

RESEARCH ARTICLE

Functional Ecology



Phenology and the physiological niche are co-adapted in a desert-dwelling lizard

Bao-Jun Sun^{1,2} | Liang Ma^{1,3} | Shu-Ran Li^{1,3} | Caroline M. Williams² |
Yang Wang^{1,3} | Xin Hao^{1,3} | Wei-Guo Du^{1,4}

¹Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

²Department of Integrative Biology, University of California, Berkeley, California

³University of Chinese Academy of Sciences, Beijing, China

⁴Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China

Correspondence

Wei-Guo Du
Email: duweiguo@ioz.ac.cn

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Abstract

1. A major goal of seasonal biology is to understand how selection on phenology and the physiological niche interact. In oviparous species, fitness variation across the growing season suggests that phenological shifts will alter selective environments experienced by embryos. We hypothesize that physiology could become co-adapted with phenology; such that embryos perform better in the environmental conditions they are adapted to compared to embryos adapted to other environments (temporal matching).
2. Here, we tested for temporal matching to seasonal changes in the environmental temperatures with toad-headed lizard, *Phrynocephalus przewalskii*, which inhabits the temperate desert steppe of China. We used a split-clutch reciprocal experiment, by incubating eggs from early- and late-breeding females at rising and falling temperature regimes, respectively, to separate the influence of intrinsic (genetic and parental) vs. extrinsic factors (developmental plasticity or acclimatization) on the performance and fitness of offspring.
3. Eggs from early-breeding females were with higher quality than those from late-breeding females, likely due to better maternal provisioning. Offspring from early-breeding females had higher selected body temperatures and metabolic rates than those from late-breeding females.
4. Falling temperatures that may indicate the end of the growing season, reduced incubation duration and increased metabolic rates for both early and late eggs, compared to rising temperatures. Late hatchlings had higher growth rates when incubated at falling compared to rising temperatures, while growth rates of early hatchlings were not sensitive to incubation temperature. Thus, growth and survival rates of late embryos were similar to early embryos under falling temperatures, despite early embryos being of generally higher quality.
5. Overall, our study confirms that “early is higher quality.” Intrinsic factors dominate offspring performance and fitness, with a general advantage for early embryos throughout the season. We found some support for temporal matching, demonstrating that late embryos with lower quality have physiological strategies that are specialized to late-season environments, allowing them to attain similar fitness in late-season environments to that of early embryos.

KEYWORDS

embryo, matching is better, metabolism, reproductive timing, seasonal nest temperature, temporal adaptation, thermal

1 | INTRODUCTION

Organisms have evolved a diversity of life-history strategies to cope with seasonal changes in their environment. As the environment changes through the breeding season, the phenotype (e.g., morphology, behaviour) and performance (e.g., growth, survival) of individuals also change (Behrman, Watson, O'Brien, Heschel, & Schmidt, 2015; Edwards & Richardson, 2004; Landa, 1992a; Pearson & Warner, 2018; Ragland & Kingsolver, 2008), which in turn may alter population dynamics. Phenotypic and performance variation among individuals across the breeding season arise from a combination of intrinsic and extrinsic effects, including genetically based differences, parental effects and direct effects of environments (Chevin, Lande, & Mace, 2010). We must understand the relative contributions of intrinsic characteristics and external environmental factors to variation in the performance of individuals across the breeding season, if we are to predict population dynamics and life-history evolution.

In seasonal environments, offspring born early in the breeding season frequently have better performance and survival than those born later in the season ("early is better"; Edwards & Richardson, 2004; Landa, 1992b; Reznick, Schultz, Morey, & Roff, 2006; Uller & Olsson, 2010; Verhulst & Nilsson, 2008; Warner & Shine, 2007; Yamahira & Conover, 2002). Seasonal variation could result from early-breeding females being higher quality, allowing them to pass on superior genes and maternally derived resources to their offspring ("earlier is higher quality" hypothesis). We refer to the combination of genetic and parental influences as intrinsic effects. In birds and reptiles, increased maternal provisioning or better-quality nest sites of early-compared to late-breeding mothers leads to higher offspring performance, in support of this hypothesis (Garcia-Navas & Jose Sanz, 2011; Olsson & Shine, 1997; Siikamaki, 1998; Verhulst & Nilsson, 2008). Alternatively, the greater fitness of early-season offspring could be determined by extrinsic factors encountered during development, such as temperature, moisture, resource availability and predation risk. In oviparous species, offspring may be particularly sensitive to environmental conditions during development, because embryos of these species develop outside the mothers' body (Pearson & Warner, 2016; Shine, 2002, 2004). For ectothermic animals, temperature is a key determinant of fitness, and incubation temperature has particularly profound effects. For example, reptile eggs laid in spring that develop at rising temperatures of spring and early summer have higher developmental success and offspring fitness, relative to eggs laid during falling temperatures in late summer (Shine, 2004), framed as the "rising temperatures are better" hypothesis. The degree to which intrinsic (genetic and parental) and extrinsic (developmental environment) effects contribute to the

pattern of "early is better" is an open question in reptiles. To differentiate between "early is higher quality" and "rising temperatures are better," we must experimentally separate the effects of intrinsic and extrinsic factors.

When forces of natural selection vary through time or space, the norms of reaction or the environmental sensitivity of fitness-relevant traits can evolve, improving fitness (Stearns, 1992). Reaction norms have been best studied in the context of local adaptation, wherein spatial heterogeneity causes populations to become adapted to their local environment, such that fitness within a given environment is higher in natal compared to non-natal genotypes (Kawecki & Ebert, 2004). However, variation in environmental conditions through time can also generate a related pattern of temporal adaptation, wherein at any given time, ecotypes that emerged under that selective environment will outperform those from other time periods (Blanquart & Gandon, 2013). The importance of temporal adaptation is well established in host-parasite coevolution (Koskella, 2014), but has been little explored in the context of seasonal adaptation. If embryos are temporally adapted to seasonal variation, it raises a third hypothesis—"matching is better." The extent to which phenology and physiology can become co-adapted is a key gap in our understanding of the ecological and evolutionary dynamics of adaptation to seasonality (Williams et al., 2017). Coadaptation between the phenological and physiological niche could occur if rates of metabolic processes or related physiological processes control performance and phenology, and if these processes are heritable through either genetic or epigenetic/parental transmission.

