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Developmental environments do not affect thermal physiology in reptiles: An experimental test and meta-analysis

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Ethics

Does your article include research that required ethical approval or permits?:
Yes

Statement (if applicable):
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Data

*It is a condition of publication that data, code and materials supporting your paper are made publicly
available. Does your paper present new data?:*
Yes

Statement (if applicable):
Experimental and meta-analytic datasets are available from: https://github.com/kris-
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Conflict of interest

I/We declare we have no competing interests

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1 **Developmental environments do not affect thermal physiology in reptiles: An experimental**

2 **test and meta-analysis**

3

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16 **Abstract**:

17 On a global scale, organisms face significant challenges due to climate change and

18 anthropogenic disturbance. In many ectotherms, developmental and physiological processes are

19 sensitive to changes in temperature and resources. Developmental plasticity in thermal

20 physiology may provide adaptive advantages to environmental extremes if early environmental

21 conditions are predictive of late-life environments. Here, we conducted a laboratory experiment

22 to test how developmental temperature and maternal resource investment influence thermal

23 physiology (critical thermal maximum: CT_{max} & thermal preference: T_{pref}) in a common skink

24 (*Lampropholis delicata*). We then compared our experimental findings more broadly across

25 reptiles using meta-analysis. In both our experimental study and meta-analysis, we did not find

26 evidence that developmental environments influence thermal physiology. Furthermore, the

27 effects of developmental environments on thermal physiology did not vary by age, taxon, or

28 climate zone (temperate/tropical) in reptiles. Overall, the magnitude of developmental plasticity

29 on thermal physiology appears to be limited across reptile taxa. Our results suggest that

30 behavioural or evolutionary processes, as opposed to developmental plasticity, may be more

31 critical in mitigating the impacts of changing thermal conditions in reptiles in the future.

32   **Introduction**

33   Climate warming and anthropogenic stressors pose significant challenges to organisms on a

34   global scale [1,2]. Rapidly increasing temperatures are a particularly significant threat for

35   ectothermic species. Indeed, increasing temperatures can drive fitness declines due to

36   physiological intolerance [3], and alter the distribution of species [4]. Inevitably, these impacts are

37   primarily mediated by how organisms change their behaviour and physiology through

38   development and evolutionary time in response to shifting environments. Phenotypic changes

39   that occur during an animal's lifetime in response to changing environments (i.e., phenotypic

40   plasticity), are important mechanisms by which ectotherms can cope with climate change over

41   short time scales [5]. However, the magnitude of plastic responses is widely trait- and species-

42   specific[5–7]

43   Temperature can also have transgenerational effects by impacting parental generations

44   [8,9]. For instance, recent evidence indicates that some ectotherms can tolerate heat events for

45   long periods [5,10]. Thermal ecology of ectotherms can also be shaped by other factors, such as

46   diet or maternal investment, which can influence physiological traits that are temperature

47   dependent [11–13]. For example, a diet high in nutrients (carbohydrate or protein) leads to higher

48   metabolic rates and CT_{max}, while a diet low in these nutrients can result in lower physiological

49   estimates [14,15]. Additionally, the resources a mother invests in her offspring (i.e., the energetic

50   provisioning of eggs) can influence metabolic processes like growth and development [16].

51   Determining how thermal and resource environments during development affect key thermal

52   physiological traits in various taxa may provide an understanding of how species may cope with

53   changing environments.

54   While phenotypic plasticity can adjust phenotypes throughout life, developmental

55   plasticity – plasticity occurring during early embryonic development – can have organisational

56   effects on phenotypes that can affect responses later in life[6]. Such effects may be adaptive or

57   maladaptive depending on whether early-life environments are predictive of late-life

58   environments. While temperature and early resource provisioning can influence thermal traits in

59   ectotherms [17], most research effort has focused on temperature, which is known to have a

60   profound effect on fitness [18,19]. In reptiles, temperatures during embryonic development are

61   known to affect phenotypes throughout ontogeny[7]. For example, incubation conditions of

62   developing reptile embryos can impact a variety of traits including sex, growth rate, morphology,

63 behaviour, and cognition[7,19,20]. However, there is a dearth of evidence linking developmental

64 factors more generally to thermal traits, and whether these differences persist through various

65 stages of ontogeny in reptiles[21,22].

