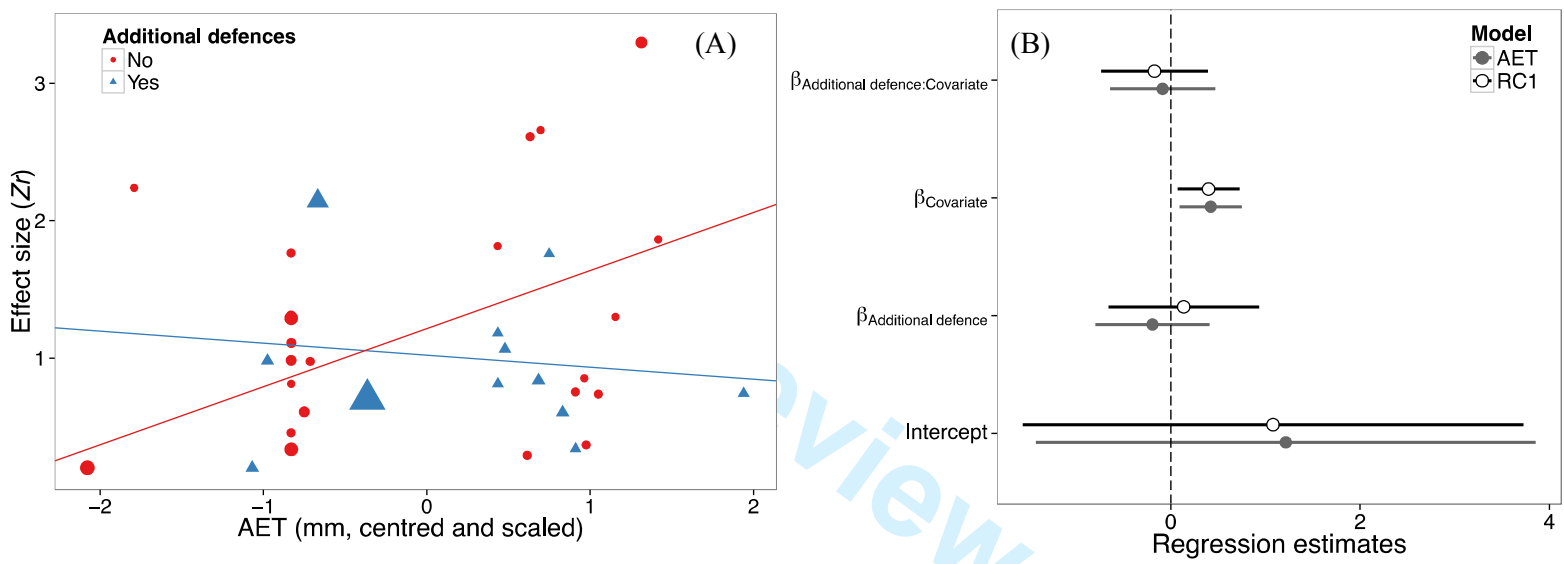
1004 **Fig. 2**



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1007 **Fig. 3**

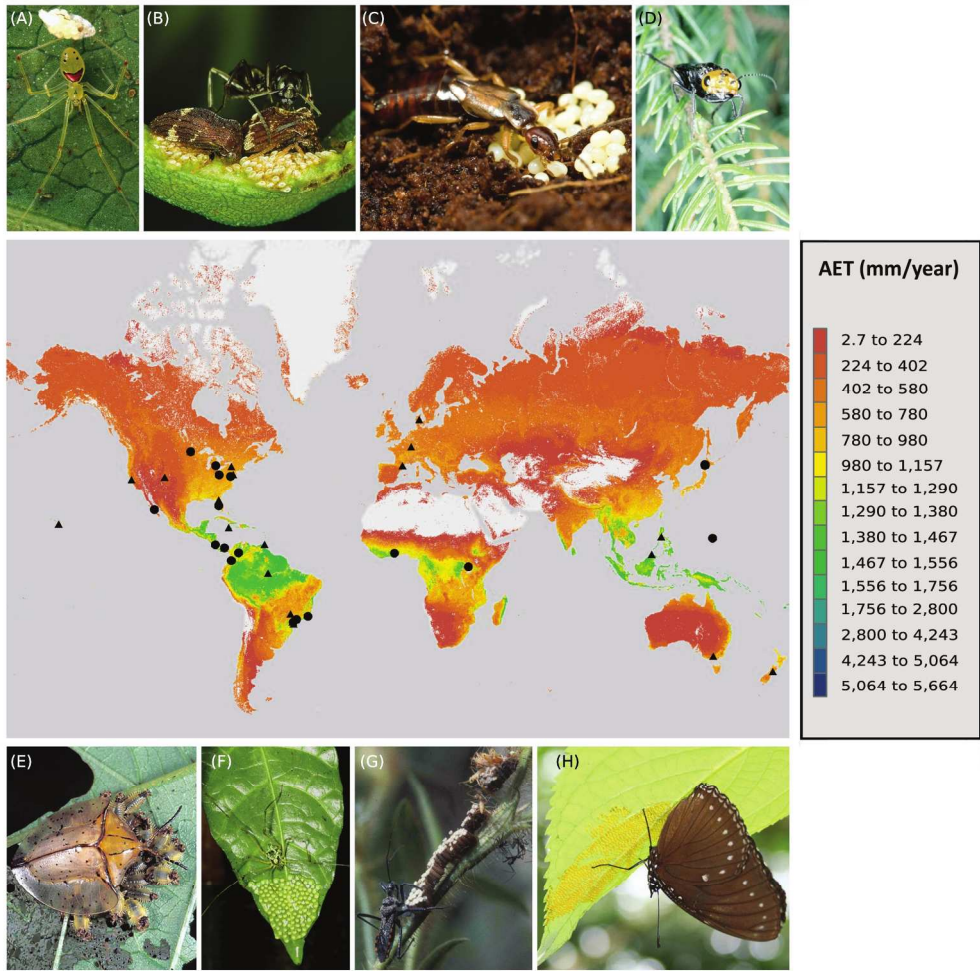


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5 1010 Table 1. Univariate-response meta-regression models and their variances, and heterogeneity. Models estimate the effect of actual  
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7 1011 evapotranspiration (AET) and the presence or absence of additional lines of offspring defence on the  $\log(OR)$  and  $Zr$  effect sizes. ‘:’ represents  
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9 1012 an interaction between the covariate (AET) and the categorical variable (additional lines of offspring defence). Heterogeneity (i.e. % variance at  
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11 1013 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  