Here, we used the toad-headed lizard, *Phrynocephalus przewalskii*, from the temperate desert steppe of China, to test three nonexclusive hypotheses of seasonal variation in offspring fitness: (a) Early is higher quality (intrinsic characteristics); (b) Rising temperatures are better (extrinsic factors); and (c) Matching is better. We reared split clutches of early (May) and late (July) embryos from different females under experimental conditions of rising (early-season) and falling (late-season) temperatures and measured embryonic and hatchling performance traits and fitness proxies. At our study site, a majority of females lay one clutch of eggs within the breeding season from late May to July, with a small proportion (16%, 6/38) of females producing a second clutch (S.-R. Li, X. Hao, & B.-J. Sun, unpublished data). It is thus likely that the late-breeding females are not due to multiple clutches, but are consistently late-breeding, as is the case for other lizard species (Ljungström, Wapstra, & Olsson, 2015). We test our three hypotheses using the framework developed for diagnosing local adaptation (Kawecki & Ebert, 2004) (Figure 1). In brief, intrinsic (including genetic and parental) effects result in a difference in intercept (Figure 1a), and "early is higher quality" results in a higher mean value for early embryos for fitness-relevant traits. Extrinsic effects

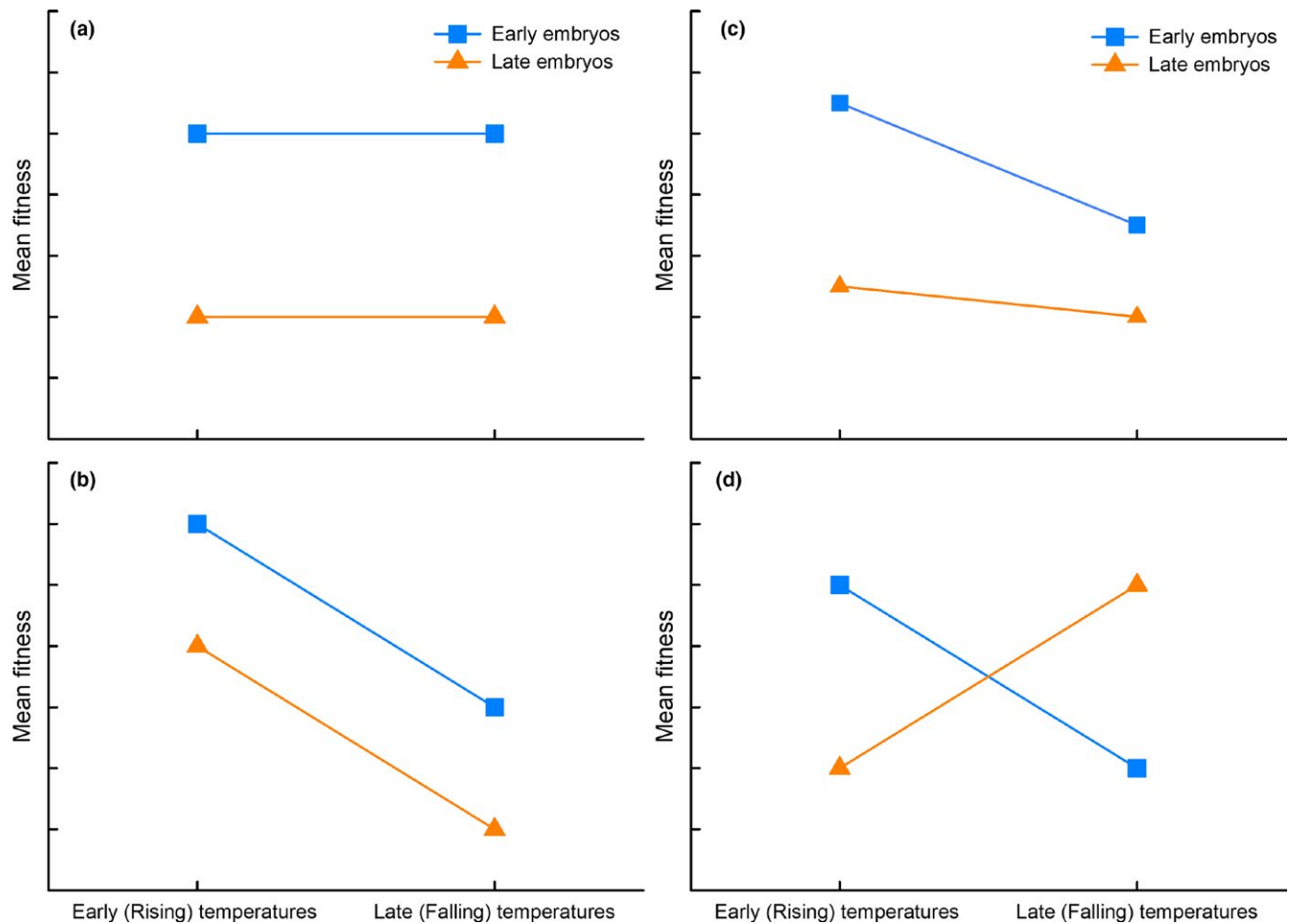


FIGURE 1 Hypothetical framework of interactions between embryos and environmental factors related to mean fitness. Pattern in (a) indicates “early is better.” Pattern in (b) indicates “rising temperatures are better.” Pattern in (c) indicates different environmental sensitivities. Pattern in (d) indicates “matching is better.”

(developmental plasticity and acclimatization) result in a significant slope, with a negative slope indicating that rising temperatures are better (Figure 1b). Differences in slope between early and late embryos indicate differences in environmental sensitivity (Figure 1c). The specific case of temporal matching requires that reaction norms cross, with early and late embryos performing better in their matching temperature conditions (Figure 1d). Unfortunately, it is impossible to test the alternative hypotheses with transplant experiments in the field, because of fixed differences in timing of laying. However, using a reciprocal common garden experiment in the laboratory, we can simulate early- and late-season temperatures to test for temporal adaptation to seasonal variation.