66   Here, we aim to determine how early developmental environments affect thermal

67 physiology (critical thermal maximum: CT_{max} & thermal preference: T_{pref}) in reptiles. CT_{max} &

68 T_{pref} are two common thermal indices used as proxies for how the environment influences

69 individual fitness and are used to predict how species distributions are predicted to shift with

70 climate change[3,23,24]. We first conduct a laboratory experiment to test how maternal investment

71 and developmental temperature both influence CT_{max} & T_{pref} in a common skink (*Lampropholis*

72 *delicata*). We then compare our experimental findings with quantitative results testing this same

73 question more broadly in reptiles using a meta-analysis.

74

Method and materials

76 *(a) Consequences of incubation temperature and resource allocation on thermal physiology: an*

77 *experimental manipulation*

78   We collected gravid *Lampropholis delicata* from populations in Sydney (Australia) and

79 transported them back to the Australian National University, where females were housed until

80 eggs (n =40) were laid. We then randomly assigned eggs (n = 20) to both a resource allocation

81 treatment ('R' - yolk removal or 'C' – control) and an incubation temperature (23°C or 28°C SD

82 $\pm$ 1.0) treatment. Yolk removal treatments followed Sinervo[25], with 15-20% of the total egg

83 mass being removed via a sterilised syringe. Control treatments were punctured with the syringe

84 without any yolk removal (*See Supplementary materials for further details on husbandry*).

85   Hatchlings from all treatments were housed in groups of 5-6 within 20 L [40 cm (l) x

86 29.5 cm (w) x 20.5 cm (h)] plastic enclosures, with UVA/UVB lighting and a 20W heat lamp in

87 each enclosure. Water was provided *ad libitum*, with enclosures misted daily. Lizards were fed

88 calcium and vitamin-dusted crickets (*Acheta domesticus*) every second day. We measured

89 thermal traits (CT_{max} and $T_{pref,}$ – for collection methods, *see Supp.*) of lizards at eight to eleven

90 months post-hatching.

91   All statistical analyses were conducted using the R environment, ver. 4.1.0 (www.r.-

92 project.org). We used linear mixed-effects models to analyse thermal traits (T_{pref} and CT_{max}). We

93 constructed models that contained the main effects of body mass, sex, incubation temperature

94   and resource treatment. We also tested for the interaction between incubation temperature and

95   resource treatment (*see Supp. for more details*). If the interaction was not significant, we

96   removed it and presented the full main effects model.

97

98   *(b) Meta-analysis of early thermal effects on thermal physiology in reptiles*

99   To understand more broadly the impact of developmental environments on thermal physiology,

100   we systematically searched for studies manipulating early developmental environments and

101   subsequently measuring thermal physiological traits. Unfortunately, few studies manipulated egg

102   resource investment and measured thermal tolerance. As such, it was only possible to focus on

103   developmental temperature manipulations. Our meta-analysis collected data on offspring's

104   thermal preference (T_{pref}) and critical thermal maximum (CT_{max}) in lizards, snakes, tortoises,

105   turtles, and tuatara.

106   In brief, we conducted a systematic literature search in Scopus, ISI Web of Science (core

107   collection), and ProQuest (dissertations and thesis) and did not apply a timespan limit. We

108   followed the PRISMA-EcoEvo (Preferred Reporting Items for Systematic Reviews & Meta-

109   Analyses in Ecology and Evolutionary biology) guidelines for reporting[26] (*see Supp. for more*

110   *details)*. Full search strings, search methods, and selection criteria are described in detail in

111   supporting information (Figs. S2&3). We obtained 485 original records, and 15 articles satisfied

112   our selection criteria.

