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RESEARCH ARTICLE

Shift in Thermal Preferences of Female Oviparous Common Lizards During Egg Retention: Insights into the Evolution of Reptilian Viviparity

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Abstract Pregnant female *Zootoca vivipara* select lower body temperatures than males or nonpregnant females, and this shift in the thermal preferendum is believed to be related to optimising the conditions for embryogenesis. Thus, subjecting embryos to the higher temperature selected by males and non-gravid females might have detrimental effects on embryonic development and on hatchling fitness, according to predictions of the "maternal manipulation" hypothesis on the evolution of viviparity. To test the role of gestation environment on embryonic development in oviparous *Z. vivipara*, we kept a number of gravid females at the temperature selected by non-gravid females in a laboratory thermal gradient, whereas control females were allowed to regulate their body temperature without restrictions. Developmental stage at oviposition was more advanced for embryos of the experimental clutches, which were heavier than those of the control group. Forced gestation temperature also affected hatching success (58.62% in the experimental treatment vs. 97.37% in the control group). In addition, hatchlings from females subjected to high temperatures during pregnancy were smaller, had shorter head length and performed worse in running trials. Our results fulfil the prediction of the "maternal manipulation" hypothesis, and suggest that the shift in female body temperature during pregnancy optimizes embryogenesis and hatchling phenotype by avoiding the negative effects of the high incubation temperatures preferred by non-gravid females.

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Introduction

Environmental maternal effects, such as mother's feeding rate or exposition to predators, and several other aspects of the maternal gestation environment have been proved to influence the phenotype and behaviour of neonatal lizards (e.g. Sorci and Clobert 1997; Shine and Downes 1999). For example, maternal thermoregulation can affect egg temperature throughout embryonic development, and maternal temperature has been demonstrated to have a great influence on offspring fitness (Rock and Cree 2003; Birchard 2004; Ji et al. 2006). Research on this topic has mainly focused on viviparous species, in which the contact between mother and embryo exists over a long period from conception to hatching (Beuchat 1988; Swain and Jones 2000), but most oviparous squamates retain eggs in utero for a considerable proportion of the embryogenesis (Shine 1983; Braña et al. 1991; Blackburn 1995), so offspring phenotypes can also be influenced by variation in the preoviposition maternal environment.

Females of some squamate species prefer lower body temperatures during pregnancy (e.g. *Podarcis muralis*: Braña 1993; *Sceloporus virgatus*: Andrews and Rose 1994; *Zootoca vivipara*: Van Damme et al. 1986). In other species, gravid females prefer higher body temperatures than other individuals in the same population (e.g. *Chalcides ocellatus*: Daut and Andrews 1993; *Hoplodactylus maculatus*: Rock et al. 2000), and this increase in body temperature would accelerate embryonic development inside the mother's body (Mathies and Andrews 1997; Shine 2006). Shift in thermal preferendum during pregnancy, especially toward lower body temperatures that retard development (but see Rodríguez-Díaz et al. 2010), is assumed to be related to optimising the conditions for embryogenesis (Beuchat 1988; Mathies and Andrews 1997; Rodríguez-Díaz et al. 2010) and could favour the evolution of extended egg retention since a longer intrauterine stay would extend the time of the developing embryos' exposure to suitable conditions (Braña and Ji 2007).

The aim of the present study was to determine whether the shift of preferred temperature in pregnant females of an oviparous lizard with prolonged egg retention avoids the negative effects that high temperatures could have on embryogenesis, as predicted by the maternal manipulation hypothesis on the evolution of viviparity (Shine 1995; Webb et al. 2006). This hypothesis posits that egg retention has evolved to control the thermal environment during embryonic development; accordingly, the shift in body temperature during pregnancy would occur because gravid females adjust thermoregulation to provide optimal thermal conditions for embryogenesis. To test this prediction, we evaluated the role of gestation environment on embryonic development, hatching success, and hatchling phenotype in oviparous *Zootoca vivipara* (Jacquin 1797), by keeping a group of gravid females at a higher temperature than they would normally select, i.e. similar to that preferred by non-gravid females of the same population, as determined in a laboratory thermal gradient (Rodríguez-Díaz et al. 2010). We chose this experimental approach rather than a possible alternative consisting of inducing oviposition (see Mathies and Andrews 1995) and then incubating the eggs under the selected thermal regime because our model more closely resembles the natural conditions of the incubation environment inside the mother's oviduct with the exception of the thermal regime applied. Our study organism is an ideal model for this task not only because females shift their preferred temperature during pregnancy, but also because they lay eggs with the embryo at quite an advanced stage of development (31–34 according to Dufaure and Hubert's 1961 developmental table; Braña et al. 1991, Rodríguez-Díaz et al. 2010). The species *Z. vivipara* also includes viviparous populations that lay soft-shelled eggs with fully developed hatchlings that emerge a few hours after oviposition (Panigel 1956). Due to the significant degree of development attained before oviposition in oviparous *Z. vivipara*, maternal thermoregulation during the pre-oviposition phase could be expected to affect developing embryos over a longer period than in most other oviparous species.