2 | MATERIALS AND METHODS

2.1 | Study species and nest temperature

The toad-headed agama (*P. przewalskii*) is a small diurnal lizard (snout-vent length [SVL] up to 60 mm), that is widely distributed in

the desert, semi-desert and grassland habitats of northern China (Zhao, Zhao, & Zhou, 1999). The lizard usually achieves maturity at the age of two years with a minimum SVL of 40 mm. In the laboratory with unlimited food access and benign thermal environments, most of females lay one clutch of eggs from May to July in each breeding season, with 1–6 eggs in each clutch and a mean clutch size ranging from 2 to 4 eggs depending on populations and body size (Wang, Ji, Zhao, Yu, & Liu, 2011; Zeng, Zhao, & Sun, 2013). Incubation temperature significantly affects incubation duration, hatching success and offspring locomotor performance, but not offspring sex (Tang et al., 2012). *P. przewalskii* is the main lizard fauna at our study site, which contains patches of sand and clusters of shrubs (Zeng et al., 2016). The site is located at the Shierliancheng Field Station, Institute of Grassland Research of the Chinese Academy of Agricultural Sciences (40° 12' N, 111° 07' E), Inner Mongolia, China.

From May to July of 2014, we located 15 nests by searching for fresh and wet soil, which indicated the entrance of nest burrows of this species. Then, we placed an iButton temperature logger (DS1921; Maxim Integrated Products Ltd.) beside the eggs in each nest to record the temperature at 1-hr intervals.

2.2 | Female collection, husbandry and reproduction

During late May (25 May–2 June) and early July (1–6 July) of 2015, we collected 35 early- and then 41 late-breeding females, respectively, at our study site. From 08:00 to 16:00 of each day, we captured gravid female lizards by hand and immediately measured the body temperature (cloacal temperature) of females. Nine copper models of similar body size to *P. przewalskii* were randomly set in the field site where the females were collected to monitor the operative temperatures (T_e) hourly by placing iButtons in the models from 08:00 to 19:00 during the period of female collection. Accordingly, we collected the operative temperatures of 9 days in late May to early June, and of 6 days in early July.

A total of 76 collected lizards were transported to our laboratory in Beijing on 3 June (early-breeding females) and 6 July (late-breeding females), respectively, where they were maintained in separate terraria (size: 350 × 230 × 210 mm) that were placed in a temperature-controlled room maintained at 24°C. A heating lamp (50 W) was hung at one end of each terrarium to provide a thermal gradient of 24–40°C during the heating period of 08:00–18:00. Food (crickets dusted with vitamin supplements) and water were provided ad libitum. The terraria were lined with 100 mm moist sand where the females laid their eggs. We checked the terraria three times a day (09:00, 13:00 and 17:00) for freshly laid eggs. The early-breeding females collected from the field in late May laid their eggs in early June, within 8.8 ± 2.8 days of entering captivity, whereas the late-breeding females laid their eggs in early July, within 3.1 ± 1.5 days of entering captivity.

2.3 | Egg incubation

A total of 189 eggs (178 fertilized eggs) were laid by 35 early- and 41 late-breeding females. The eggs were weighed (± 0.001 g) immediately once found. A total of 11 and 14 eggs of early- and late-breeding females from different clutches were selected randomly to determine the embryonic stage according to the classification scheme of the developmental stage in lizards (Dufaure & Hubert, 1961). The remaining eggs ($n = 153$) from the early-breeding ($n = 71$) and late-breeding ($n = 82$) females were incubated separately in glass jars (57 × 75 mm; diameter × height) with moist vermiculite (-220 kpa). The jars were covered with plastic wrap and were then randomly assigned to the rising and falling temperature regimes using a split-clutch design. Rising temperatures mimic the thermal environment within a nest from late May to early July, whereas falling temperatures mimic the nest temperatures from July to August. Given that the average incubation duration of *P. przewalskii* eggs in natural nests is 43 days (38–50 days, see details in Li et al., 2018), the eggs assigned to the rising temperature regime were incubated at $24 \pm 3^\circ\text{C}$, $26 \pm 3^\circ\text{C}$ and $28 \pm 3^\circ\text{C}$ in sequence for 13 days at each temperature regime. The eggs assigned to the falling temperature regime were incubated at $28 \pm 3^\circ\text{C}$, $26 \pm 3^\circ\text{C}$ and $24 \pm 3^\circ\text{C}$ in sequence for 13 days at each temperature regime (see detailed references in Supporting

Information Figure S2). After 39 days, all of the eggs were transferred to the thermal treatment of $26 \pm 3^\circ\text{C}$ until they hatched. As a result, eggs from the two thermal treatments experienced rising and falling temperatures, respectively, but the same mean temperature of 26°C . We checked the jars every three days, and water was added to maintain the moisture conditions, if necessary.

2.4 | Hatchling traits

Towards the end of incubation, we checked the jars three times daily for new hatchlings. Incubation duration was recorded as the days from oviposition to hatching, while hatching success was calculated as the percentage of hatchlings relative to incubated eggs in each treatment. Hatchling lizards ($n = 90$) were individually measured (SVL to 0.01 mm, body mass to 0.001 g). After measurements, the hatchlings were randomly assigned to one of six terraria (600 × 450 mm) and raised in a temperature-controlled room at 24°C. The set-up of the terraria and heating schedule for thermoregulation were same as that used for the adult females. Each terrarium contained 8–10 hatchlings of a similar age from both early and late seasons. To minimize potential thermal differences between terraria, we rotated the positions of terraria on the shelf every day. Water and food (larvae of mealworms and crickets dusted with vitamin supplements) were provided ad libitum.

2.4.1 | Selected body temperatures

On day 15 after hatching, the selected body temperature of a subsample of lizards with a similar age ($n = 60$) was measured in a 1,500 × 800 × 400 mm tub within a temperature-controlled room maintained at 20°C. Two 275 W heating lamps were hung at one end of the tub to generate a thermal gradient of 20–60°C. In each trial, six hatchlings were released in the tub for 1-day acclimation. The cloacal temperature of each hatchling was then measured with an UNT-325 electronic thermometer ($\pm 0.1^\circ\text{C}$; UNI-Trend Technology, Shanghai, China) at 09:00 and 15:00, respectively. The average selected body temperature was calculated as the mean value of the body temperature at the two time points in each day (Shu, Sun, & Du, 2010).