113   Multilevel meta-analytic (MLMA) models were constructed using the *rma.mv* function in

114   the *metafor* package (version 3.8)[27]. We used the acclimation response ratio (ARR) as our

115   effect size [28]. Sampling variance for the ARR was derived in Pottier et al.,[29]. Study, phylogeny,

116   and study species were designated as random effects and we included an observation-random

117   effect (effect size ID). A model that included only study, species and effect size ID was best

118   supported over one with phylogeny, so we present meta-analytic results from a model without

119   phylogeny. Studies often had more than two temperature treatments. As such, we derived all

120   pairwise effect size comparisons. This, however, does induce a correlation between effect size

121   sampling errors , which we controlled for through the inclusion of a sampling (co)variance

122   matrix derived by assuming effect sizes are correlated by r = 0.5[30]. Thermal trait (T_{pref} or

123   CT_{max}), life stage at measurement (hatchling, juvenile or adult), climate zone (temperate or

124   tropical), and major taxonomic group (lizard, snake, tuatara or turtle) were included as fixed

125   factors in separate multi-level meta-regression (MLMR) models. We also tested for publication

126   bias using a MLMR model with sampling variance and standard error as predictors [31] and

127   visually explored publication bias using a funnel plot (*see Supp. for more details*). We present

128   effect size heterogeneity by constructing prediction intervals [32] and presenting I^2 using the

129   *orchaRd* package (version 2.0)[33].

130

131   **Results**

132   *a)Incubation temperature and resource allocation consequences on thermal preference and*

133   *critical thermal maximum*

134   Hatchling *Lampropholis delicata* (n=40) were measured for thermal preference (T_{pref}) and

135   critical thermal maximum (CT_{max}) with (n=10) per resource treatment (yolk removal and control)

136   by incubation temperature (23 & 28°C). Mean T_{pref} was 31°C ±0.47 (mean ±SE) and ranged

137   from 20.99–34.26°C. Mean CT_{max} was 43.04°C ±0.23 and ranged from 38.6–45.2˚C. We did not

138   detect any effect of incubation temperature, yolk treatment, sex, or body mass on T_{pref} or CT_{max}

139   (Figure 1A|B; Table 1).

140   *(b) Meta-analysis of early thermal effects on thermal physiology in reptiles*

141   Across reptiles, developmental temperatures did not influence thermal traits (T_{pref} or CT_{max}), but

142   heterogeneity was high (ARR =0.05, 95% CI:-0.28-0.37; I^2_{Total} = 99.53%, Prediction Interval: -

143   1.23-1.32; Fig. 2A, n = 69 effects from 14 species). Overall, we found no evidence for

144   publication biases (*β*=-0.81, 95%CI=-1.92-0.3, *p=0.15*; Fig S4; for further details see electronic

145   supplementary materials). Species effects ($I^2_{Species}$ = 70.57%) drove most of the heterogeneity in

146   ARR, but thermal traits were not influenced by life stage, climate zone, or major taxonomic

147   group (i.e., snakes, turtles, lizards) (Fig. 2B|C). While there was a significant increase in thermal

148   traits in snakes, this was driven by a single species (*Nerodia sipdedon*) (Fig 2D), and given the

149   small sample sizes, we need to caution whether any true differences between snakes and other

150   groups exists.

151

152   **Discussion**

153   Genetic adaptation and phenotypic plasticity are two competing hypotheses for how ectotherms

154   can cope with warming temperatures associated with anthropogenic climate change [3,34–36].

155   Plastic responses occurring early in development can have anticipatory and long-lasting effects

156   on organisms, with significant implications for how they cope with environmental stressors.

157   We show that early developmental environments do little to modify thermal

158   physiological traits (CT_{max} & T_{pref}) in most reptile taxa. Both our experimental and meta-analytic

159   approaches suggest that the magnitude of developmental plasticity on thermal indices appears to

160   be canalised across reptile taxa. For example, our meta-analysis indicated that for every 1°C

161   change in developmental temperature, we only expect a 0.05°C change in thermal physiology.