Materials and Methods

Gravid females of *Zootoca vivipara* (snout-vent length: mean ± SD, 52.71 ± 5.18 mm) were collected from an oviparous population in Las Señales (León, northern Spain), between 1,650 and 1,750 m.a.s.l., during late June of 2007 and were kept until oviposition in plastic terraria (50 × 40 × 30 cm; length x width x height) in the Zoology laboratory of the University of Oviedo. A maximum of 6 lizards was housed in each terrarium. Cages contained refuges and moist peat, a substrate suitable for egg laying. All lizards were provided with water ad libitum and mealworms twice a day.

Female *Z. vivipara* prefer a lower body temperature during pregnancy (mean body temperature ± SD: 32.33 ± 1.27°C; $n = 64$) than do adult males or non pregnant adult females (34.05 ± 1.07°C; $n = 155$; data from this population: Rodríguez-Díaz et al. 2010). If pregnant females prefer lower body temperatures to optimize embryonic development, even at the cost of some increase in incubation time, then incubating eggs in utero at the higher temperatures preferred by non-gravid females can be expected to have some detrimental effects on embryogenesis, and thus on hatchling phenotypes. To test this hypothesis, we kept a group of 27 gravid females in incubators at a constant temperature of 34°C, which is close to the mean temperature preferred by males and non-gravid females, for 6 h a day (11:00–17:00 h). This period of 6 h is roughly the average daily time they spend thermoregulating in the field. Because of the uniformly high air temperature and the lack of a radiant heat source, females are unable to perform behavioural thermoregulation, and their body temperature should approach air temperature inside the incubator; in fact, a sample of cloacal temperatures of these females, measured with a quick-reading cloacal *Schultheis* thermometer (to the nearest 0.1°C; Miller and Weber, Inc.) at the end of their daily period in the incubator, verified that their mean body temperature was indeed close to that sought (mean body temperature ± SD; 33.70 ± 0.30°C, $n = 19$). A fluorescent light was placed inside the incubator so that the photoperiod was the same for both groups of lizards. Before and after the daily period in the incubator, we let the lizards thermoregulate in a terrarium with a 60 W bulb from 9:00 to 11:00 h, and from 17:00 to 19:00 h. Another group of gravid females ($n = 19$) was allowed to thermoregulate without restrictions under these conditions from 9:00 to 19:00 h. At other times of the day all lizards were maintained at room temperature (mean laboratory temperature ± sd: minimum, 18.56 ± 2.75°C, $n = 25$; maximum, 26.68 ± 4.53°C, $n = 25$). In this study, lizards that oviposited at least 1 week after the experimental treatment had started were used in order to guarantee that the experimental conditions were able to affect embryonic development.

Clutches were collected from the terraria and weighed within a few hours of the time of oviposition, and embryonic stage at oviposition was determined for one egg from each clutch according to the developmental scale of Dufaure and Hubert (1961). We used plastic containers with moistened vermiculite as substrate (proportion distilled water/vermiculite 1/1 by weight) to incubate the eggs individually. Incubation temperature was set at 25°C, a temperature which has resulted in high hatching success and normal hatchling phenotypes in previous studies (Rodríguez-Díaz et al. 2010). Containers were rotated inside the incubator daily to minimize possible effects of temperature gradients on development and were periodically checked to verify that the vermiculite was still moist. Protocols for the incubation of control eggs were the same as those described for experimental eggs.