2.4.2 | Metabolic rates

One day after the selected body temperature measurement, the resting metabolic rate (RMR) of the hatchlings ($n = 60$) was measured at four environmental temperatures (22°C, 26°C, 30°C and 34°C) in a random order using a respirometry system (Sable Systems International, Henderson, NV). We used respiratory gas exchange by estimating CO_2 production rate as a proxy for metabolic rate. Before the test, the hatchlings were fasted for 12 hr and were allowed to acclimate to the test temperature for 2 hr. The metabolic rate of the lizards was tested in a closed-circuit system with a volume of 116.7 ml. Each lizard was enclosed within a chamber of the circuit that had been placed in an incubator set at the test temperature.

At the beginning of the measurement, the circuit system was open to the air scrubbed of water and CO₂ through a tube with a flow rate of 240 ml/min to stabilize the baseline. The circuit system was then transferred to a closed cycle, and the rate of carbon dioxide production (VCO₂) in the closed-circuit system was continuously recorded secondly for at least 10 min. The metabolic rates were then calculated as the CO₂ production per gram body mass per hour (ml g⁻¹ hr⁻¹), with the equation of MR = VCO₂ × volume/body mass, where VCO₂ is the CO₂ production rate in percentage (%/hr) in the closed circuit and volume is 116.7 ml of the closed circuit. All measurements of lizards in the incubators (MIR554-PC, Sanyo, Japan) were conducted from 10:00 to 18:00, to minimize the effect of circadian rhythms.

2.4.3 | Growth rate and survival rate

After the hatchlings ($n = 90$) had been kept in the laboratory for 20–22 days to determine the behavioural and physiological traits assessed in this study, they were measured and released to five field enclosures (5 m × 5 m) covered with anti-bird nets in the natural habitat of our field study site where the lizards were collected. The hatchlings from each treatment were randomly assigned to five enclosures, with each enclosure containing a mix of 15–20 hatchlings from different seasons and incubation treatments. Hatchlings from early-breeding females were released during early August, while young from late-breeding females were released during early September. We added supplementary food (larva of mealworm) twice a week (about 1.5 g hatchling⁻¹ week⁻¹) for hatchlings in the enclosures to ensure food was available ad libitum. On September 21, 2015, all hatchlings in the enclosures were recaptured and re-measured (SVL to 0.01 mm, body mass to 0.001 g) to calculate the specific growth rate (SGR = [Ln (SVL or BM) – Ln (initial SVL or initial BM)]/days) and survival rate of hatchlings before winter. After the measurements, the recaptured lizards were returned to the field enclosures where they overwintered. On May 18, 2016, the hatchlings in the enclosures were recaptured again to calculate the survival rate of hatchlings.

2.5 | Statistical analysis

Before the analysis, the normality of the distribution and homogeneity of all variances in the data were tested with the Kolmogorov–Smirnov test and Bartlett's test. In cases where assumptions of normality were violated, we used nonparametric analyses to detect between-treatment differences. Mann–Whitney U test was used to analyse differences in operative temperature, female body temperature and nest temperature. Two-sample t tests were performed to analyse seasonal variation in female body size and reproductive output, while one-way ANOVA was conducted to analyse the developmental stage of freshly laid eggs. Linear mixed models were used to analyse incubation duration, hatchling SVL, hatchling body mass, selected body temperature, RMR and specific growth rates (SGR), with reproductive timing and developmental temperatures as

fixed factors, female identity as a random factor and maternal SVL or initial egg mass as a covariate. The effects of enclosures on SGRs in SVL and BM of hatchlings were redundant and thus not included in our statistical models. We included days of growth as a covariate in the analysis of SGR. The hatching success and survival rate were analysed with the chi-square test. We used Tukey's honestly significant difference test for pair-wise comparisons.

3 | RESULTS

3.1 | Seasonal changes in ambient temperature, body temperature and nest temperature

The operative temperature ($Z = -3.092$, $df = 180$, $p = 0.002$) of the locations where females were collected was significantly higher in early July than in late May (Supporting Information Figure S1). Correspondingly, female body temperatures when they were collected were 1.3°C higher in early July (36.0°C) than in late May (34.7°C) during the active period of each day from 08:00 to 16:00 ($Z = -2.384$, $df = 83$, $p = 0.017$; Supporting Information Figure S1). Temperatures inside natural nests showed noticeable seasonal changes, increasing during the early-breeding season (late May to July) and decreasing during the late-breeding season (July to August), both daily and weekly (Supporting Information Figure S2a,b). The mean nest temperature during the early- and late-breeding season, which was 25.3°C and 25.7°C, respectively, was not different significantly ($Z = -0.405$, $df = 15$, $p = 0.685$).

3.2 | Female body size and reproduction

Early-breeding females were larger and heavier and produced larger eggs than late-breeding females (Table 1). However, clutch size did not change seasonally (Table 1). After the effect of maternal SVL was removed statistically, eggs from early-breeding females were

TABLE 1 Body size and reproductive traits of early- and late-breeding females of *Phrynocephalus przewalskii*

	Early-breed- ing	Late-breeding	Statistical significance
Female SVL (mm)	52.01 ± 0.43 ($n = 35$)	48.12 ± 0.62 ($n = 41$)	$t = 4.974$, $df = 74$, $p < 0.0001$
Female mass (g)	4.099 ± 0.107 ($n = 35$)	3.246 ± 0.132 ($n = 41$)	$t = 4.915$, $df = 74$, $p < 0.0001$
Egg mass (g)	0.604 ± 0.021 ($n = 35$)	0.522 ± 0.012 ($n = 41$)	$t = 3.472$, $df = 74$, $p = 0.0009$
Clutch size	2.5 ± 0.1 ($n = 35$)	2.4 ± 0.1 ($n = 41$)	$t = 0.575$, $df = 74$, $p = 0.567$

Note. Values are expressed as means ± SE. Two-sample t tests were used to compare seasonal differences in body size and reproductive traits. Statistically significant differences are indicated in bold.

still larger ($F_{1,73} = 6.769$, $p = 0.011$) than those from late-breeding females, with no seasonal change in clutch size ($F_{1,73} = 2.526$, $p = 0.116$).