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14 1014 phylogeny.

Model	Fixed effects	Random effects	Heterogeneity (Var <sub>Species</sub> ) %	Heterogeneity (Var <sub>Order</sub> ) %	Heterogeneity (Var <sub>Phylogeny</sub> ) %	Total heterogeneity %
Log( <i>OR</i> )						
models						
Model	Additional lines of defences +	Species + Order	29.62	19.42	30.10	79.15
AET	AET + Additional lines of defences:AET	+ Phylogeny				
<i>Zr</i> models						
Model	Additional lines of defences +	Species + Order	29.46	14.37	56.17	98.53
AET	AET + Additional lines of defences:AET	+ Phylogeny				

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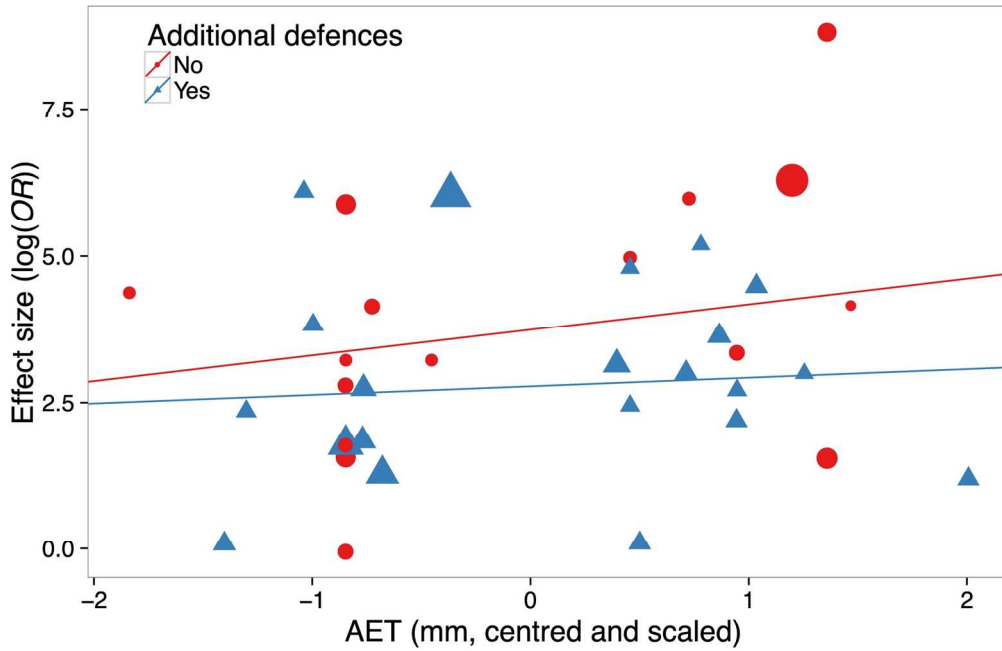
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Geographic distribution of the species included in the meta-analysis (some points are overlapped).

Fig. 1  
218x215mm (300 x 300 DPI)





