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Phil. Trans. R. Soc. B 2009 **364**, 1049-1058
doi: 10.1098/rstb.2008.0251

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The influence of context-dependent maternal effects on population dynamics: an experimental test

S. J. Plaistow^{1,*} and T. G. Benton²

¹*School of Biological Sciences, University of Liverpool, Biosciences Building, Crown Street, Liverpool L69 7ZB, UK*

²*Institute of Integrative & Comparative Biology, University of Leeds, Miall Building, Leeds LS2 9JT, UK*

Parental effects arise when either the maternal or paternal phenotype influences the phenotypes of subsequent generations. Simple analytical models assume maternal effects are a mechanism creating delayed density dependence. Such models predict that maternal effects can very easily lead to population cycles. Despite this, unambiguous maternal-effect mediated cycles have not been demonstrated in any system. Additionally, much evidence has arisen to invalidate the underlying assumption that there is a simple positive correlation between maternal performance and offspring performance. A key issue in understanding how maternal effects may affect population dynamics is determining how the expression of parental effects changes in different environments. In this study, we tested the hypothesis that maternal effects influence population dynamics in a context-dependent way. Populations of the soil mite, *Sancassania berlessei*, were set up at high density (500 eggs) or low density (50 eggs), with eggs that were either laid by young mothers or old mothers (a previously documented maternal effect in this system). The influence of maternal age on both population and egg and body-size dynamics was only observed in the populations initiated under low density rather than high density. This difference was attributable to the context-dependence of maternal effects at the individual level. In low-density (high food) conditions, maternal effects have an impact on offspring reproductive performance, creating an impact on the population growth rate. In high density (low food), maternal effects impact more on juvenile survival (not adult size or reproduction), creating a smaller impact on the population growth rate. This context dependence of effects at the population level means that, in fluctuating populations, maternal effects cause intermittent delayed density dependence that does not lead to persistent cycles.

Keywords: parental effects; population dynamics; the maternal effect hypothesis; life-history; soil mites; context-dependence

1. INTRODUCTION

Parental effects arise when parental phenotypes influence offspring phenotypes over and above directly transmitted genetic effects (Falconer 1989; Mousseau & Fox 1998*a,b*; Uller 2008). Interest in the influence that parental effects have on population dynamics can be traced as far back as Park's (1935) demonstration that changes in the quality of the maternal environment of flour beetles had considerable consequences for the fitness of the offspring. Later, important work by Wellington (1957) and Chitty (1960) emphasized the importance of 'individual quality' for population dynamics; however, Leslie (1959) was the first to explicitly consider maternal effects (as a mechanism creating differences between cohorts of individuals born at different times) from a population-dynamic perspective (Beckerman *et al.* 2002). The subsequent realization that delayed density dependence can destabilize population dynamics and in some cases, promote cyclic dynamics (May 1974; Schaffer & Kot 1986; Turchin

1990; Berryman 1992), led to a resurgence of interest in maternal effects at the population level (Rossiter 1991, 1994; Ginzburg & Taneyhill 1994; Crone & Taylor 1996; Crone 1997; Ginzburg 1998; Inchausti & Ginzburg 1998; Ginzburg & Colyvan 2004).

The 'Maternal effects hypothesis' proposes that a positive correlation between maternal quality and offspring quality causes populations to cycle (Boonstra & Boag 1987; Rossiter 1994; Boonstra *et al.* 1998). Using a simple, unstructured, deterministic model, Ginzburg & Taneyhill (1994) successfully modelled the multi-generational cycling often found in populations of forest Lepidoptera. Later, Inchausti & Ginzburg (1998) provided further support for the maternal effects hypothesis by successfully modelling small mammal cycles in Northern Europe. However, the maternal effect hypothesis remains controversial since natural cycles in abundance may have alternative causes, such as an inter-cohort dynamics or trophic interactions (Krebs *et al.* 1995; Hudson *et al.* 1998; Hanski *et al.* 2001; Smith *et al.* 2006). For example, a key prediction of the Ginzburg formulation of the maternal effects hypothesis was purported to be that the cycle periods occurring between two and six generations will never be observed (Ginzburg & Colyvan 2004). However,

* Author for correspondence (s.plaistow@liv.ac.uk).