3.3 | Embryonic development at rising and falling temperatures

The developmental stage of embryos at oviposition was more advanced in eggs from early-breeding females (stage 31.7 ± 0.4 , $n = 11$) than late-breeding females (stage 29.7 ± 0.3 , $n = 14$) ($F_{1,23} = 15.712$, $p = 0.0006$). Incubation duration was significantly affected by reproductive timing ($F_{1,49,626} = 4.581$, $p = 0.037$) and incubation temperature ($F_{1,38,891} = 82.831$, $p < 0.001$), but not by the interaction of these two factors ($F_{1,38,891} = 0.004$, $p = 0.953$). Eggs from early-breeding females had an incubation duration that was 1.4 days shorter than those from late-breeding females (38.2 vs. 39.6 days), whereas eggs incubated at falling temperatures hatched out 2.4 days earlier than those incubated at rising temperatures (37.7 vs. 40.1 days) (Figure 2a). Hatching success was significantly higher for eggs from early-breeding females (70.4%) than late-breeding females (48.8%) ($X^2 = 7.36$, $df = 1$, $p = 0.007$), but was not affected by incubation temperature (Rising: 55.8% vs. Falling: 61.8%) ($X^2 = 0.57$, $df = 1$, $p = 0.451$) (Figure 2b).

3.4 | Hatchling traits

Hatchlings from early-breeding females were larger and heavier than young from late-breeding females (Table 2). After the effects of maternal SVL or initial egg mass were removed as covariates, hatchlings from early-breeding females were neither larger ($F_{1,38,619} = 3.493$, $p = 0.069$), nor heavier ($F_{1,45,418} = 0.004$, $p = 0.951$), than young from late-breeding females (Figure 3a,b). Neither the body size nor mass of hatchlings was affected by incubation temperature or

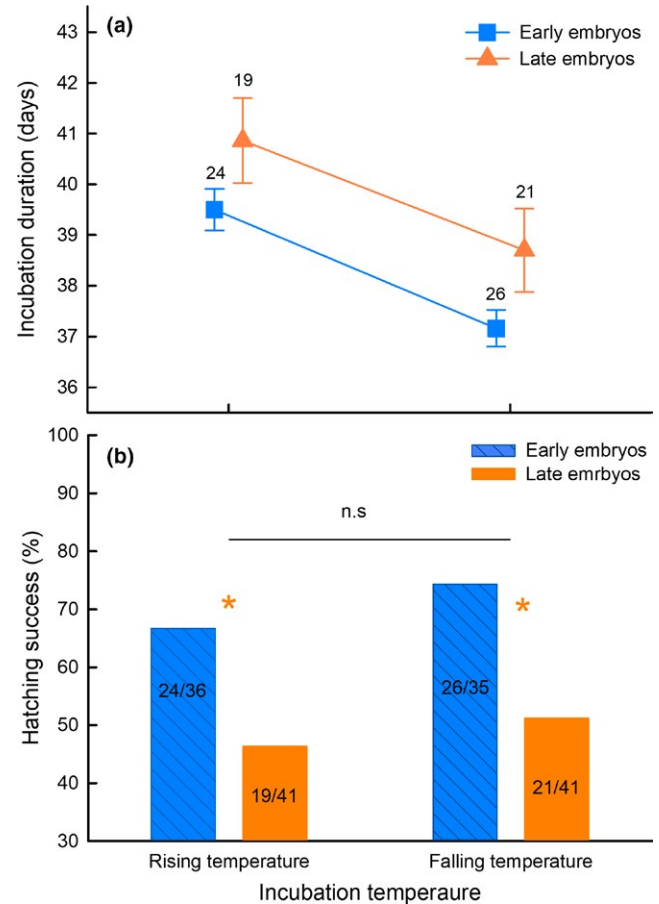


FIGURE 2 Incubation duration (a) and hatching success (b) of eggs from early- and late-breeding *Phrynocephalus przewalskii* females. The numbers above the bars (a) and in the volumes (b) indicate the sample size. Data are shown as mean \pm SE. Asterisks indicate the significant difference in hatching success between early and late embryos

TABLE 2 Statistical results of the effects of reproductive timing (early vs. late), incubation temperature (rising vs. falling) and their interaction on the snout-vent length (SVL), body mass (BM), selected body temperature (Tsel), resting metabolic rate (RMR) and specific growth rates (SGR) of SVL and BM in *Phrynocephalus przewalskii* hatchlings

	Reproductive timing	Incubation temperature	Interaction
Hatchling SVL	$F_{1,46.734} = 9.873$, $p = 0.003$	$F_{1,46.804} = 2.839$, $p = 0.099$	$F_{1,46.804} = 1.538$, $p = 0.221$
Hatchling BM	$F_{1,47.274} = 5.382$, $p = 0.025$	$F_{1,42.057} = 0.820$, $p = 0.370$	$F_{1,42.057} = 0.600$, $p = 0.443$
Tsel	$F_{1,56} = 9.584$, $p = 0.003$	$F_{1,56} = 0.315$, $p = 0.577$	$F_{1,56} = 0.385$, $p = 0.538$
RMR	$F_{1,55} = 135.019$, $p < 0.0001$	$F_{1,55} = 13.504$, $p = 0.001$	$F_{3,165} = 2.183$, $p = 0.145$
SGR-SVL	$F_{1,57.826} = 4.360$, $p = 0.041$	$F_{1,57.826} = 7.764$, $p = 0.007$	$F_{1,57.826} = 12.158$, $p = 0.001$
SGR-BM	$F_{1,57.008} = 15.179$, $p < 0.001$	$F_{1,57.008} = 7.913$, $p = 0.007$	$F_{1,57.008} = 10.049$, $p = 0.002$

Note. Linear Mixed Models were used to determine the effects with female identity as a random factor for Hatching SVL, BM, Tsel and RMR, and enclosures as a random factor for SGR-SVL and SGR-BM. The days of growth were also included as a covariate in the analysis of SGR-BM given the significant relationship between these two parameters. Test temperatures were repeated measures in the analysis of RMR. Statistically significant differences are indicated in bold.

