

# The high invasion success of fall armyworm is related to life-history strategies across a range of stressful temperatures

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## Abstract

**BACKGROUND:** Insects living in unfavorably high or low temperatures are predicted to display a fast or slow life-history strategy. Here, we examined life histories of fall armyworm (FAW), a globally important invasive species with a broad ecological niche, at five constant temperatures of 13, 19, 25, 31 and 37°C, to study life-history responses to different temperatures.

**RESULTS:** In our experiment, FAW had lower lifetime fecundity at unfavorable temperatures, a finding that is consistent with the idea that FAW can shift resources from reproduction to other functions under stressful conditions—such as heat or cold tolerance. Given the adverse effects of stressful temperatures, life-history strategies arise from individuals having limited remaining resources to allocate towards vital functions like survival or reproduction. Here we show plasticity in life-history strategies adopted at different temperatures. Rather than simply varying along a fast–slow continuum, FAW at unfavorably high temperatures exhibited lower daily fecundity and longer reproductive lifespans, and at unfavorably low temperatures showed a shorter peak in reproduction later in life, compared with FAW at 25°C. Such patterns, if adaptive, could suggest a strategy mitigating reproductive and mortality risk in unfavorable environments, however, this remains to be tested.

**CONCLUSION:** Our analysis suggests that the high invasion success of FAW may result from their ability to adjust life-history strategies, across a range of stressful temperatures, in a way that reduces not only mortality, but also fecundity loss. The adoption of such strategies may be instrumental for the global invasion success of FAW.

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**Keywords:** life-history strategy; lifespan; reproduction; *Spodoptera frugiperda*; survival

## 1 INTRODUCTION

How the life histories of invasive insects change in response to environmental variation is critical for determining whether such species are likely to have a significant economic impact under local environmental conditions.<sup>1,2</sup> For insects, temperature is a key environmental factor that impacts their life-history strategy, that is, the combination of the timing of growth, survival and reproduction.<sup>3,4</sup> At unfavorable temperatures, invasive insects may lower fecundity by shifting resources from reproduction to heat or cold tolerance.<sup>5,6</sup> Given the adverse effects of stressful temperatures, variation in life-history strategies can arise from individuals having limited resources to allocate towards vital functions such as survival or reproduction.<sup>7,8</sup> A commonly seen pattern is that life-history strategies move along a fast–slow continuum in response to stressful temperatures. At high temperatures insects display a fast strategy characterized by early reproduction and shorter reproductive lifespans, whereas at low temperatures they display a slow strategy characterized by delayed reproduction and longer reproductive lifespans.<sup>9,10</sup> Because trade-offs between reproduction and survival are pervasive, the repertoire of life-history strategies are constrained and

thus can be described accurately along a single axis with high allocation to reproduction at one end and high allocation to survival at the other.<sup>11</sup> Despite considerable empirical support for the link between temperature and fast or slow strategies,<sup>12</sup> it has become evident that this pattern is not ubiquitous. An alternative strategy that has also been documented, is one that allows individuals to

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mitigate increased mortality while also maintaining reproductive output.<sup>13–15</sup> Understanding the physiological relationship between temperature and life-history strategies is key to predicting population outbreaks worldwide and ensuring timely pest management.<sup>16</sup>

Overlaying this general relationship between temperature and life-history strategy it has also been suggested that invasive species demonstrate faster life histories than their non-invasive counterparts.<sup>17,18</sup> This is because early reproduction is likely to be favored when populations are yet to reach carrying capacity and in stressful environments where there is increased mortality risk. However, studies are emerging that show not all invasive species necessarily adopt strategies consistent with a fast life history.<sup>19,20</sup> Some cross-species comparisons provide evidence that long-lived species with slow life histories are also able to establish stable populations in invaded environments.<sup>21,22</sup> Recent population comparisons, by contrast, show that within species, invasive populations exhibit “trade-off” life-history strategies compared with native populations.<sup>23</sup> However, neither type of study provides information about cause and effect. Are species with certain life histories more likely to be invasive? Or are species that become invasive selected to have specific life-history strategies? To predict which species are more likely to become invasive and how populations of species that are invasive are likely to respond to differing local conditions it is necessary to document within-species life-history responses to differing temperatures.