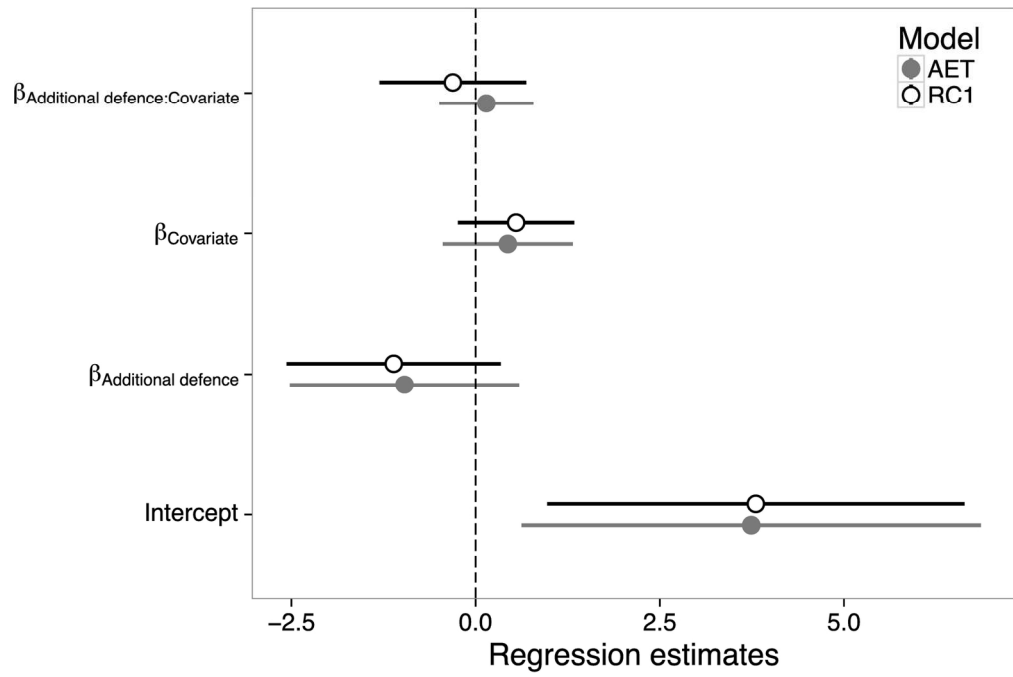
(A) Relationship between actual evapotranspiration (AET) and the effect size [log(OR)] of the probability of brood survival until the end of the experiment of arthropod parental removal.

Fig. 2A  
154x99mm (300 x 300 DPI)

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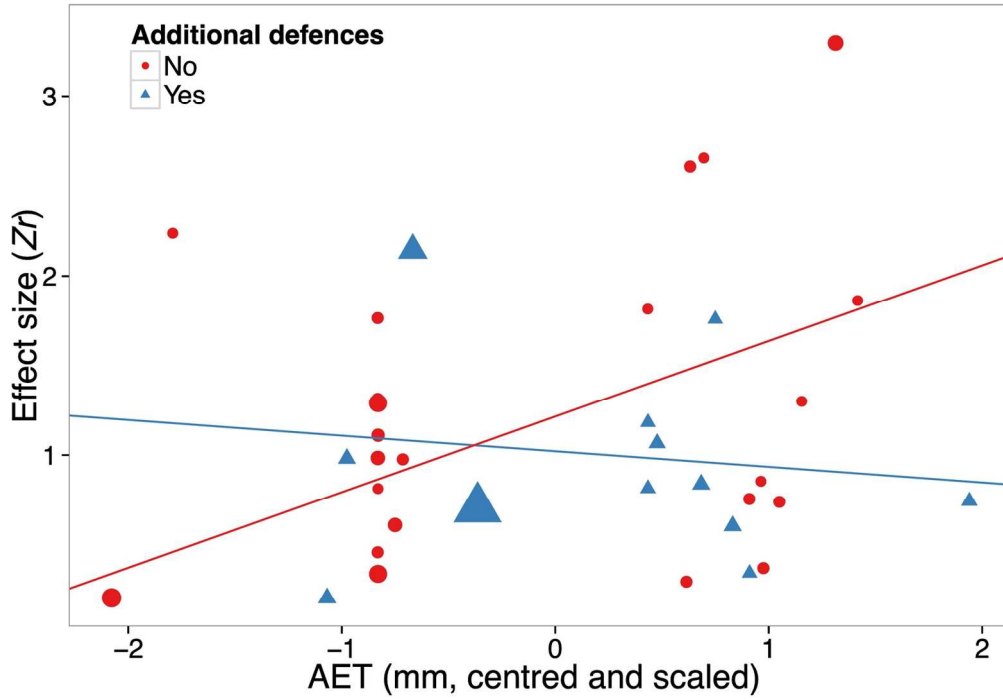
(B) Phylogenetic meta-regression model estimates for the log(OR) effect sizes.

Fig. 2B

154x102mm (300 x 300 DPI)

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(A) Relationship between actual evapotranspiration (AET) and the effect size  $Z_r$  of the intensity of brood mortality in the experiment of arthropod parental removal.