One contribution of 12 to a Theme Issue 'Evolution of parental effects: conceptual issues and empirical patterns'.

Greenman *et al.* (2005) showed that such a gap in periodicity is a general feature of single-species, discrete-time, structured models, whether or not they incorporated a maternal effect. Therefore, observation of long-period cycles does not necessarily implicate maternal effects. Moreover, distinguishing between alternative hypotheses contributing to cyclical dynamics can be extremely difficult, particularly when more than one mechanism is in operation within the same population (but see Kendall *et al.* 2005). In short, the generality of the maternal effects hypothesis has been questioned because: (i) most organisms do not show cyclical population dynamics (Benton *et al.* 2001), (ii) early maternal effects' models are over simplistic (Benton *et al.* 2001), (iii) field studies have often failed to detect maternal effects (Weiner *et al.* 1997; Myers *et al.* 1998; Ergon *et al.* 2001*a,b*; Banks & Powell 2004), (iv) the assumptions of the early maternal effects models were never properly tested (Plaistow *et al.* 2006).

Normally, maternal effects are modelled as a single generation, positive association between the average quality of the parental generation and the average quality of their offspring (Ginzburg & Taneyhill 1994; Inchausti & Ginzburg 1998; Benton *et al.* 2001; Kendall *et al.* 2005). The simplicity of these models is underpinned by the assumption that parents in low-density cohorts are in better condition and give rise to higher quality offspring than parents in high-density cohorts. However, as the interest in maternal effects as adaptations has grown, and researchers have studied them in more detail (Mousseau & Fox 1998*a*; Marshall & Uller 2007; Räsänen & Kruuk 2007), our understanding of the nature of maternal effects has changed. For example, we now know that maternal effects sometimes have a negative effect on the fitness of offspring (Bernardo 1996*b*; Einum & Fleming 2000; Mayhew 2001; Plaistow *et al.* 2006; Marshall & Uller 2007); that maternal effects may often last for longer than a single generation and interact in complex ways (Bernardo 1996*a*; Fox & Savalli 1998; Hercus & Hoffman 2000; Magiafoglou & Hoffmann 2003); and that the expression of maternal effects may be context-dependent, influencing different traits and creating different patterns of trait (co)variation in different environments (Berven 1990; Gliwicz & Guisande 1992; Parichy & Kaplan 1992; Bernardo 1996*b*; Rossiter 1998; Czesak & Fox 2003; Lardies *et al.* 2004; Marshall & Keough 2004; Räsänen *et al.* 2005; Plaistow *et al.* 2006; Marshall & Uller 2007), or even disappearing in some environments (Weiner *et al.* 1997; Rossiter 1998; Ergon *et al.* 2001*a*). Maternal effects may also be dynamic in some instances, with mothers changing how they provision their offspring over time or in different environments (Marshall & Keough 2006; Plaistow *et al.* 2007), and may result from the combined effect of selection on maternal or offspring strategies (Uller 2008). Given that maternal effects are far more complex in reality than a simple positive correlation between maternal and offspring quality, the simple 'maternal effects create cycles' hypothesis is clearly undermined. This begs the question 'do maternal effects contribute to variation in population dynamics, and if so, how?'

Rossiter (1998) stated that 'our difficulty in determining the contribution of maternal effects to fitness is at least partly due to our inability to understand how the expression of parental effects can be modified by the environment'. If we replace the word 'fitness' with 'population dynamics' then we very much set the scene for this paper. From a population dynamic perspective, context-dependent and dynamic maternal effects are particularly important because the very life-history traits that are affected (e.g. survival, offspring size and number), can themselves determine the subsequent environment that mothers experience and respond to (Park 1935; Beckerman *et al.* 2005; Benton *et al.* 2005; Plaistow *et al.* 2007). Thus, complex maternal effects will lead to complex patterns in the dynamics, feeding, in turn, into complex patterns of phenotypic dynamics. Consequently, there is a real need to characterize and quantify context-dependent maternal effects over time in different systems (Plaistow *et al.* 2006; Marshall & Uller 2007). Such investigations really need to be experimental (Rossiter 1994), because statistical modelling of censused populations in the field will rarely (if ever) have the power to separate maternal effects from changes in other extrinsic and intrinsic aspects of the immediate neonate environment (Albon *et al.* 1987; Lindström 1999). However, experiments on populations in the field are often fraught with practical difficulties leading to small sample sizes (of individuals or population-level replication) and therefore often have low power. Field-based experimental approaches have included switching offspring between their natal environment and some other environment (Mihok & Boonstra 1992; Myers *et al.* 1998; Ergon *et al.* 2001*a*), while others have manipulated maternal condition (Banks & Powell 2004). Typically, maternal effects were not detected in these field-based studies. This could be because maternal effects were swamped by an individual's response to the current environment (Ergon *et al.* 2001*a*; Banks & Powell 2004). Alternatively, it could be that the small number of traits measured in these studies, and the limited range of environmental conditions in which they occurred, were often not sufficient to detect context-dependent maternal effects.