162   Our findings are consistent with those of other ectotherm systems, which show that

163   developmental plasticity has little impact on adult heat tolerance [6,37–39]. Nonetheless, we

164   detected significant species-specific heterogeneity ($I^2_{Species}$= 70.57%), suggesting substantial

165   differences across species that cannot be ignored. Such variability may be driven by species

166   differences in micro-habitat selection of nests or nesting phenology in the wild and whether

167   developmental conditions in the field corroborate with conditions chosen for laboratory

168   experiments. It has been indicated in other studies[40–43] that differences in nest depth, nest

169   location, clutch density or maternal condition may select for developmentally plastic responses

170   in offspring.

171   Across reptile taxa, plasticity in thermal physiology also did not differ by age, taxon or

172   climate zone. We expected that the earlier age at which thermal traits were measured would be

173   more likely to detect effects of early environments. In addition, tropical species are expected to

174   maintain body temperatures near their thermal limits, and an increase in temperature can push

175   these species to physiological extremes compared to temperate species [3,36]. Greater thermal

176   variability in temperate regions should select for greater plasticity. However, our meta-analysis

177   does not support these hypotheses, and instead, the microthermal environments and behavioural

178   flexibility may be a more important driving mechanism as to whether species respond plastically

179   to developmental environments or not [3,44]. Future studies looking at the autocorrelation between

180   early and late developmental environments would be fruitful in helping elucidate species-specific

181   responses to thermal environments.

182   Overall, our results indicate that most reptiles may have limited developmental plasticity

183   in thermal traits, relying instead on energetically expensive behaviours (i.e. thermoregulation)

184 [3,45] or responses that operate on slower time scales (i.e. local adaptation) [35,46]. These data

185 collectively serve as valuable insights into possible responses that are plausible under changing

186 thermal conditions.

187

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359   **Tables & Figures**

360   Table 1. Model outputs coefficients for testing wither sex, body mass, incubation temperature,

361   resource, or the interaction between resource and temperature had an effect on T_{Pref} or CT_{Max} in

362   hatchling *Lampropholis delicata*. Est. value describes the estimated coefficient value and 95% CI

363   describes the lower and upper bound of the 95% credible interval for each coefficient value.

364   Intercept is the estimated mean of each thermal trait from the null model.

| Thermal Index	Covariate	Estimate	l-95% CI	u-95% CI	p value
	(Intercept)	**30.94**	**28.67**	**33.20**	**0.00**
	Body Mass	0.44	-0.97	1.86	0.53
	Sex	0.30	-2.50	3.09	0.83
Tpref	Incubation Temperature	-0.35	-2.36	1.66	0.72
	Resource	0.19	-1.83	2.20	0.85
	Incubation Temperature*Resource	-0.22	-4.31	3.87	0.91
	(Intercept)	**43.27**	**42.17**	**44.37**	**0.00**
	Body Mass	-0.41	-1.08	0.25	0.21
	Sex	-0.03	-1.35	1.28	0.96
CTmax	Incubation Temperature	-0.18	-1.14	0.78	0.70
	Resource	-0.24	-1.20	0.71	0.61
	Incubation Temperature*Resource	-0.52	-2.47	1.44	0.59