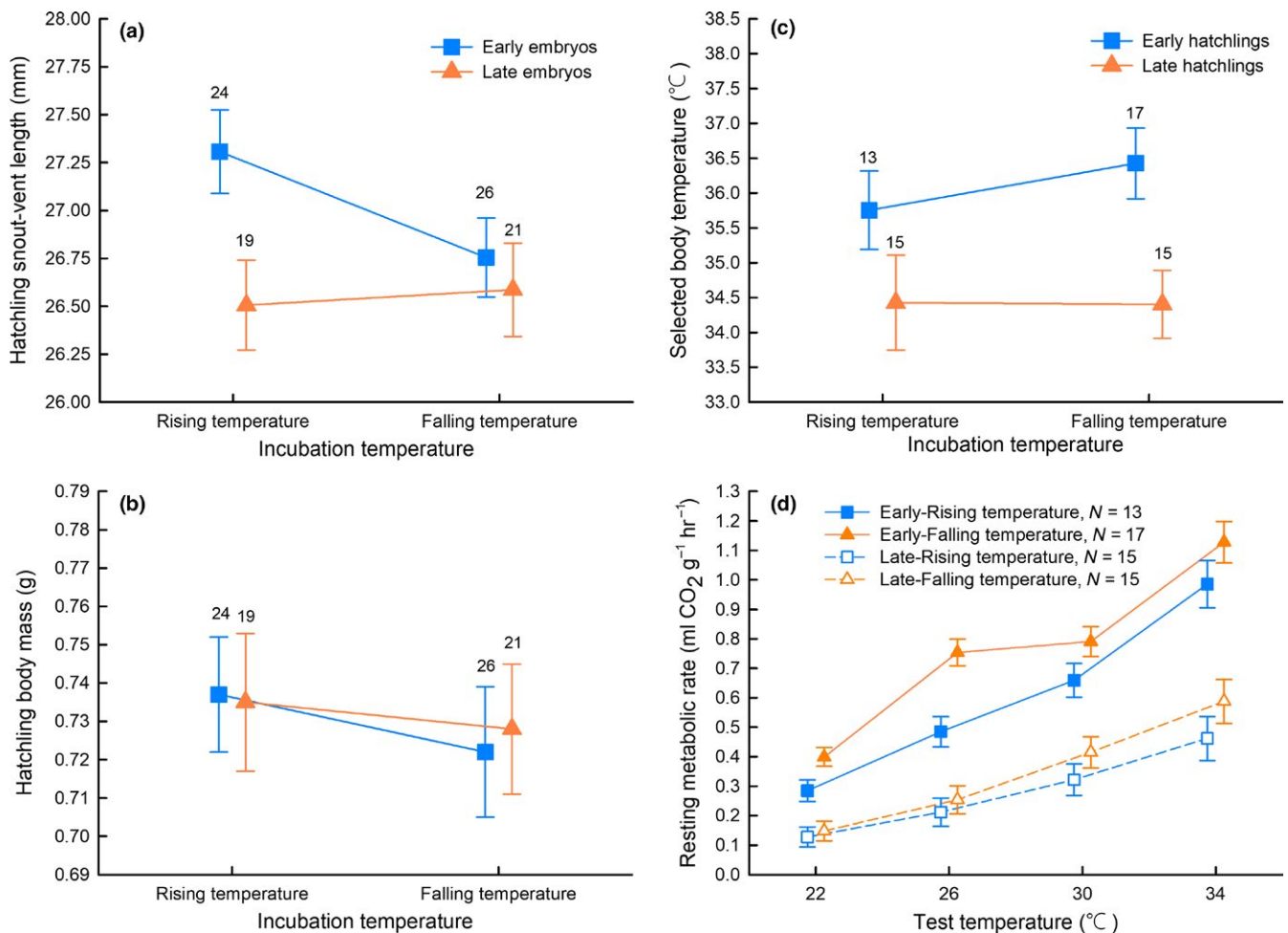


FIGURE 3 Snout-vent length (a), body mass (b), selected body temperature (c) and resting metabolic rates (d) of *Phrynocephalus przewalskii* hatchlings from early and late eggs incubated at rising and falling temperature regimes, respectively. The numbers above the bars indicate the sample size. Data are shown as least square means \pm SE

the interaction of reproductive timing and incubation temperature (Table 2; Figure 3a,b).

Hatchlings from early-breeding females had higher selected body temperatures (36.14 ± 0.38 °) than young from late-breeding females (34.33 ± 0.42 °), regardless of the incubation temperatures that was experienced (Table 2; Figure 3c). The RMR of hatchlings was significantly affected by reproductive timing and incubation temperature, but not by the interaction of these two factors (Table 2). Hatchlings from early-breeding females had higher average metabolic rates (0.686 ± 0.053 ml g^{-1} hr^{-1}) than young from late-breeding females (0.316 ± 0.052 ml g^{-1} hr^{-1}). Furthermore, hatchlings incubated at falling temperatures had higher average metabolic rates (0.560 ± 0.051 ml g^{-1} hr^{-1}) than young incubated at rising temperatures (0.442 ± 0.054 ml g^{-1} hr^{-1}) (Figure 3d).

The SGR of SVL and body mass were significantly affected by reproductive timing, incubation temperature and the interaction of these two factors (Table 2). The growth rate of hatchlings from early-breeding females were not different between rising (SVL: 0.0021 ± 0.0004 mm mm^{-1} day^{-1} ; BM: 0.0051 ± 0.0012 g g^{-1} day^{-1}) and falling incubation temperatures (SVL: 0.0019 ± 0.0003 mm mm^{-1} day^{-1} ; BM: 0.0047 ± 0.0011 g g^{-1} day^{-1}). However, hatchlings from

late-breeding females had a higher growth rate when incubated at falling incubation temperatures (SVL: 0.0023 ± 0.0004 mm mm^{-1} day^{-1} ; BM: 0.0038 ± 0.0013 g g^{-1} day^{-1}) than at rising incubation temperatures (SVL: 0.0002 ± 0.0004 mm mm^{-1} day^{-1} ; BM: -0.0036 ± 0.0013 g g^{-1} day^{-1}) (Figure 4a,b).