Our approach is therefore to study maternal effects experimentally using easily manipulated, replicable, populations of an invertebrate in controlled environmental conditions. This approach allows us to conduct experiments at the individual and population levels and therefore dissects the population level consequences of maternal effects in a finer way than is otherwise possible.

(a) *Maternal effects in soil mites*

The soil mite, *Sancassani berlesei*, is an ideal system in which to study maternal effects. At the population level, initiating populations with eggs laid by different types of mothers enables us to study the influence that maternal provisioning of offspring has on transient population dynamics. For example, populations that were initiated with different sized eggs had different transient population dynamics for at least three generations (Benton *et al.* 2005). Populations initiated with eggs that are the same size, but laid by different

aged mothers, showed a similar response (Benton *et al.* 2008). The population dynamical effects appear to arise via two mechanisms. Firstly, maternal effects alter the competitive environment for offspring generating cohort effects (Beckerman *et al.* 2005). Secondly, studies at the individual level show that the maternal effects may last for multiple generations and interact in complex ways (Plaistow *et al.* 2004). A fully factorial, multi-environment study showed that when multiple traits were measured, an environmental perturbation that generated maternal effects (i.e. caused females to lay different types of eggs) was still detectable in the life histories of descendents three generations later (Plaistow *et al.* 2006). In high-food environments, the maternal effect primarily influenced a tradeoff between fecundity and survival and resulted in increasing differences in the average size of eggs that females in different treatment groups laid over the course of the experiment. By contrast, in low-food environments the maternal effect had little influence on the size of the eggs that females laid, consequently the egg size converged over the course of the experiment. In another experiment, an age-related dynamic shift in the size and number of eggs that soil mites laid was also greater in high-food environments compared to low-food environments (Plaistow *et al.* 2007).

Our individual-level studies of soil mites suggest that the exaggeration and the transmission of differences in egg size and number from one generation to the next increases in high-food environments, but decreases in low-food environments. Consequently, we hypothesized that maternal effects would be more likely to persist, and have a bigger influence on population dynamics, in high-food environments compared to low-food environments (Plaistow *et al.* 2006). In this study, we tested this hypothesis. We created maternal effects by initiating populations with eggs from young mothers or old mothers (see Benton *et al.* (2008) for details of the maternal-age effect) and we varied the food environment by changing the initial density from high (500 eggs) to low (50 eggs). This study is different from our previous population experiments (Benton *et al.* 2005, 2008) because on this occasion, we also manipulated the environmental context (high and low density) in which an artificially created maternal effect operated. We predicted that the transient population dynamics of populations initiated with eggs from young and old mothers at a high density (high competition and thus low-food environment) would be more similar than the transient population dynamics of populations initiated with eggs from young and old mothers at a low density (high-food environment).

2. MATERIAL AND METHODS

(a) *Study organism*

Soil mites, *S. berlessei* (Michael), are commonly found in soil, poultry litter and stored food products. Our populations were first collected in an agricultural manure heap in 1996, 1998 and 2002 and have been kept in stock cultures (approx. $1\text{--}2.5 \times 10^{-5}$ individuals) ever since. Stocks are fed a level half-teaspoonful of yeast granules per day, and so the populations equilibrate around a food-limited carrying capacity (as evidenced by the small size of individuals when they are removed from the stock culture). The life cycle consists of five

stages. Eggs hatch and emerge as six-legged larvae before moulting into protonymph, tritonymph and finally an adult (females: 0.79 ± 0.17 mm, range 0.47–1.17 mm, $n=64$; males: 0.72 ± 0.11 , range 0.55–1.02 mm, $n=39$). Eggs typically hatch 2–5 days after being laid, and maturation can occur from 4–50 and more days after hatching (Beckerman *et al.* 2003). Females typically live for approximately 10–25 days depending upon environment and rates of offspring provisioning (see Plaistow *et al.* 2007).