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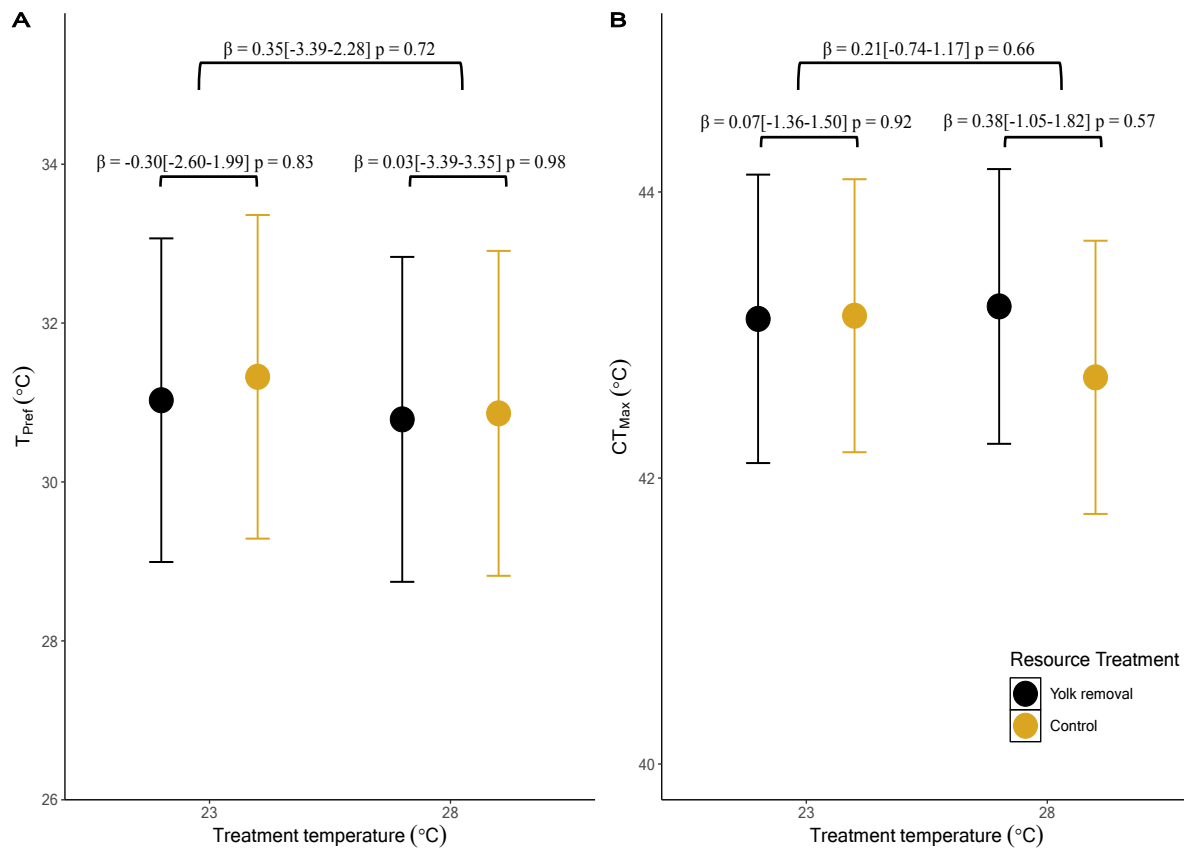
368   Figure 1. Thermal indices across different incubation temperatures and resource treatments for

369   hatchling *Lampropholis delicata* (n=10 per temperature and treatment). (A) Thermal preference

370   (T_{pref}) in lizards incubated at 23 & 28°C for each resource treatment (yolk ablation & control).

371   (B) Critical thermal maximum (CT_{max}) in lizards incubated at 23 & 28°C for each resource

372   treatment. Bars above plots indicate pairwise comparisons of thermal indices between treatment

373   temperature and the interaction between treatment temperature and resource treatment. Means

374   and 95% confidence intervals are provided along with the *p*-value for each contrast.