We assessed the effect of the gestation environment on clutch mass, embryonic stage at oviposition, length of incubation time (from oviposition to hatching), percentage of eggs that hatched successfully, and several hatchling phenotype traits: head length, abdomen length, snout-vent length (SVL), tail length, robustness (size-corrected hatchling mass), and locomotor performance. The morphological traits were measured in vivo using a digital caliper (to the nearest 0.01 mm; Vogel, Germany). Sex determination was carried out by eversion of hemipenes in males by applying gentle forceps pressure at the base of the tail (Harlow 1996).

Hatchling locomotor performance was tested 2 days after hatching. Before the running trials, hatchlings were kept for 30 min in an incubator at a high temperature (32°C), thus ensuring the same conditions for all hatchlings, i.e. a body temperature that maximizes locomotor performance in *Z. vivipara* (Van Damme et al. 1991). They were then made to run along a 1-meter-long corridor and videofilmed laterally with a Nikon videocamera. Whenever they stopped, we gently pushed them with a paintbrush. Three variables were measured on video recordings at 30 frames per second: (a) maximum sprint speed: speed in the fastest five consecutive frames; (b) number of stops during the entire run (two or more consecutive frames without moving); and (c) maximum distance covered between stops.

Statistical Analysis

All data were checked for normality (Kolgomorov-Smirnov test) and homocedasticity (Levene's test) prior to further statistical analysis. A Mann–Whitney *U*-test was carried out to analyse stage of embryonic development at oviposition because this variable did not meet the above assumptions, even after logarithmic transformation. A Generalized Linear Model using binomial errors and logit link function was carried out to assess differences in hatching success between the control and experimental group.

A one-factor analysis of variance was carried out to analyse between group differences in the mean incubation time for each clutch and a one-factor analysis of covariance (covariate: female mass) was carried out to examine clutch mass. Nested mixed model ANOVAs or ANCOVAs were performed to analyse the remaining variables. Treatment, sex, and their interaction were used as fixed effects and clutch as a random effect nested within the treatment, in order to control family effect. We included SVL as covariate in the analyses of several size related variables: tail length, body mass, sprint speed, and the longest distance done without pauses during trials. In the analyses of SVL, head length, and abdomen length, egg mass was used as covariate. The significance level for all tests was set at $\alpha = 0.05$. All statistical analyses were conducted with Statistica software (StatSoft, Inc., version 6.0, 2001).

Results

Control females oviposited eggs with embryos at Dufaure and Hubert's (1961) stages 33 and 34, whereas embryos from females kept at 34°C during the experimental period were more advanced, some even reaching stage 35 (Mann–Whitney *U*-test, Z adjusted $= -2.66$; $P < 0.01$; Fig. 1a). This advance in embryonic development at oviposition did not significantly affect incubation time at 25°C (ANOVA, $F_{1,37} = 2.878$; $P = 0.098$).

Hatching success was lower in the experimental group (58.62%, $n = 145$; Control group: 97.37%, $n = 76$; Wald χ^2 (1) $= 19.434$, $P < 0.001$). This difference in hatching success is not connected with the between-treatment differences in developmental stage at oviposition, as differences in hatching success were still found for stage 34, which is the most frequent embryo stage in both experimental groups (Wald χ^2 (1) $= 12.024$, $P < 0.001$; Fig. 1b). Clutch size did not differ between treatments (ANCOVA with female SVL as covariate: $F_{1,31} = 2.438$; $P = 0.129$), but clutches of the experimental group were on average heavier than those of the control group (ANCOVA with female mass: $F_{1,29} = 5.306$; $P = 0.029$).

Family effects were significant for all of the hatchling traits analysed ($P < 0.05$ for all cases). As has been previously found in the same population (Braña 2008; Rodríguez-Díaz et al. 2010), SVL, abdomen, and tail length of hatchlings varied according to sex, with the SVL and abdomen being longer in females (SVL: $F_{1,117} = 68.69$, $P < 0.001$; abdomen length: Table 1), and the tail being longer in males (Table 1). Furthermore, hatchling males were more robust than females (body mass with SVL as covariate; Table 1). There were no differences between sexes as regards head length or locomotor performance.