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), is a pest noctuid moth that damages more than 353 plant species, but prefers maize.<sup>24</sup> For maize alone, economic losses from FAW can reach between 15% and 73% worldwide.<sup>25–27</sup> Native to the Americas, FAW lives year-round in tropical and subtropical regions and undergoes seasonal migrations as far north as temperate North America.<sup>28–30</sup> Outside their native distribution, FAW are highly invasive. After recent introductions into West Africa in 2016,<sup>31–34</sup> southwest India in 2018,<sup>35–37</sup> and China in 2019,<sup>38,39</sup> FAW has spread to neighboring countries at an alarming rate.<sup>40–43</sup> Covering an impressive range of climatic and ecological conditions, FAW is an excellent model species that can be used to test for plastic life-history responses to temperature. At present, global agriculture is under increasing threat from FAW. Given the rapidly escalating economic impact, FAW has long been used for laboratory research. Over the course of laboratory rearing, 25°C is largely recognized as close to the FAW optimal temperature for growth, survival and fecundity.<sup>44,45</sup> Our baseline assumption is that FAW at 25°C show a normal life history and thus can act as an appropriate control group to compare with FAW housed at other temperatures.

The routes taken during the course of FAW invasion have been reconstructed meticulously.<sup>46,47</sup> Previous studies have notably shown that the vast majority of invasive populations in Africa and subsequently in Asia were native to the Americas, and acted as a bridgehead for further invasion.<sup>48</sup> FAW have a wide niche in their native area and possibly worldwide, covering an impressive range of temperature conditions.<sup>49</sup> This broad ecological distribution poses the question of whether FAW invasion success results (at least in part) from its ability to respond to extreme temperature variation. By comparing key life-history traits of FAW (total and reproductive lifespan, age at the start of reproduction, and total and daily fecundity) at a range of temperatures, we addressed the question: does variation in temperature cause FAW life histories to vary along a fast–slow continuum, with individuals at high temperatures (37 and 31°C) having early reproduction and

shorter reproductive lifespans, and individuals at low temperatures (19 and 13°C) having delayed reproduction and longer reproductive lifespans? Or alternatively, do FAW show other kinds of life-history strategies? Our analysis reveals the types of life-history strategies likely to be linked to successful invasion, which will be helpful for developing a FAW forecasting program and improving FAW management in global agriculture.