Reproductive timing and incubation temperature did not affect the survival rate of hatchlings before winter (Early-rising: 66.7%; Early-falling: 73.1%; Late-rising: 68.4%; Late-falling: 66.7%) ($X^2 = 4.99$, $df = 3$, $p > 0.05$). However, hatchlings from late-breeding females that were incubated under rising temperature regimes (10.5%) had lower post-hatching survival rates through the winter than early hatchlings developed at rising (37.5%) ($X^2 = 5.09$, $df = 1$, $p = 0.024$) or falling temperatures (38.5%) ($X^2 = 4.57$, $df = 1$, $p = 0.033$) (Figure 4c).

4 | DISCUSSION

Our experimental study allowed us to untangle intrinsic and extrinsic influences on offspring performance across the season, in an organism that has marked variation in reproductive timing across the season, which results in strong fitness consequences. We tested three

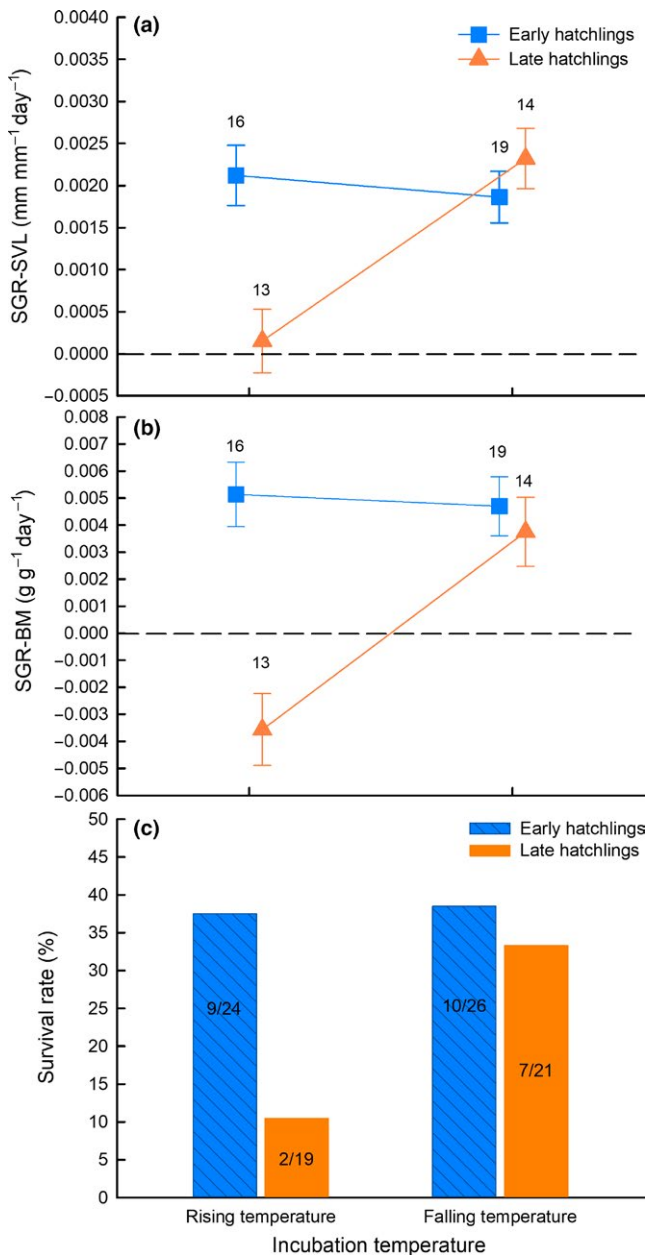


FIGURE 4 Specific growth rates (SGR) in (a) snout-vent length (SVL, mm mm⁻¹ day⁻¹) and (b) body mass (BM, g g⁻¹ day⁻¹) and (c) posthatching survival rate over winter of *Phrynocephalus przewalskii* hatchlings from early and late eggs incubated at rising and falling temperature regimes, respectively. The numbers above the bars in (a) and (b), and numbers in the volumes in (c) indicate the sample size. Data are shown as mean ± SE

alternate and nonexclusive hypotheses: (a) Early is higher quality; (b) Rising temperatures are better; and (c) Matching is better. Overall, we found the strongest support for “Early is higher quality,” suggesting that intrinsic (genetic plus parental) effects dominate variation in performance and fitness across the growing season in this species. Early- compared to late-breeding females produced embryos with shorter incubation duration, higher hatching success, resulting in faster growing and larger hatchlings with consistently high overwinter survival. Better performance of offspring from early-breeding

females will make them more competitive and valuable than late ones (Garcia-Navas & Jose Sanz, 2011; Olsson & Shine, 1997; Uller & Olsson, 2010; Verhulst & Nilsson, 2008; Warner & Shine, 2007). Consequently, early offspring, with greater fitness, have a disproportionately high contribution to population recruitment and seasonal declines in fitness of hatchlings are normal in oviparous species (Landa, 1992b; Reznick et al., 2006; Varpe, Jorgensen, Tarling, & Fiksen, 2007; Warner & Shine, 2007; Yamahira & Conover, 2002).

Performance advantages of offspring from early-breeding females may arise from genetic or maternal effects, because eggs were separated between temperature treatments after oviposition. In lizards and other oviparous species, oviposition timing is heritable and repeatable (Ljungström et al., 2015; Rutschmann et al., 2016; Saastamoinen & Hanski, 2008; Visser et al., 2011). For example, larger females in sand lizards generally lay eggs earlier, and the butterflies that can fly at low temperatures generally initiate oviposition earlier (Ljungström et al., 2015; Saastamoinen & Hanski, 2008). These results suggest that there could be genetic differences between early and late females. However, maternal effects on offspring performance are ubiquitous in lizards (Wang, Li, Zeng, Liang, & Du, 2017; Noble, Stenhouse, & Schwanz, 2018), and we consider maternal effects the most likely origin of the “early is higher quality” pattern that we observed. Greater body size of early-compared to late-breeding females likely gave rise to greater investment in embryos, leading to a higher hatching success (Uller & Olsson, 2010). Alternatively, late-breeding females experienced hotter temperatures during gestation, which may have imposed a negative effect on egg quality and hatchability (e.g., antioxidants and immune; Saino, Romano, Ambrosini, Ferrari, & Moller, 2004). However, the maternal thermal environment does not affect the hatching success of eggs within a wide range of temperatures (25–32°C) in *Takydromus* lizards (Du, Lu, & Shen, 2005). In this case, the effect of body temperature difference between early and late females (1.3°C) on egg hatchability, if any, would be trivial. We have focused on temperature as a key aspect of seasonality, but these maternal effects could have been influenced by other ecological factors such as food availability and predation risk, which also vary throughout the season, and likely contributed to seasonal variation in reproductive investment and offspring quality (Du, 2006; Varpe, 2017; Wang et al., 2017).