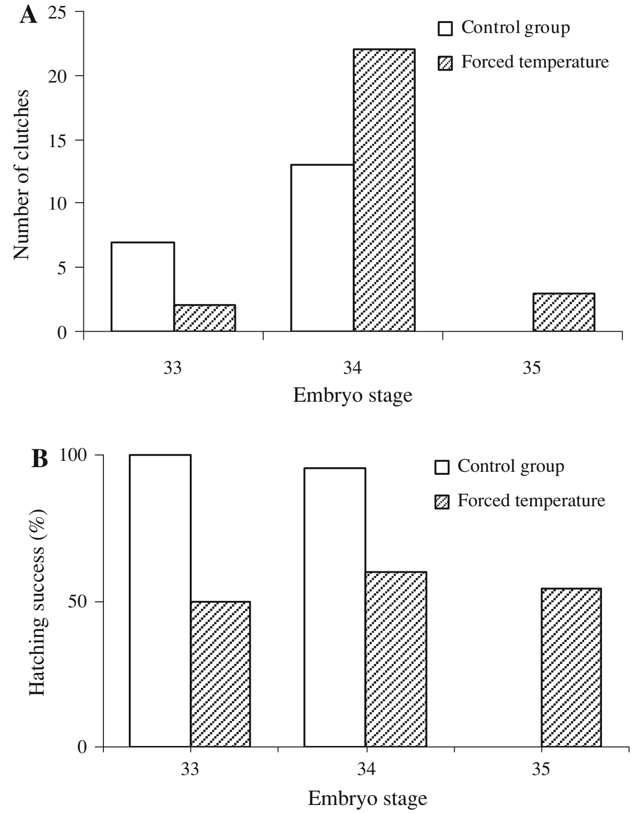

Fig. 1 **a** Development stages at oviposition of embryos of oviparous *Z. vivipara* in control clutches and in clutches oviposited by females subjected to forced temperature while pregnant, according to the stages described by Dufaure and Hubert (1961). **b** Percentage of hatching success for each of the embryo stages in control and experimental groups

Control hatchlings were marginally larger (ANCOVA with SVL as the dependent variable and egg mass as the covariate: $F_{1,117} = 4.04$, $P = 0.050$) and had larger heads (Table 1). The other morphological traits analysed do not differ between treatments. Hatchlings from the control group performed better in the running tests: control hatchlings ran faster (Fig. 2), paused less frequently, and covered larger distances without stopping than those from the forced temperature treatment (Table 1).

Discussion

Maternal temperature has been widely reported to affect traits influencing offspring fitness (Beuchat 1988; Shine and Harlow 1993; Mathies and Andrews 1997; Wapstra 2000) and females are expected to evolve a more accurate control of body temperature during pregnancy. In fact, gravid females of several lizard species shift their preferred body temperatures (Braña 1993; Gvoždík and Castilla 2001), which are generally less variable (Mathies and Andrews 1997; Shine 2006). Our results show that maintaining the comparatively high temperature preferred by non-pregnant females during pregnancy has detrimental effects on development and could ultimately influence hatchling fitness. These results concur with the predictions of the "maternal manipulation" hypothesis (Shine 1995; Webb et al. 2006), which sets out the adaptive advantages of egg retention in the evolutionary transition from oviparity to viviparity.

Results from incubations at 34°C in the postovipositional phase reported in a previous paper on the same oviparous population used in the present study (Rodríguez-Díaz et al. 2010) suggested that the shift in thermal preference of pregnant females towards lower body temperatures might be explained by the fact that the temperature preferred by females when non-gravid has detrimental effects on developing embryos. In the present study, new data support this same conclusion. Although the two studies differ in the phase in which the experimental thermal conditions were applied (before or after oviposition), there is an overlap with regard to the embryonic development stages affected by the two thermal incubation regimes. This is because, in the current study, females from the forced temperature treatment retained their eggs until a more advanced embryo stage. The effects on hatchling phenotype of gestation temperature at 34°C, even if applied for just 6 h a day during the later stages of egg retention, were similar to the effects of external incubation at constant 34°C from oviposition to hatching (see Rodríguez-Díaz et al. 2010). This result parallels the findings reported by Braña and Ji (2007) in the lacertid *Podarcis muralis*, in which high temperature experienced by embryos during the early external incubation period only, produced similar phenotypic responses to those produced by the same constant temperature applied during the whole incubation period (Braña and Ji 2000). Interestingly, the embryonic stages affected by high temperatures were probably very similar in the experiment by Braña and Ji (2007) and in the present study, with the affected developmental stages ranging from 26–28 to 34: *P. muralis* lay eggs containing embryos at stages 26–28 (Braña et al. 1991), and it takes 14–15 days to attain stage 34 at 26°C (Dhouailly and Saxod 1974), thus the 13 days of treatment at a higher temperature of 32°C in the Braña and Ji (2007) study, will certainly have affected the range of development stages between 26–28 and 34; in turn, *Z. vivipara* were under the forced temperature regime in the present study for 7–10 days, and most eggs were laid at stage 34 (see results), hence, according to the development timetable of Hubert (1985), development would have been at stages 26–28 when the treatment was initiated.