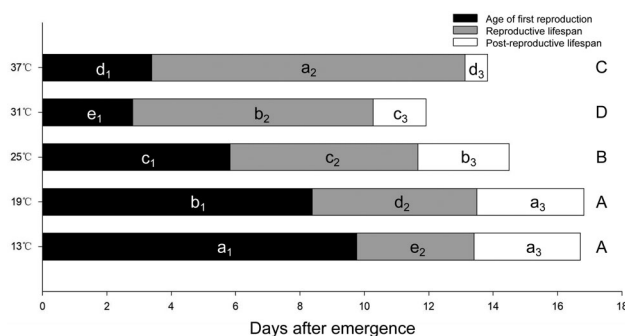
## 2 MATERIALS AND METHODS

### 2.1 Biological material and experimental design

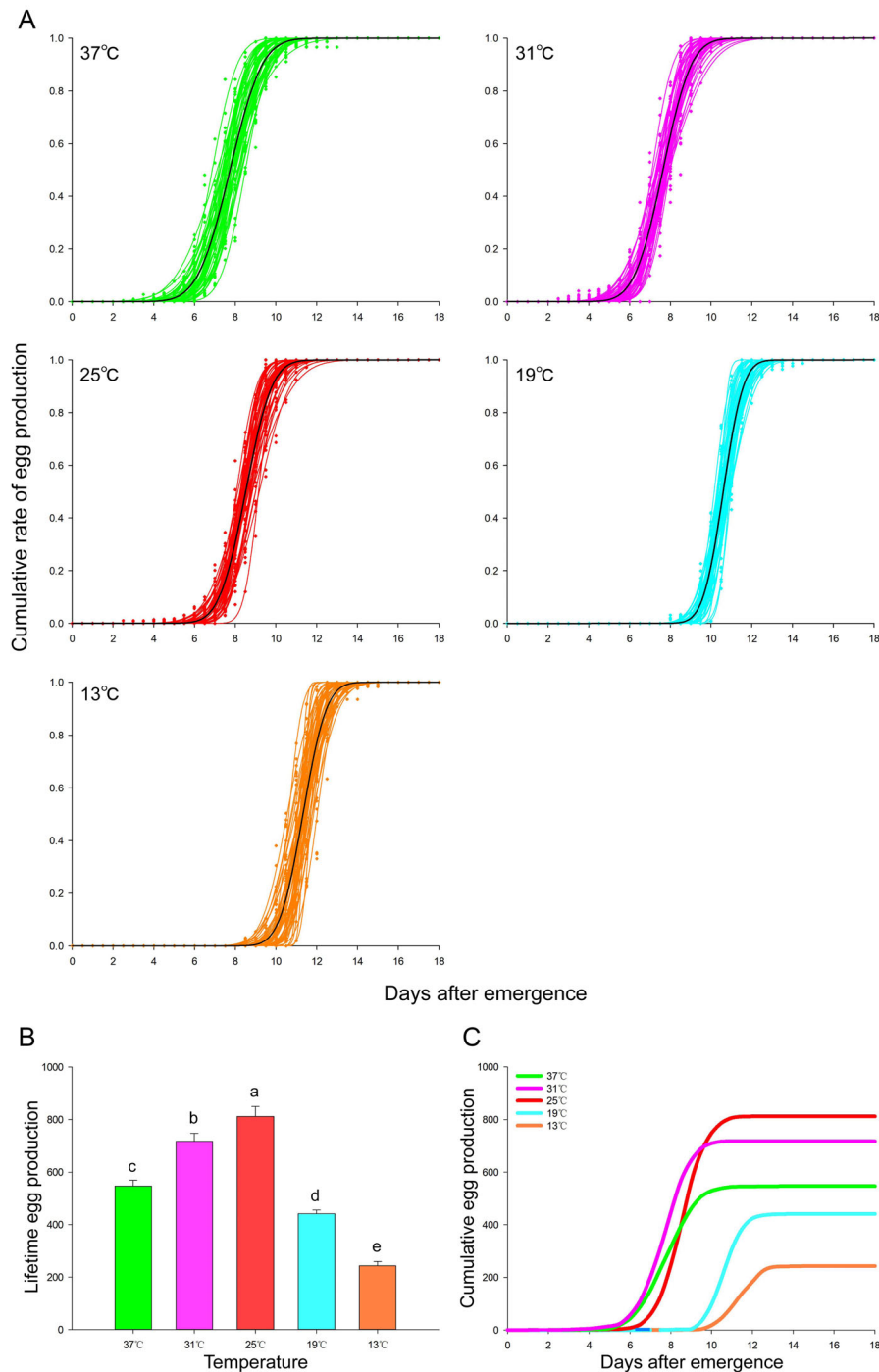
Fall armyworm larvae were obtained from Hengcao Biotechnology Co Ltd. Larvae were individually reared within compartments in a plastic container (40 × 38 × 4 cm high), on a modified artificial diet of wheatgerm, soybean bran, casein and brewer's yeast (Figure S1). Emerging FAW adults were then paired and introduced into a plastic container (16 × 22 × 8 cm high), where they were provided with honey diluted at 10%, once a day. FAW were bred in this way for three generations, in a strictly controlled environment (25 ± 1°C, 75% ± 5% relative humidity [RH], 16:8 h light/dark photoperiod), prior to our experiment.

After three generations, 120 newly emerged (<24 h) adults (1:1 sex ratio) were isolated and transferred to incubators (KBF720, Binder) where they were kept at one of five constant temperatures (37, 31, 25, 19 and 13°C, each ± 0.2°C) under 75% ± 5% RH and a 16:8 h light/dark photoperiod (120 adults × 5 temperatures = 600 adults in total). The 25°C condition corresponds to that used for the rearing of laboratory populations and is largely recognized as close to the species' optimal conditions for growth, survival and fecundity<sup>44,45</sup> and can thus be considered a control.