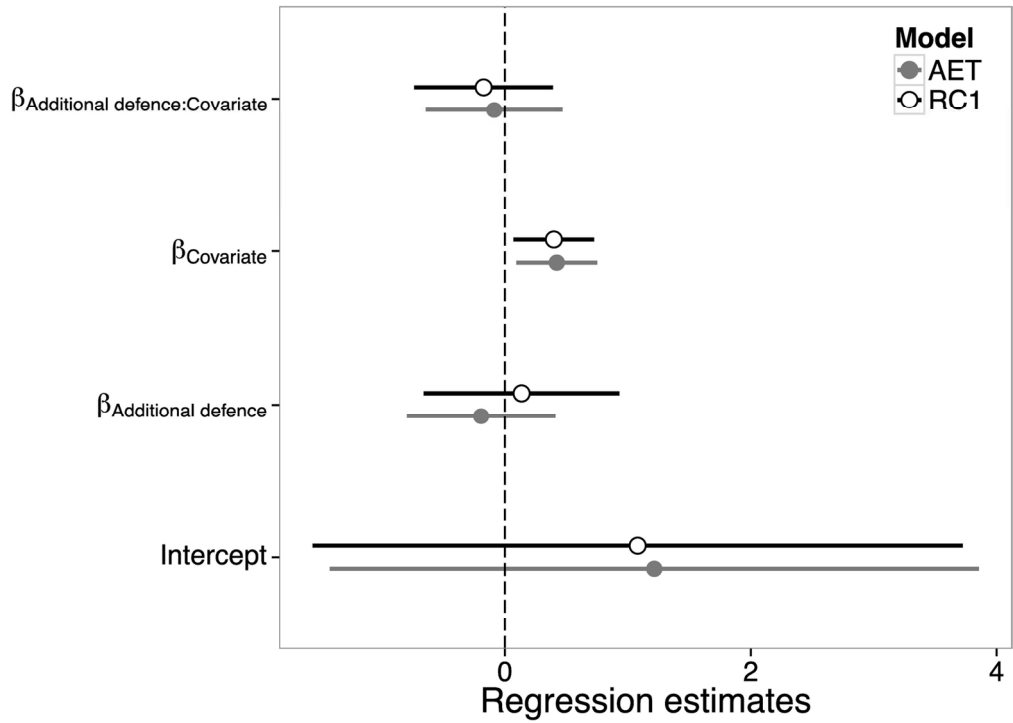
Fig. 3A

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(B) Phylogenetic meta-regression model estimates for the Zr effect sizes.

Fig. 3B

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3 **Macroecology of parental care in arthropods: higher mortality risk leads to higher**  
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10 Eduardo S. A. Santos, Pedro P. Bueno, James D. J. Gilbert, Glauco Machado  
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15 APPENDIX S1. SUPPLEMENTAL METHODS  
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18 (1) PCA to synthesize climatic variables  
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21 We used a principal component analysis (PCA) to summarize the 19 climatic  
22 variables (see Table S2) into uncorrelated orthogonal axes, and performed the PCA on  
23 the correlation matrix of the data, with Varimax factor rotation, using the function  
24 *principal* from the R package *psych* (R version 3.0.2; R Core Team, 2014; Revelle, 2016).  
25  
26 The correlation matrix was calculated with a sample size of 42 observations per  
27 climatic variable (see Table S3 for more details). As suggested by Budaev (2010), we  
28 calculated the Kaiser–Meyer–Olkin (KMO) measure of sampling adequacy of the  
29 correlation matrix used in the PCA, which indicated that the matrix was adequate for a  
30 PCA (KMO = 0.789). The first rotated principal component (RC1) is a measure of the  
31 abiotic conditions at a locality, as explained in Section II.1 of the main text (see Table S2  
32 for factor loadings).  
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48 (2) Assembly of phylogenetic tree used in meta-analytic models  
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51 Given that no phylogenetic study published so far comprises all species  
52 included in our data set (Dataset S1), we assembled different phylogenies in order to  
53 obtain the super-tree depicted in Fig. S3. This super-tree includes 45 species belonging  
54 to the following arthropod orders: (1) ARACHNIDA: Acari (pink branch), Opiliones  
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3 (red branches), Araneae (orange branches), (2) CRUSTACEA: Decapoda (grey branch),  
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5 (3) HEXAPODA: Dermaptera (dark-blue branches), Embioptera (light-blue branch),  
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7 Hemiptera (green branches), Hymenoptera (light-brown branch), Lepidoptera (purple  
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9 branch), and Coleoptera (dark-brown branches). The backbone of the super-tree (node  
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11 1), i.e. the relationship among arachnids, crustaceans, and hexapods, is based on Regier,  
12  
13 Shultz & Kambic (2005). The relationship among arachnid orders (node 2) is based on  
14  
15 Shultz (2007), and the internal phylogeny of the order Opiliones is based on Sharma &  
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17 Giribet (2011), which provides data on interfamilial relationships (node 3), and  
18  
19 Caetano & Machado (2013), which provide data on generic relationships within the  
20  
21 family Gonyleptidae (node 4). The phylogeny of the major groups within the order  
22  
23 Araneae (node 5) is based on Coddington (2005). The topology of the family  
24  
25 Theridiidae is partially based on Agnarsson (2004) (node 6) and Arnedo, Agnarsson &  
26  
27 Gillespie (2007) (node 7), according to which *Theridion impressum* should be included in  
28  
29 the genus *Phylloneta*, sister group to *Theridion sensu stricto*. The topology of the clade  
30  
31 Dionycha (node 8) is based on Bayer & Schoenhofer (2013) and Ramírez (2014). The  
32  
33 relationship among insect orders (node 9) is based on Ishiwata *et al.* (2010). Within the  
34  
35 order Hemiptera, the topologies of the clades Cimicomorpha (node 10) and  
36  
37 Cicadomorpha (node 11) are based on Schuh, Weirauch & Wheeler (2009) and Cryan *et*  
38  
39 *al.* (2004), respectively. Specifically, for the Pentatomoidea (nodes 12 and 13), the  
40  
41 generic relationship is based on Grazia, Schuh & Wheeler (2008) and Tsai, Kudo &  
42  
43 Yoshizawa (2015). Finally, the generic relationships among genera of the family  
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45 Chrysomelidae (node 14) are based on Gómez-Zurita, Hunt & Vogler (2008).  
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(3) Power analysis