Our results show that intrauterine incubation temperature can influence embryonic development in an oviparous species, as has been previously found in viviparous species

Table 1 Effects of treatment (forced body temperature during intrauterine incubation) and sex on morphology and locomotor performance of *Zootoca vivipara* hatchlings

Hatchling traits	Effects		
	Treatment	Sex	Interaction
Morphology			
Head length	**F1,117 = 5.820*** **C > T**	*F*1,117 = 0.398 ns	*F*1,117 = 1.512 ns
Abdomen length	*F*1,117 = 0.170 ns	**F1,117 = 110.75***** **M < F**	*F*1,117 = 2.920 ns
Tail length	*F*1,116 = 1.039 ns	**F1,116 = 6.741*** **M > F**	*F*1,116 = 42.618 ns
Body mass	*F*1,117 = 0.007 ns	**F1,117 = 5.760*** **M > F**	*F*1,117 = 0.304 ns
Locomotor performance			
Sprint speed	**F1,117 = 21.164***** **C > T**	*F*1,117 = 0.035 ns	*F*1,117 = 0.325 ns
Distance	**F1,117 = 6.329*** **C > T**	*F*1,117 = 0.005 ns	*F*1,117 = 0.898 ns
Number of stops	**F1,115 = 4.309*** **C < T**	*F*1,115 = 0.758 ns	*F*1,115 = 0.157 ns

Statistical tests correspond to single effects and between-factor interactions in nested ANOVAs (for number of stops) or ANCOVAs (for tail length, hatchling mass, sprint speed, and distance with SVL as covariate; and head and abdomen length with egg mass as covariates). Although not shown, random factor (clutch) effects were significant for all traits analyzed

Symbols immediately after *F* values represent significant levels: ns $P > 0.05$, * $P < 0.01$, *** $P < 0.001$

M male, *F* female, *C* control, *T* treatment. Significant effects are in bold type

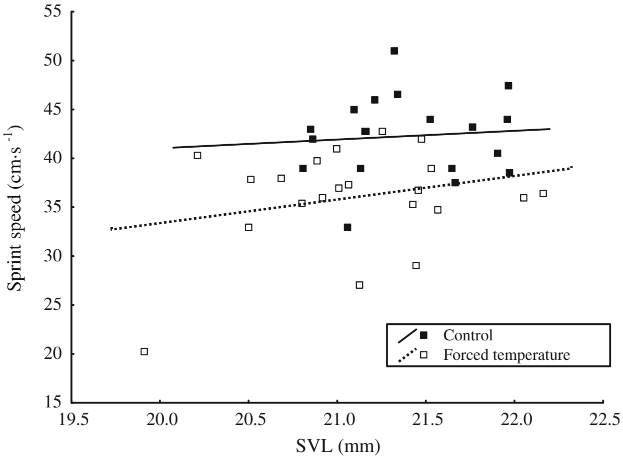

Fig. 2 Relationship between maximal sprint speed and snout-vent length (SVL) of hatchling *Z. vivipara* from control and forced temperature groups. *Squares* represent the mean values for each clutch

(Beuchat 1988; Mathies and Andrews 1997). Some of the females forced to maintain high temperature during pregnancy oviposited eggs with embryos at stage 35, one stage more advanced than the maximal reached by the embryos of eggs laid by control females. There seems to be an almost absolute upper limit around this stage in the extent of development attainable in utero for oviparous populations of *Z. vivipara*: a previous study on the same population dealing with the limitations of egg retention beyond the normal time of oviposition also showed that stage 35 was the maximal reached in utero before egg-laying (Rodríguez-Díaz and Braña 2011). However, F1 hybrids between oviparous and viviparous populations lay eggs containing embryos that can surpass this stage of intrauterine development and reach stage 36 (Arrayago et al. 1996), but these eggs have thin and incompletely calcified eggshells (Heulin et al. 1992), thereby probably favouring respiratory exchanges.