(b) *Experimental set up*

In order to obtain enough eggs to set up the population experiment, 150 males and 150 females were taken from stock cultures that had been maintained at equilibrium since 2002 and placed into each of two 5 cm diameter containers fitted with breathable mesh lids and filled with a plaster of paris base. Both containers were kept in an incubator at 24°C and provisioned with ad libitum balls of yeast until the females were producing large clumps of eggs on a daily basis. Six days later, the adults were transferred into two fresh containers. The following day, 600 eggs were collected from each container and placed into two 10 cm diameter pots to create a cohort of adults from whom the experimental eggs were harvested. After two days, approximately 50 per cent of the eggs had hatched, and each 10 cm pot was provisioned with 7×1 mm balls of yeast a day. Six days later, approximately 50 per cent of individuals had matured. Eight days later, adults were transferred to a fresh pot to ensure that all eggs collected on the following day would be laid on the same day and would have been laid by mothers that were 9 days old. The following day, batches of 50 eggs from 'older' 9 day old mothers were removed from the two pots and randomly allocated to one out of five culture tubes containing 50 eggs (Low density) and five culture tubes containing 500 eggs (High density). Eggs from 'younger' 3 day old mothers were obtained in an identical fashion, but the set-up procedure was started 6 days later such that the 3 and 9 day old mother populations could be set up synchronously. No obvious difference in the mortality of the egg-laying 3 and 9 day old mothers was observed. This set up resulted in four different types of population: Older high-density (OH), Older low-density (OL), Younger high-density (YH), and Younger low-density (YL) (figure 1).

(c) *Maintenance, counting and measuring of populations*

Samples of 20 eggs from all 20 population tubes were photographed at the beginning of the experiment in order to compare the size of the eggs from the younger and older mothers. Photos were taken at a magnification of $\times 15$, using a Canon Powershot S40 digital camera connected to a Vision Engineering (Woking, UK) 'Lynx' head-up stereomicroscope. The length of each egg was then measured from tip to tip using the IMAGEJ 1.28u image analysis package (<http://rsb.info.nih.gov/ij>). Each day, all tubes received two drops of water and a single ball of active dried yeast, sieved for conformance ($1.08 \text{ mg} \pm \text{s.e. } 0.03$, $n=100$). We counted the numbers of eggs, juveniles and adults under a Leica MZ8 binocular microscope using a hand-held tally counter, and a sampling grid scratched onto the plaster base of the tube. Initially, all adults, juveniles and eggs were counted throughout the tube, but after numbers exceeded 500, the juveniles and eggs were counted from a randomly selected quarter of the tube. In order to get information also on the size dynamics of eggs and females in each treatment over time, each quarter of each population tube was also photographed each day up until day 36 of the experiment