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3 The issue of a power analysis in the context of meta-analyses in ecology and  
4 evolution has been treated recently by Lajeunesse (2013). Lajeunesse provides  
5 guidance as to how and when to employ power analysis to assess the validity of meta-  
6 analytic results. One useful piece of information is a simulation that shows (Lajeunesse,  
7 2013, Fig. 22.2B, p. 352) that when the meta-analysis sample size reaches approximately  
8 40 effect sizes, the width of the 95% confidence interval of the effect size stabilizes. It  
9 means that increasing the number of effect sizes above this number causes very little  
10 improvement in the power of the meta-analysis. On this basis, we argue that our  
11 overall sample size ( $N = 76$  effect sizes) is almost twice as large as Lajeunesse's  
12 simulation suggestion of a reasonable sample size (i.e. a more sensitive study) for a  
13 hypothesis-testing meta-analysis. Nevertheless, we calculated the power ('soft'  
14 retrospective approach,  $\rho^Z_{\text{two-tailed}}$ ) of the analysis of  $Zr$  effect sizes including the  
15 moderators (AET and additional defences). The statistical power of a test allows one to  
16 answer the following question "how should one interpret a meta-analysis that fails to  
17 reject a null hypothesis?", as the definition of power is the probability of detecting a  
18 significant finding when it, in fact, exists (Cohen, 1988). Therefore, in the case of our  $Zr$   
19 results the interpretation of the following estimates of statistical power would allow  
20 readers to evaluate how they view the non-significant result of the effect of AET on  
21 broods that have additional defences (see Section III.2 of the main paper). The results  
22 from the power analysis (Table S4) suggest that our study had reasonable power to  
23 detect nonzero effect sizes using a random-effects model, which could be ultimately  
24 interpreted as the observed effects having biological basis that is not due to sampling  
25 error.  
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56 (4) Supplementary results using latitude as a predictor variable  
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3 For continuity with the macroecological literature, we also conducted a meta-  
4 regression with latitude as a predictor variable of the  $\log(OR)$  and  $Zr$  effect sizes of the  
5 benefits of offspring attendance. Latitude was originally coded in decimal degrees, in  
6 such a way that southern latitudes presented negative values and northern latitudes  
7 positive values. These data were centred and scaled prior to inclusion in the meta-  
8 analytic model, which followed exactly the same protocol as the analyses reported in  
9 the main text.  
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19 We found no significant effect of the latitude on the magnitude of the  $\log(OR)$   
20 effect size of the probability of brood survival (meta-regression slopes:  $\beta_{[No\ additional\ defence:latitude]}$   
21  $= -0.321$ , 95% C.I. =  $-1.556$  to  $0.913$ ;  $\beta_{[Additional\ defence:latitude]}$  =  $-0.246$ , 95% C.I. =  
22  $-0.740$  to  $0.247$ ; interaction term:  $\beta_{[Additional\ defence:latitude]}$  =  $0.074$ , 95% C.I. =  
23  $-1.197$  to  
24  $1.346$ ). When investigating the interaction between latitude and the presence of  
25 additional lines of offspring defence, we found that in the absence of additional  
26 defences, there was a negative effect of latitude on the magnitude of the intensity of  
27 brood mortality ( $Zr$ ; meta-regression slope:  $\beta_{[No\ additional\ defence:latitude]}$  =  $-0.457$ , 95% C.I. =  
28  $-0.939$  to  $0.024$ ). However, the effect was not statistically significant. In the presence of  
29 additional defences, the effect of the latitude covariate was positive, but again non-  
30 significant ( $Zr$ ; meta-regression slope:  $\beta_{[Additional\ defence:latitude]}$  =  $0.179$ , 95% C.I. =  $-0.554$  to  
31  $0.912$ ; interaction term:  $\beta_{[Additional\ defence:latitude]}$  =  $0.636$ , 95% C.I. =  $-0.135$  to  $1.408$ ).  
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46 In conclusion, the results of the analyses using latitude as predictor variable  
47 were all non-significant – both for species with and without additional lines of  
48 offspring defence. These findings contrast with those presented in the main text, in  
49 which the intensity of brood mortality was influenced by our proxies of biotic  
50 interactions. We interpret this discrepancy as evidence that the causal link between  
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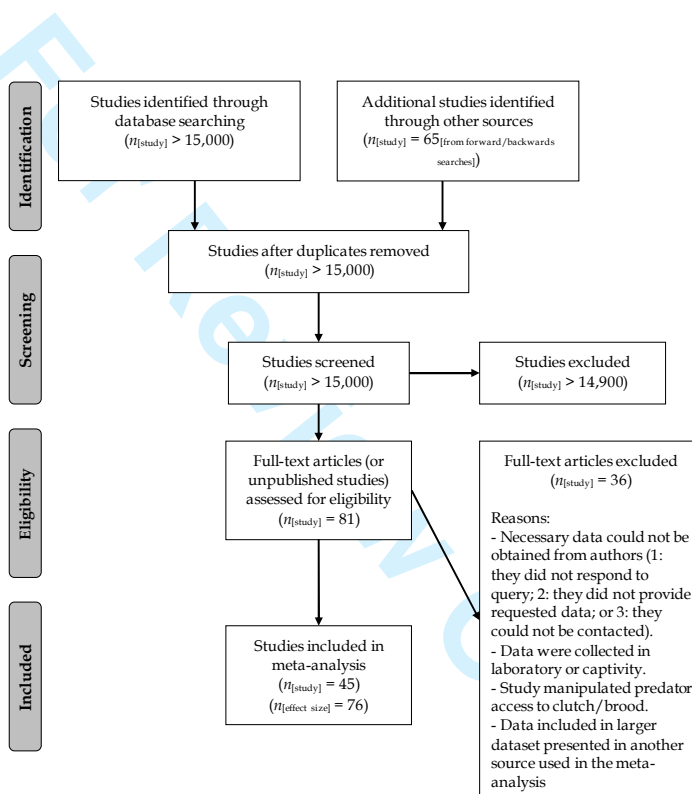