To determine the life-history strategy of adult females kept at each temperature, females were each introduced into individual plastic containers (16 × 22 × 8 cm high), with a randomly selected male from the same temperature, and fed daily with honey (diluted to 10%). The experimental females were then monitored from emergence to death—recording survival and the number of eggs laid each day. This allowed us to calculate key adult life-history traits, including: total fecundity, daily fecundity, age at the start of egg laying, and reproductive and adult lifespans. The experiment was conducted in two temporal blocks, and thus different populations were provided. In each block,



**FIGURE 1.** Reproductive schedules for fall armyworm (FAW) kept at five different temperatures. Mean time in days for age of first reproduction (black), reproductive lifespan (gray), post-reproductive lifespan (white) and adult lifespan (all portions of the bar combined) for females at 37, 31, 25, 19 and 13°C. Different lower case letters indicate significant differences within a life-history category, and different upper-case letters represent significant differences across the full adult lifespan.



**FIGURE 2.** Lifetime reproduction dynamics for fall armyworm (FAW) females at five temperatures. (A) Temporal allocation of egg production. Colored points and curves represent individuals' cumulative proportion of eggs produced over time. For each individual, data are fitted with the cumulative density function of a normal distribution with mean  $\mu$  and standard deviation  $\sigma$ . Black curves are obtained using the average values of  $\mu$  and  $\sigma$  for each temperature treatment. (B) Mean lifetime egg production per temperature treatment (with 95% confidence intervals). Data are from 231 individuals ( $n_{37^\circ\text{C}} = 47$ ,  $n_{31^\circ\text{C}} = 43$ ,  $n_{25^\circ\text{C}} = 43$ ,  $n_{19^\circ\text{C}} = 48$ ,  $n_{13^\circ\text{C}} = 50$ ). Different letters indicate significant differences among temperatures. (C) Schematic representation of lifetime dynamics of cumulative egg production at each temperature. The curves were obtained as the product of average allocation schedules (black curves in A) and average lifetime fecundities (B).

60 individuals (1:1 sex ratio) were kept in each of the five constant temperature treatments (300 adults in total).

## 2.2 Statistical analyses

We collected the summary statistics for measured traits (Table S1), and analyzed these traits using mixed-model analyses of variance.

Response variables were transformed when required to improve normality and reduce heteroscedasticity of the residuals. Models included temperature (37, 31, 25, 19 and 13°C) as a fixed effect, population nested in temperature and block as random effects (Table S2).

To illustrate more clearly how female investment in reproduction varied across time, individual fecundity data (Figure S2) were

transformed into the rate of egg production by dividing each female's daily egg production by their lifetime production. For each female, the dynamics of the cumulative reproductive rate over time were then fitted with the cumulative density function of a normal distribution with mean  $\mu$  and standard deviation  $\sigma$  via nonlinear regression. Biologically,  $\mu$  and  $\sigma$  represent the age at peak fecundity and the duration of peak fecundity, respectively (Figure S3 and Table S3).<sup>50</sup> The distribution of both traits was analyzed after proper transformation. The traits of all temperature treatments were positively correlated (Pearson's correlation coefficient  $r = 0.599$ ,  $p < 0.0001$ , after log-transformation for  $\mu$  and square-root transformation for  $\sigma$ ), and within each temperature treatment ( $r_{37^\circ\text{C}} = 0.787$ ,  $r_{31^\circ\text{C}} = 0.898$ ,  $r_{25^\circ\text{C}} = 0.929$ ,  $r_{19^\circ\text{C}} = 0.743$ ,  $r_{13^\circ\text{C}} = 0.831$ ; Figure S4). For each trait ( $\mu$  and  $\sigma$ ), differences between temperatures were thus examined using analysis of covariance (ANCOVA; the other trait as independent variable, and temperature as factor) after Box–Cox transformation of the response variable and withdrawal of outliers. When the duration of fecundity peak ( $\sigma$ ) acted as the response variable, there was a significant interaction between the age at peak fecundity ( $\mu$ ) and temperature ( $p$  of temperature  $\times \mu < 0.0001$ , Figure S4 and Table S4). We then focused on the pairwise comparisons of temperatures using the same approach (Table S5). A similar protocol was used with the variable order reversed: when the age at fecundity peak ( $\mu$ ) acted as the response variable, the interaction between the duration of fecundity peak ( $\sigma$ ) and temperature was also significant ( $p$  of temperature  $\times \sigma < 0.0001$ , Table S6). Then we further made comparisons between pairs of temperatures (Table S7).