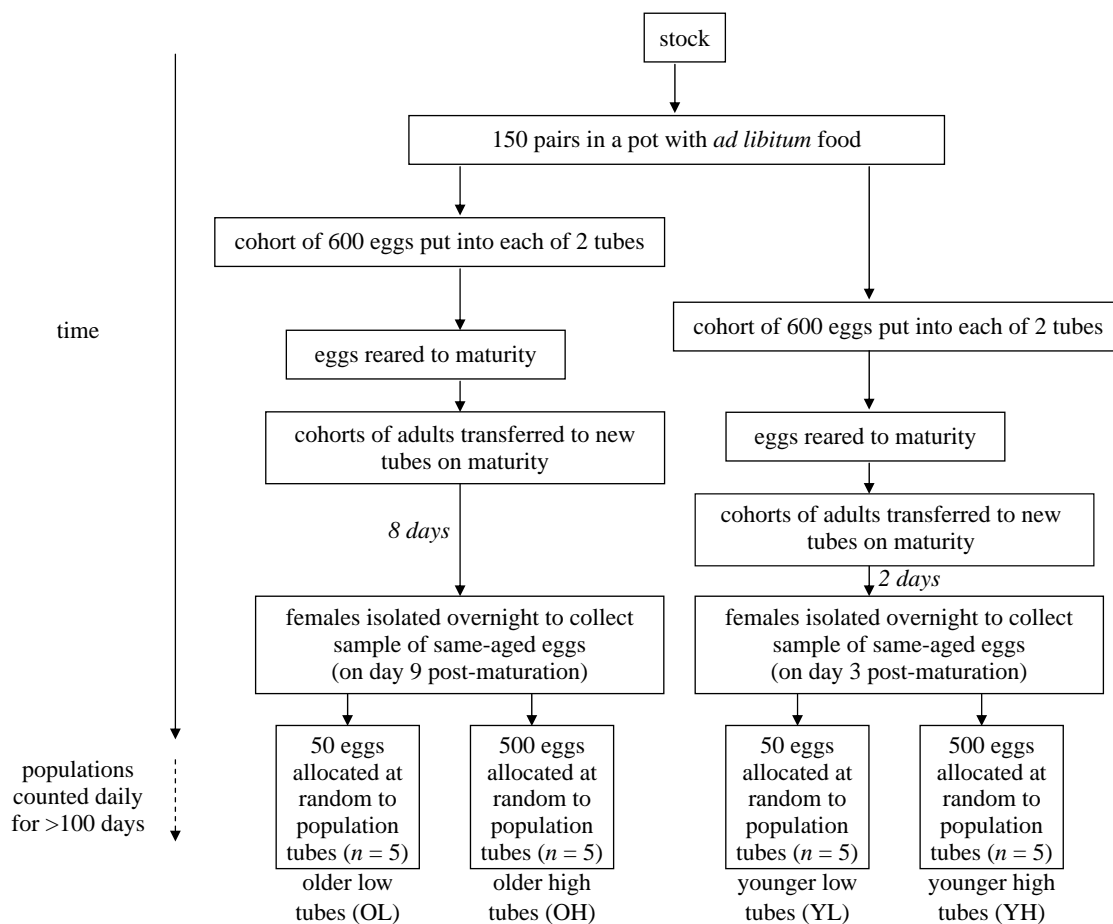


Figure 1. A schematic of the experimental set up used to produce synchronous batches of eggs from 3 and 9 day old mothers. Once collected, the eggs were used to set up high density (500 eggs) and low density (50 eggs) in order to test the prediction that the influence of maternal effects on population dynamics is context-dependent.

and most week days up until day 81 of the 110 day experiment. However, due to time constraints, it was not possible to measure images from all days. Therefore, we measured images from days at key stages of the first 81 days of the 110 day population time-series. Although, we aimed to measure 10 eggs and 10 females from each tube, resulting in a total of 50 measurements per treatment per day, the actual number measured per treatment varied depending upon image quality and the current age structure of the population at that time.

(d) Statistical analysis

Differences in the size of eggs used to set up the different populations were tested for using a linear mixed-effects model (LME) with the different treatment groups fitted as a four-level factor (OH, OL, YH, YL) and tube fitted as a random term. The results are presented with degrees of freedom and likelihood ratio test statistics (LRT). Owing to temporal changes in the auto-covariance structure of the time series, fitting standard autoregressive models to the data is not appropriate (for example, with density-dependent generation time, there is no fixed lag in the dynamics), so a formal statistical test is not possible that accounts for the temporal non-independence of the data. Instead, we use an approximate method to guide our assessment of when the time series are significantly different. We estimated the 95 per cent confidence intervals using bootstrap re-sampling for the five replicates within each treatment group at each time point. In cases where the confidence intervals (CIs) did not overlap, we assumed that the time series were different (Benton *et al.* 2005, 2008). The alternative method of bootstrapping the

difference between means is slightly less conservative, but produces quantitatively similar results (Benton *et al.* 2008). Little weight should be put on differences observed at a single time point, but periods where the CIs do not overlap for several days are clearly significantly different. To describe the time series for egg and female size dynamics, we fitted generalized additive models (GAMs) with gamma errors and a log-link function. As there are gaps in the data at different parts of the time series, we found that the default cross-validation routine (generalized cross-validation (GCV)) to control the smoothness over-fitted the data in periods where data were sparse. We therefore restricted the smoothness to a spline of 6° of freedom (using the argument $k=7$). The overall spline fit was plotted with its standard errors, and statistical significance was informally assessed by the difference between predicted GAM fits relative to the s.e. of the fit. All analyses were conducted in R (R Core Development Team 2005) and included the libraries Hmisc (Harrell 2006), Design (Harrell 2005), MASS (Venables & Ripley 2002), nlme (Pinheiro *et al.* 2006) and mgcv (Wood 2006).