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3 environmental conditions and the benefits of parental care is captured better using  
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5 actual evapotranspiration and climatic variables than latitude *per se*.  
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For Review Only

## Supplementary figures

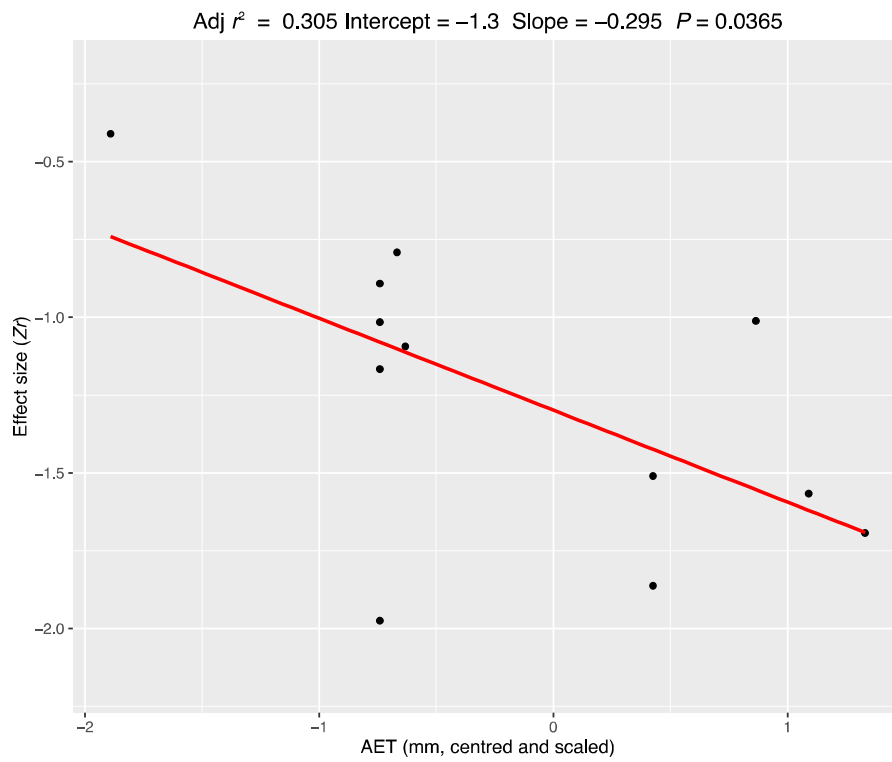
Fig. S1. PRISMA flow diagram of our literature search and data collection.



From: Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group (2009). Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. *PLoS Med* 6(6): e1000097. doi:10.1371/journal.pmed1000097

For more information, visit [www.prisma-statement.org](http://www.prisma-statement.org)