### 3 RESULTS

#### 3.1 FAW do not show fast life histories at high temperatures

Examining the traits (daily and total fecundity, age of first egg production, reproductive and adult lifespan; Table S1) showed substantial differentiation in life-history strategies among the five temperatures. We found that all examined traits varied by temperature, whereas within temperature there were no significant differences between populations (Table S2).

Compared with control groups (25°C), the total fecundity of FAW females at unfavorably high temperatures (37°C and 31°C) was lower, and so was the mean daily fecundity (Table S1). FAW females at high temperatures started reproducing earlier, and also had a shorter adult lifespan (Figure 1 and Table S1). However, contrary to a classic fast life history, which is characterized by shorter reproductive lifespans, FAW females at high temperatures showed a prolonged reproductive lifespan (Figure 1 and Table S1). Our results further suggested that females living at high temperatures reached peak fecundity earlier but spread their egg production over a longer period than control groups (Figure 2, Tables S3, S5 and S7).

#### 3.2 FAW do not show slow life histories at low temperatures

At unfavorably low temperatures (19°C and 13°C) FAW females had lower lifetime egg production and lower mean daily production (Table S1). FAW females living in low temperatures initiated reproduction later than control groups and had a longer adult lifespan (Figure 1 and Table S1). However, in contrast to a typically slow life-history strategy, which is characterized by longer reproductive lifespans, FAW females at low temperatures had a

shortened reproductive lifespan (Figure 1 and Table S1). Further, FAW females at low temperatures concentrated their egg production around a fecundity peak that was both later and briefer than in control groups (Figure 2, Tables S3, S5 and S7).

#### 3.3 Intermediate life histories in FAW at 31 and 19°C

The impact of temperature on the life histories of FAW is a gradual process. FAW females at 31°C or 19°C showed intermediate values between those at 37°C and control groups (25°C), or between those at 13°C and control groups, in many key life-history traits such as reproductive lifespan, daily and total fecundity (Figures 1 and 2, and Table S1). For  $\mu$  (age at peak fecundity) and  $\sigma$  (duration of fecundity peak), FAW females at 31°C/19°C displayed intermediate values between control groups and females at 37°C/13°C (Figure 2 and Table S3). For the other traits (that is, age at the start of reproduction and adult lifespan), FAW females at 31 and 19°C shared the same value as those at 37 and 13°C, respectively (Figure 1 and Table S1).

#### 3.4 FAW overall exhibit plastic responses to unfavorable temperatures

Overall, the life-history strategy of FAW at high or low temperatures is very different from a typically fast (early reproduction and shorter reproductive lifespans) or slow (delayed reproduction and longer reproductive lifespans) life history. FAW females adopted a life-history strategy characterized by early reproduction but elongated reproductive lifespans at high temperatures, and by delayed reproduction but shortened reproductive lifespans at low temperatures (Figure 2 and Table S3). These life histories may reflect strategies that are selected to mitigate reproductive and mortality risk in unfavorable environments, although the adaptive significance of this variation remains to be tested.

### 4 DISCUSSION

Being heterothermic poikilotherms, insects are very sensitive to variations in temperature. In many insects, including those that are invasive, temperature affects traits such as growth, survival and reproduction.<sup>51,52</sup> Thus the population dynamics of these insects are largely dependent on temperature. Accordingly, there has long been considerable interest in the relationship between temperature and the life histories of invasive pests, with the aim of predicting outbreaks and population dynamics.<sup>53,54</sup>

Many studies indicate that life-history traits, especially reproduction, are adversely affected by unfavorable temperatures.<sup>12,55</sup> In accordance with this, we found FAW had greatly reduced fecundity at unfavorable temperatures. One possible explanation for this is that FAW are inefficient at acquiring resources at unfavorable temperatures.<sup>56,57</sup> Another plausible explanation for low fecundity in FAW kept at unfavorable temperatures lies in a possible shift of resources between fecundity and heat/cold tolerance. Indeed, previous empirical studies have shown that insects shift resources from reproduction towards heat or cold tolerance at unfavorable temperatures.<sup>56</sup> Therefore, a similar shift may drive FAW fecundity differences between 25°C and unfavorable temperatures. Another explanation could involve trade-offs between larval and adult performance; however, in our experiment individuals all experienced the same rearing conditions and those experiencing different adult temperature treatments did not differ in larval traits (egg hatching and larval survival) (Figure S5).