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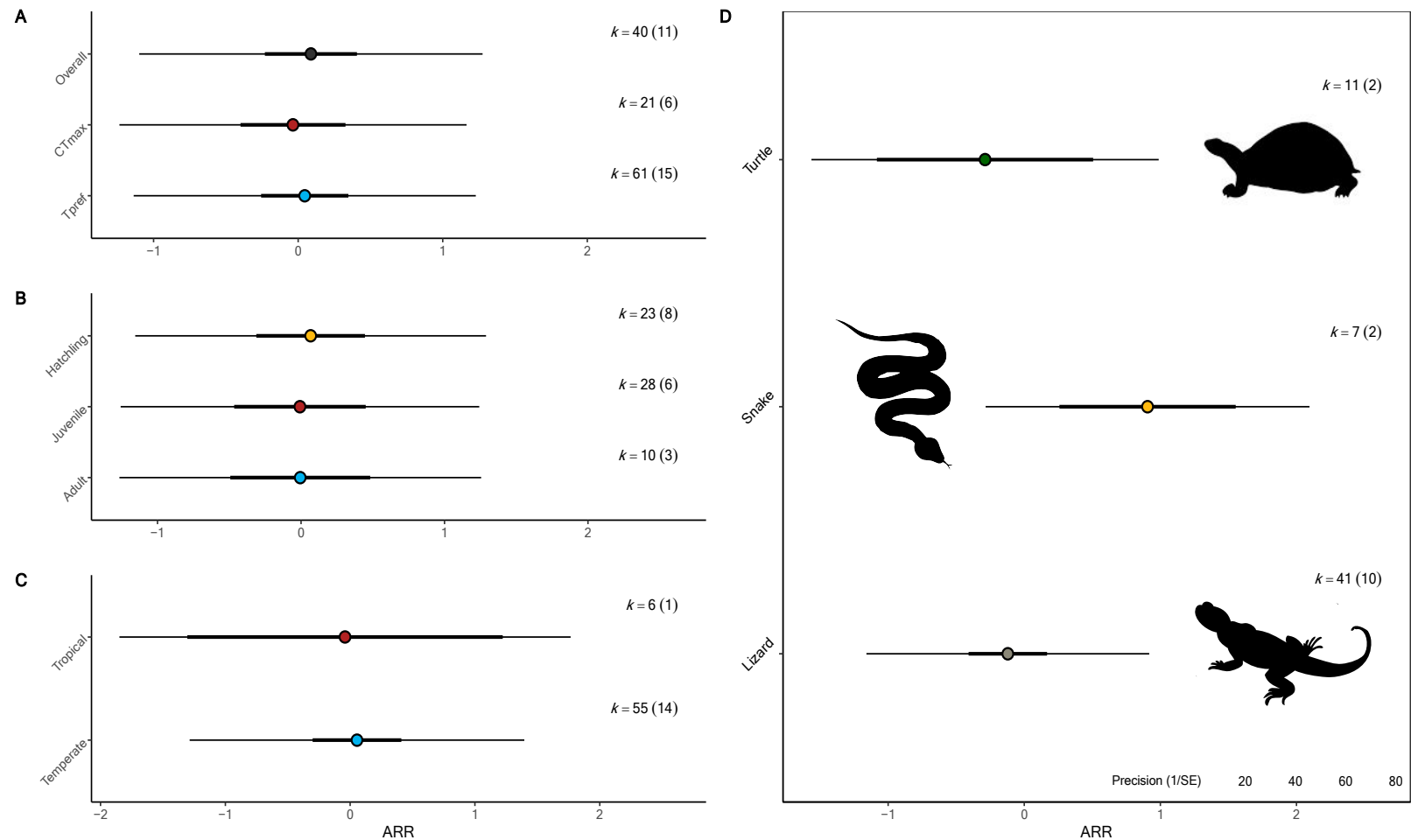
Figure 2. The magnitude of the effect of developmental temperature on thermal indices (T_{pref} & CT_{max}) in reptiles (A) concerning age class of thermal physiological measurement (B), climate zone (C), and taxon (D). Mean meta-analytic ARR estimates (circles) with their 95% confidence intervals (thicker error bars) and prediction intervals (thinner error bars). Data points from each study from the meta-analysis are scaled by precision (inverse of standard error), and k is the number of effect sizes with the number of species in

381 brackets. ARR is the acclimation response ratio. 95% confidence intervals not overlapping 0 are statistically significant. Graphs were

382 constructed using the *orchaRd* package[47]. Tuatara was removed for visual purposes due to the small number of effect sizes (n=3)

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