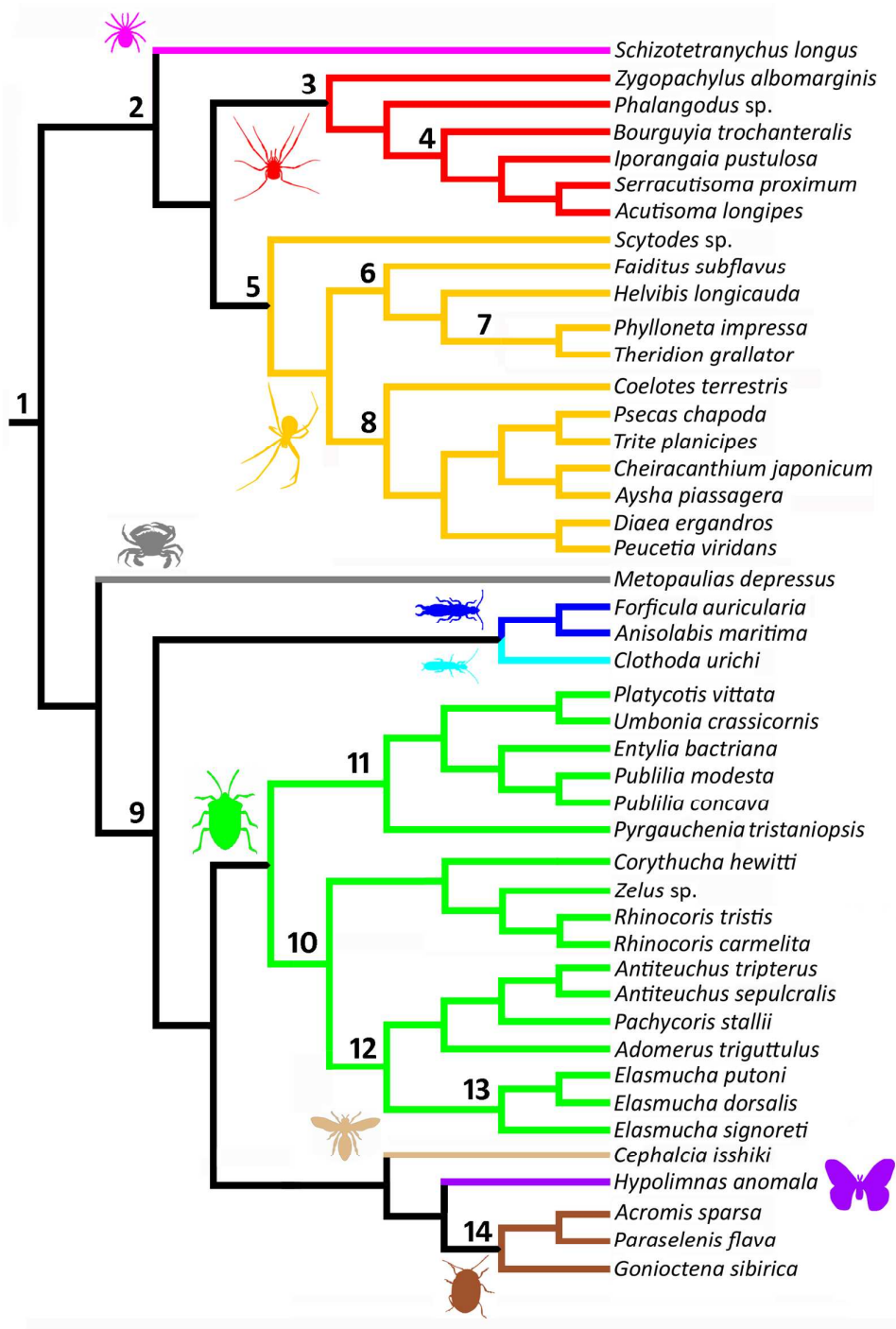
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3 Fig. S2. Relationship between actual evapotranspiration (AET; centred and scaled) and  
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5 the effect size  $Zr$  of the intensity of brood mortality in non-guarded broods (removal  
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7 group) with no additional offspring defence.  
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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	<i>Apollophanes punctipes</i>
2	Eberhard (1974)	Study was not manipulative experiment	<i>Lyssomanes jemineus</i>
3	West & Alexander (1963)	Study was not manipulative experiment	<i>Anurogryllus muticus</i>
4	Filippi <i>et al.</i> (2001)	Study was not manipulative experiment	<i>Parastrachia japonensis</i>
5	Thiel (1999)	Experiment conducted in marine environment	<i>Leptocheirus pinguis</i> , <i>Casco bigelowi</i> , <i>Dyopedos monacanthus</i>
6	Wyatt (1986)	Insufficient information to calculate effect size	<i>Bledius spectabilis</i>
7	Suzuki (2001)	Experiment not conducted in the wild	<i>Nicrophorus quadripunctatus</i>
8	Satou <i>et al.</i> (2009)	Experiment not conducted in the wild	<i>Nicrophorus quadripunctatus</i>
9	Gundermann <i>et al.</i> (1997)	Experiment not conducted in the wild	<i>Coelotes terrestris</i>
10	Tsukamoto & Tojo (1992)	Experiment not conducted in the wild	<i>Parastrachia japonensis</i>
11	Halffter <i>et al.</i> (1996)	Experiment not conducted in the wild	<i>Copris incertus</i>
12*	Edgerly (1987)	Insufficient information to calculate effect size	<i>Clothoda urichi</i>
13*	Tallamy & Denno (1981)	Insufficient information to calculate effect size	<i>Gargaphia solani</i>
14*	Crespi (1990)	Insufficient information to	<i>Elaphrothrips tuberculatus</i>