Mechanistically, the higher growth rates of early hatchlings may have resulted from higher selected body temperatures leading to higher metabolic rates. Higher body temperatures enhance energy assimilation (Qu, Li, Gao, Xu, & Ji, 2011) and rates of intermediary metabolism (Dmitriew, 2011; Stoks, De Block, & McPeck, 2006). The fitness consequences of higher rates of growth and metabolic processes could be context-dependent—providing better performance when food is abundant as in the current experiment, but imposing a cost if resources are limited (Glazier, 2015; Le Henanff, Meylan, & Lourda, 2013; Olsson & Shine, 1997).

We found no support for “Rising temperatures are better”—most traits we measured, including hatching success and hatchling size and mass, showed limited sensitivity to incubation temperature, suggesting a relative insensitivity to extrinsic effects. One exception was

incubation duration, which was faster under falling temperatures. The shortening of incubation duration confers selective advantages and is thus a mechanism to speed development prior to the onset of winter, because prolonged incubation increases the risk of embryos being exposed to predation or lethal extremes of temperature and moisture, and decreases the opportunity of prewinter growth and winter survival in many oviparous species (Olsson & Shine, 1997; Warner & Shine, 2007; While, Uller, McEvoy, & Wapstra, 2009). Moreover, early and late embryos shorten their incubation using different mechanisms under their natural (matched) temperature conditions. Embryos from late-breeding females with less advanced stages achieved shortened incubation duration at falling incubation temperatures (Figure 2a). In contrast, eggs from early-breeding females contained embryos in advanced developmental stages, which could shorten the incubation duration (Ma, Sun, Li, Sha, & Du, 2014; Sun et al., 2013).

Interestingly, we found some support for “Matching is better”: growth rate and hatchling survival over winter reacted differently to temperatures in early and late embryos, such that hatchlings from late breeders with generally lower qualities had much lower growth rate and survival than early embryos under early-season (rising) temperatures, but similar growth rate and survival under late-season (matching) temperatures. Our results indicate that late eggs have developed strategies to maximize offspring fitness in lizards, which minimize the costs of seasonal variation in reproductive timing. Higher quality early embryos could maintain performance across all incubation temperature environments, while lower-quality late embryos specialize on late-season environments in order to maximize performance. Early-breeding females may reproduce on the basis of both reserved resources and current acquisition (capital breeding), which enable them to allocate more resources to embryos that may perform well across all incubation temperature environments as a “generalist” (Ejsmond, Varpe, Czarnoleski, & Kozłowski, 2015; Varpe, 2017). In contrast, late-breeding females are more likely to reproduce with only current acquisition (income breeding) (Ejsmond et al., 2015; Varpe, 2017), which may constrain resource allocation, leading to low quality embryos. The lower-quality late-season embryos could be subject to a generalist–specialist trade-off, which prevents them from attaining high fitness across all incubation temperature environments and requires specialization (Angilletta, Wilson, Navas, & James, 2003).

The partial signature of temporal matching that we detected could arise through either genetic differences between late and early-breeding females, or through parental effects resulting from environmental conditions during gestation, including maternal provisioning and epigenetic modifications. Given that the early- and late-breeding mothers are different groups of females in our study, the seasonal variation might be due to genetic differences between early- and late-breeding females, but future research needs to verify this hypothesis. However, the reproductive periods of offspring from early- and late-breeding females overlap considerably (Li et al., 2018), suggesting that unless there is assortative mating then gene flow would likely prevent the adaptive differentiation of genes leading to temporal adaptation (Sultan & Spencer, 2002).

Maternal effect is another potential source of the temporal matching that we detected. Females might enhance metabolic rates

and growth rates of hatchlings by depositing different proportions of energetic and hormonal resources in eggs (i.e., maternal effect, Dmitriew, 2011; Reed & Clark, 2011). For example, female birds supply more testosterone to eggs laid later for the “catch-up” growth of chicks to compensate for the disadvantage of later hatching (Tomita et al., 2011). The metabolic regulation caused by plasticity could set the paces of energetic allocation, in turn control the rate of embryonic differentiation and development. Developmental temperature shapes mitochondrial function and the metabolic enzyme activity of embryos (Sun, Li, Gao, Ma, & Du, 2015), which potentially have carry-over effects to regulate the energetic metabolism of offspring (Seebacher & Grigaltchik, 2014; Watkins, 2000). The phenotypic effects of rising and falling temperatures might diverge between early and late eggs, if these eggs show different patterns in the plasticity of embryonic stage-dependent development in response to temperature (Eme et al., 2015).

5 | CONCLUSION

We found strong support for “early is high quality” in *P. przewalskii*, with a general advantage for early-season embryos throughout the season. Early vs. late temperature conditions had a relatively small effect on performance and fitness, suggesting that intrinsic factors mediated by maternal effects are likely the dominant factor driving variation in fitness across the growing season. However, we demonstrate that lower-quality late-season embryos have physiological strategies that are specialized to late-season environments, allowing them to attain similar fitness to early-season embryos. We conclude that physiology and phenology can be co-adapted to match offspring phenotypes to the selective environment that they experience during development in seasonal environments.

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AUTHOR CONTRIBUTIONS

B.-J.S., L.M., S.-R.L. and W.-G.D. conceived the ideas and designed methodology; B.-J.S., L.M., S.-R.L., X.H. and Y.W. collected the data; B.-J.S., C.M.W. and W.-G.D. analysed the data and led the writing of

the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dj7f25r> (Sun et al., 2018).

ORCID

Bao-Jun Sun  <http://orcid.org/0000-0002-7318-6059>

Caroline M. Williams  <http://orcid.org/0000-0003-3112-0286>

Wei-Guo Du  <http://orcid.org/0000-0002-1868-5664>

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