Thus, a trade-off between larval and adult performance is unlikely to explain our results.

Because of the adverse effects of stressful temperatures, the life-history strategies of ectotherms are expected to covary with temperature, and many species experiencing unfavorable temperatures adopt a classic fast or slow strategy. At high temperatures, they generally display fast strategies characterized by early reproduction and shorter reproductive lifespans, which increase reproductive output at the cost of reduced longevity. At low temperatures, by contrast, they display slow strategies characterized by delayed reproduction and longer reproductive lifespans, which increase survival at the cost of lower fecundity.<sup>9,10,22</sup> Although our results indicated a strong effect of temperature on the life-history strategy of FAW, it did not vary along the expected fast–slow continuum. Instead, FAW in our experiment adopted life-history strategies characterized by early reproduction combined with elongated reproductive lifespans at high temperatures, and by delayed reproduction combined with shortened reproductive lifespans at low temperatures. Why FAW adopt such strategies at unfavorable temperatures, rather than a classic fast or slow one remains to be tested.

When exposed to unfavorable temperatures, FAW may allocate limited resources to either survival or reproduction by altering their life-history strategy, thus altering their life history along a fast–slow continuum. Here, we additionally showed that at high and low temperatures FAW showed a shift in the timing and duration of egg production, from elongated to shortened reproductive lifespans, a strategy that could reduce not only mortality, but also fecundity loss. At unfavorably high temperatures, FAW with early reproduction may have high fecundity, and reproductive lifespan extension may reduce mortality by preventing total lifespan shortening. Besides, prolonged reproduction may facilitate invasion success by mitigating the effects of reproductive failure associated with maladaptation to a novel environment.<sup>58</sup> At unfavorably low temperatures, high survival could be selected for via delayed reproduction, and reproducing quickly may minimize the amount of time spent at a demographically precarious small population size, and thus promote successful invasion.<sup>18</sup> The ability of FAW to adjust their life histories in this way may be instrumental for their high invasion success. However, the life-history strategies shown here at stressful temperatures in the laboratory need to be confirmed with further field investigations. Laboratory results cannot be directly extrapolated to field populations because laboratory experiments are simplified systems.<sup>59,60</sup> Moreover, determining whether the strategies shown here are instrumental in FAW invasion success would require experimental releases. Additional study on life-history strategies of other closely related moth species living in unfavorable temperatures would help confirm if this strategy is general.

Noticeably, FAW individuals at 31°C or 19°C showed an intermediate fecundity and life history between those at 37°C and control groups (25°C), or between those at 13°C and control groups, respectively. A temperature of 31°C or 19°C seems to be favorable relative to that of 37°C or 13°C. This suggests that FAW populations in temperate regions may be more invasive than those in tropical and cold-temperate regions. We would predict that despite the wide niche covering diverse climatic and ecological environments, FAW may be more devastating to temperate regions (around 24°N and 24°S latitudes) than tropical and cold-temperate regions. Our prediction has been confirmed by data of FAW native distribution which suggests the populations in southern North America (around 25°N latitude) and central South

America (around 23°S latitude) pose more of a problem than do other native populations.<sup>49</sup> We would therefore expect this prediction to be robust to the inclusion of more regions.

In conclusion, our analysis cements the idea that the life-history strategies of FAW are phenotypically plastic, and are shaped by the temperature environment that individuals experience. Such plasticity is likely to have played an instrumental role in determining the success of this highly invasive species. However, during invasion the ways that life histories shift at unfavorable temperatures seem more complex than once thought, with a simple selection for a fast or slow life-history strategy not found in all species. Therefore, our results highlight that the high invasion success of FAW is not due to having life histories along the fast–slow continuum, but may result from their ability to adopt life-history strategies that reduce not only mortality, but also fecundity loss, when experiencing unfavorable conditions. The adoption of such strategies may be instrumental for the global invasion success of FAW.

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## CONFLICTS OF INTEREST

The authors declare that they have no conflict of interests.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://datadryad.org/stash/share/VZ1eoA50BJ3-ZRVGDiff4yDt66Qc49o32WC9sxddfNw>, reference number <https://doi.org/10.5061/dryad.2jm63xsq7>.

## SUPPORTING INFORMATION

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

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