In our study, the main effect of high temperature during the intrauterine incubation is reduced hatching success, which would significantly lower the reproductive success of females. The experimental treatment also influenced hatchling phenotypes: hatchlings that experienced higher temperature inside their mother's oviduct at the end of the retention phase were smaller, had shorter heads, and performed worse during running trials. Even though clutches of the forced temperature treatment were heavier, hatchlings from this experimental treatment were smaller in length, which seems to be contradictory. This pattern could be explained by, on the one hand, the between-treatments difference in egg hydration at oviposition. Eggs of lizards, with flexible eggshells, absorb water and swell as embryonic development proceeds (Packard 1991; Qualls and Andrews 1999) and the eggs of the forced temperature group contained more developed embryos than the control eggs. On the other hand, higher incubation temperatures usually produce smaller hatchlings (Atkinson 1994; Mathies and Andrews 1997; Braña and Ji 2000), which may be linked to the acceleration of metabolic rates and reduction of metabolic efficiency as a result of high temperatures (Packard and Packard 1988; but see Angilletta et al. 2000). The head length difference is important to note as it, along with body size, has an influence on bite capacity, an important ecological attribute in adult *Z. vivipara* because of its influence on prey selection (Herrel et al. 2001; Verwaijen et al. 2002) and also probably on male reproductive success (Braña 1996; Gvoždík and Van Damme 2003). The final point, that experimental hatchlings exhibit slower sprint speed, stop more frequently, and cover shorter distances without stopping, could be detrimental to their fitness. Although evidence for positive correlation of locomotor performance with Darwinian fitness is somewhat contradictory (see, e.g. Garland and Losos 1994; Clobert et al. 2000), it is generally thought that individuals with outstanding locomotor capacity may be better able to capture prey and escape from predators or have advantages in social hierarchies (e.g. see Garland et al. 1990; Robson and Miles 2000). For a viviparous population of our study species, Le Galliard et al. (2004) demonstrated that under dietary restriction, differences in locomotor performance (endurance) at hatching were retained 1 year later and positively influenced fitness (survival).

The effects resulting from our experimental conditions arise from the exposition of developing embryos to high temperatures for just a few hours per day. Females from treatment and control groups were exposed to the same temperatures for 18 h per day, including during the night, when they experienced the same minimum temperatures (mean ± SD, 18.56 ± 2.75°C). For only 6 h per day both groups experienced slight differences in body temperature: control females could freely thermoregulate, keeping a narrow range of body temperatures (mean, 32.33°C; see Rodríguez-Díaz et al. 2010), and experimental females maintained a mean temperature of 33.70°C (see Materials and Methods). Experimental studies have shown effects of mean of (Braña and Ji 2000; Andrews et al. 2000) as well as variance in (Shine and Harlow 1996; Du and Ji 2006) incubation temperatures on development. In this study, overall mean temperature and variance were very similar in both experimental groups and hence they would not explain the differences obtained between groups. It is therefore reasonable to assume that the most likely explanation to account for the differences observed is in fact that females were kept for a certain period at temperatures which were above an upper thermal limit suitable for development.

Taken together, our findings show that temperatures similar to those preferred by non-gravid females applied during the later phase of egg retention considerably reduce hatching success and produce hatchling phenotypes exhibiting characteristics that are likely to be connected with low fitness, a finding previously reported by Mathies and Andrews (1997) in the viviparous lizard *Sceloporus jarrovi*. In conclusion, the shift in preferred body temperature during pregnancy would avoid the negative effects of high incubation temperatures on hatchling fitness and, as predicted by the maternal manipulation hypothesis on the evolution of viviparity, would provide the thermal environment that optimises hatchling traits, suggesting that this shift in the thermoregulatory pattern could have been an important component in the evolution of extended egg retention.

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