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1			calculate effect size	
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4	15	Favila (1993)	Experiment not conducted	<i>Canthon cyanellus</i>
5				
6			in the wild	
7	16	Honbo & Nakamura	Insufficient information to	<i>Elasmucha putoni</i>
8		(1985)	calculate effect size	
9				
10	17	Filippi <i>et al.</i> (2000)	Predation level	<i>Parastrachia japonensis</i>
11			manipulated	
12				
13	18	Aoki (1997)	Experiment conducted in	<i>Caprella sp.</i>
14			marine environment	
15				
16	19	Eggert <i>et al.</i> (1998)	Experiment not conducted	<i>Nicrophorus vespilloides</i>
17			in the wild	
18				
19	20	Filippi-Tsukamoto <i>et al.</i>	Predation level	<i>Parastrachia japonensis</i>
20		(1995)	manipulated	
21				
22	21	Halfpfter & Matthews	Could not locate source	<i>Copris fricator</i>
23		(1966)	material	
24				
25	22	Klostermeyer (1942)	Insufficient information to	<i>Euborellia annulipes</i>
26			calculate effect size	
27				
28	23*	Kudo (1990)	Insufficient information to	<i>Elasmucha putoni</i>
29			calculate effect size	
30				
31	24	Maschwitz & Gutmann	Study was not	<i>Elasmucha fieberi</i>
32		(1979)	manipulative experiment	
33				
34	25	Melber & Schmidt (1975a)	Study was not	<i>Elasmucha sp.</i>
35			manipulative experiment	
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37	26	Melber & Schmidt (1975b)	Study was not	<i>Elasmucha sp.</i>
38			manipulative experiment	
39				
40	27	Melber <i>et al.</i> (1980)	Could not locate source	<i>Elasmucha grisea</i>
41			material	
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43	28	Neiswander (1944)	Could not locate source	<i>Forficula auricularia</i>
44			material	
45				
46	29	Pukowski (1933)	Insufficient information to	<i>Nicrophorus sp.</i>
47			calculate effect size	
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49	30	Thiele (1977)	Study was not	Tribe Pterostichini (14
50			manipulative experiment	species)
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52	31	Trumbo (1991)	Experiment not conducted	<i>Necrophorus orbicollis</i>
53			in the wild	
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55	32	Tyndale-Biscoe (1984)	Experiment not conducted	<i>Copris diversus</i>
56			in the wild	
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33	Weyrauch (1929)	Insufficient information to calculate effect size	<i>Forficula auricularia</i>
34	Edwards (1988)	Study was not manipulative experiment	<i>Kheper nigroaeneus</i>
35	Punzo (1998)	Predation level manipulated	<i>Eremobates marathoni</i>
36	Ruttan (1990)	Predation level manipulated	<i>Theridion pictum</i>

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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	<b>0.796</b>
BIO2	Mean diurnal range [mean of monthly (max temp - min temp)]	<b>-0.421</b>
BIO3	Isothermality (BIO2/BIO7) (* 100)	<b>0.863</b>
BIO4	Temperature seasonality (standard deviation *100)	<b>-0.95</b>
BIO5	Maximum temperature of warmest month	0.239
BIO6	Minimum temperature of coldest month	<b>0.891</b>
BIO7	Temperature annual range (BIO5-BIO6)	<b>-0.942</b>
BIO8	Mean temperature of wettest quarter	0.268
BIO9	Mean temperature of driest quarter	<b>0.915</b>
BIO10	Mean temperature of warmest quarter	<b>0.435</b>
BIO11	Mean temperature of coldest quarter	<b>0.879</b>
BIO12	Annual precipitation	<b>0.549</b>
BIO13	Precipitation of wettest month	<b>0.636</b>
BIO14	Precipitation of driest month	-0.060
BIO15	Precipitation seasonality (coefficient of variation)	<b>0.449</b>
BIO16	Precipitation of wettest quarter	<b>0.611</b>
BIO17	Precipitation of driest quarter	0.113
BIO18	Precipitation of warmest quarter	0.197
BIO19	Precipitation of coldest quarter	<b>0.503</b>
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 ( $\rho^Z_{\text{two-tailed}}$ )		
		$\bar{\mu}$	95% C.I.	$\sigma^2(\bar{\mu})$	Small $\bar{\mu} = 0.2$	Medium $\bar{\mu} = 0.5$	Large $\bar{\mu} = 0.8$
		No additional defence	23	0.422	0.092 to 0.751	0.0422	0.997
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 <i>et al.</i>	1999
ref12	Soerensen	2007
ref13	Gillespie	1990
ref15	Taylor	1997
ref16	Machado & Oliveira	1998
ref17	Machado & Oliveira	2002
ref18	Requena <i>et al.</i>	2009
ref19	García & Machado	2014
ref20	Buzatto <i>et al.</i>	2007
ref21	Mora	1990
ref22	Diesel	1989
ref24	Choe	1989
ref25	Kudo <i>et al.</i>	1995
ref28	Miller & Zink	2012
ref29	Kölliker & Vancassel	2007
ref31	Eberhard	1975
ref32	Santos & Albuquerque	2001
ref33	Kudo <i>et al.</i>	1989
ref34	Kudo	2002
ref36	Kudo & Nakahira	1993
ref38	Williams <i>et al.</i>	2005
ref40	Zink	2003
ref41	Stegmann & Linsenmair	2002
ref42	Gilbert <i>et al.</i>	2010
ref43	Nakahira & Kudo	2008
ref44	Kudo <i>et al.</i>	1992
ref45	Nafus & Schreiner	1988
ref47	Billick <i>et al.</i>	2001
ref48	Evans	1998
ref49	Faeth	1989
ref50	Kudo & Ishibashi	1996
ref51	Mori <i>et al.</i>	1999
ref52	Olmstead & Wood	1990
ref53	Ralston	1977
ref54	Windsor	1987
ref55	Wood	1976
ref56	Wood	1976
ref57	Rossi <i>et al.</i>	2013

reference

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