3. RESULTS

(a) Population dynamics

As in a previous experiment (see Benton *et al.* 2008), eggs from younger mothers tended to hatch and mature earlier than eggs from the older mothers irrespective of population density at set-up (figure 2*c–f*). This effect persisted into the F₂ generation, although the difference was less pronounced in the high-density populations (figure 2*d,f*). Eggs from younger mothers

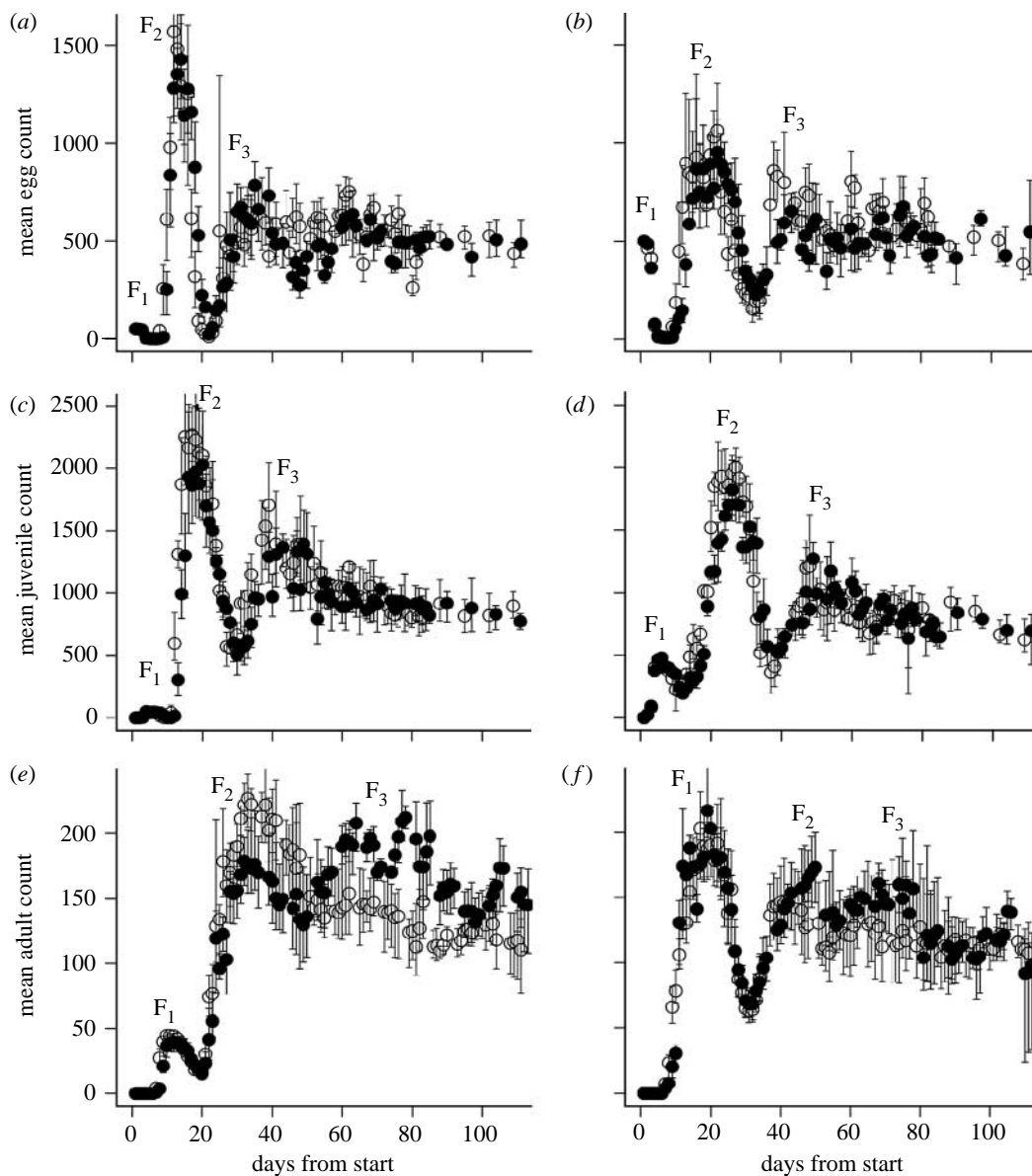


Figure 2. Differences in the transient dynamics of populations initiated with eggs that were laid by either younger 3 day old (white points) or older 9 day old mothers (black points). The left-hand panels show population counts of (a) eggs (c) juveniles and (e) adults from populations that were initiated at low-density (50 eggs). The right-hand panels show population (b) counts of eggs (d) juveniles and (f) adults from populations that were initiated at high density (500 eggs). In all cases, the error bars represent bootstrapped 95% confidence intervals. The individual cohorts are marked on the figures as F₁, F₂ and F₃ and were identified by inspection of the age-structured dynamics.

hatched into females that produced marginally higher *per capita* numbers of juveniles in both high- and low-density populations (figure 2*c,d*). This maternal effect had no influence on the number of F₂ adults recruiting into the population in the high-density treatment and the dynamics settled down to a noisy equilibrium (figure 2*f*). By contrast, in the low-density populations, the maternal effect led to differences in the number of adults recruiting into the F₂ cohort (figure 2*e*) and subsequently drove differences in the transient dynamics of the two treatments that had still not converged in the adult time series at the end of the experiment 110 days (3–4 generations) later (figure 2*e*).

(b) Age structure

The different starting densities in the high- and low-density treatments resulted in substantial differences in the age structure of populations. In the low-density

treatment, a small number of highly fecund females in the F₁ generation resulted in populations with very low adult : juvenile ratios. Individuals in the F₁ cohort had largely died by the time the majority of the F₂ cohort had hatched, resulting in little overlap between the F₁ and F₂ cohorts (figure 3, black points). By contrast, in the high-density treatment, the intense competition in the F₁ generation resulted in small females with low *per capita* fecundities (approx. 100 females produce more than 1000 eggs in the F₂ generation, figure 2*b*) creating a large degree of overlap between the F₁ and F₂ cohorts and an adult : juvenile ratio that was approximately double that of the low-density populations (figure 3, white points). The increased competition for resources and the inter-cohort, asymmetric, competition between F₁ and F₂ generations in high-density treatments swamped any differences in F₂ recruitment of the OH and YH treatments (figure 2*f*).

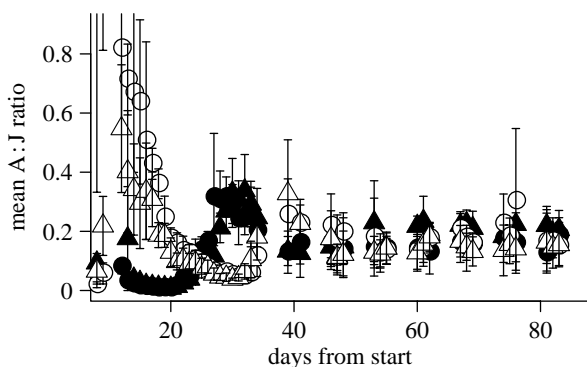


Figure 3. Differences in the adult:juvenile (A:J) ratio (mean \pm 95% CI) of populations initiated at low density (black points), and high density (white points). Populations initiated with eggs from young mothers are plotted as circles; populations initiated with eggs from old mothers are plotted as triangles.

(c) Egg size dynamics

There was no difference in the size of the eggs used to initiate the different populations at the start of the experiment (mean \pm s.e.; Old high = 0.177 ± 0.0011 , Old low = 0.179 ± 0.0011 , Young high = 0.176 ± 0.0010 , Young low = 0.177 ± 0.0011 ; LRT, treatment = 4.57, d.f. = 3, $p = 0.21$). In order to describe the change in egg size dynamics in the OH, YH, OL, YL treatments 3482 egg sizes were measured with an average of 44.08 ± 15.09 (mean \pm s.e.) measurements per treatment per day. The egg size dynamics differed between treatments, with effects both due to the initial density of eggs at set-up and due to maternal age. In populations initiated at high-density (OH, YH), all F1 mothers laid larger eggs than those they had hatched from (figure 4b, days 10–25). The dynamics of the OH and YH treatments were broadly parallel after this point with individuals in the OH populations tending to lay similarly sized or larger eggs than individuals in YH populations. Egg size decreased as populations approached equilibrium in both treatments. By contrast, in the low-density populations, OL and YL females tended to lay smaller eggs in the F1 cohort compared to the size of eggs at set-up. However, the different body sizes of OL and YL females resulted in a divergence in egg size as the F1 cohorts aged (figure 4a, days 10–30, see Plaistow *et al.* 2007). These differences in the size of eggs laid drive further differences in the body size of females recruiting approximately 10 days later (figure 4c, days 30–40). In low-food environments, the close association between female body size and the size of eggs that a female can lay (Plaistow *et al.* 2007) led to subtle asynchronous oscillations in egg sizes in the different treatments. There was a reduction in egg size variation in all treatments as populations approached equilibrium and female body sizes began to converge (figure 4a,b).

(d) Female size dynamics

In order to describe the change in female size dynamics, 2304 measurements of female body size were made with an average of 30.76 ± 2.35 (mean \pm s.e.) measurements per treatment per day. In the low-density treatments (YL, OL), the F1 cohort of females matured at maximal body size (approx. 1–1.2 mm, figure 4c),

with very high *per capita* fecundity (approx. 25 females produce more than 1500 eggs in the F2 generation, (figure 2a)). However, OH females were larger than YH females in the F1 cohort, i.e. there was a maternal effect (figure 2d, day 10). Subsequently, the constraint that the body size has on the size of eggs a female can lay (see Plaistow *et al.* 2007) and the different offspring provisioning strategies generated by the maternal effect (Benton *et al.* 2008) were sufficient to generate differences in the size and number of juveniles developing in the F2 cohort. This resulted in differences in the number (figure 2c) and size (figure 4c) of OL and YL females recruiting into to the F2 generation. From this point onwards, female body size remained small (approx. 0.7 mm) with subtle asynchronous oscillations in the size dynamics of the OL and YL treatments (figure 4c) that closely mirrored differences in the egg size dynamics of the two treatments 10–20 days previously (figure 4a). Conversely, in the high-density populations, the intense competition for resources in the F1 generation resulted in females that matured at much smaller body sizes (approx. 0.8 mm, figure 4d), with a much lower *per capita* fecundity (approx. 100 females produce more than 1000 eggs in the F2 generation, figure 2b). There was no difference in the size of OH and YH females recruiting into the F1 adult cohort and as a result there was no difference in the subsequent size dynamics of OH and YH populations (figure 4d). Overall the body size of females in both treatments declined slightly as the populations approached equilibrium (figure 4d), mirrored by a decline in the egg size (figure 4b).

4. DISCUSSION

In this study, we demonstrate a context-dependent influence of maternal effects on transient population dynamics. Subtle differences in the provisioning of eggs by young and old mothers resulted in multigenerational differences in the transient dynamics of populations initiated at low density. However, populations initiated at high density showed more similar population dynamics despite the fact that the initial eggs came from the same young and old mothers. The reason for this difference is that the differential provisioning of eggs by young and old mothers caused differences in their offsprings' life histories. These differences were accentuated by the high-resource/low-density environment, leading to further differences in the size of the F1 eggs, creating an even stronger grand-maternal effect in the F2 generation. By contrast, in the high-density populations, competition was so strong that all surviving F1 females matured at close to the minimal size, and consequently all F1 females laid eggs of the same size, thereby swamping the original maternal effect and synchronizing the transient dynamics of young and old mother populations.

To our knowledge, no other study has ever previously demonstrated context-dependent maternal effects on population dynamics, although several have previously shown that the relative strength and even the direction of maternal effects on offspring phenotype can change depending upon the local environmental conditions (Gliwicz & Guisande 1992; Parichy & Kaplan 1992;

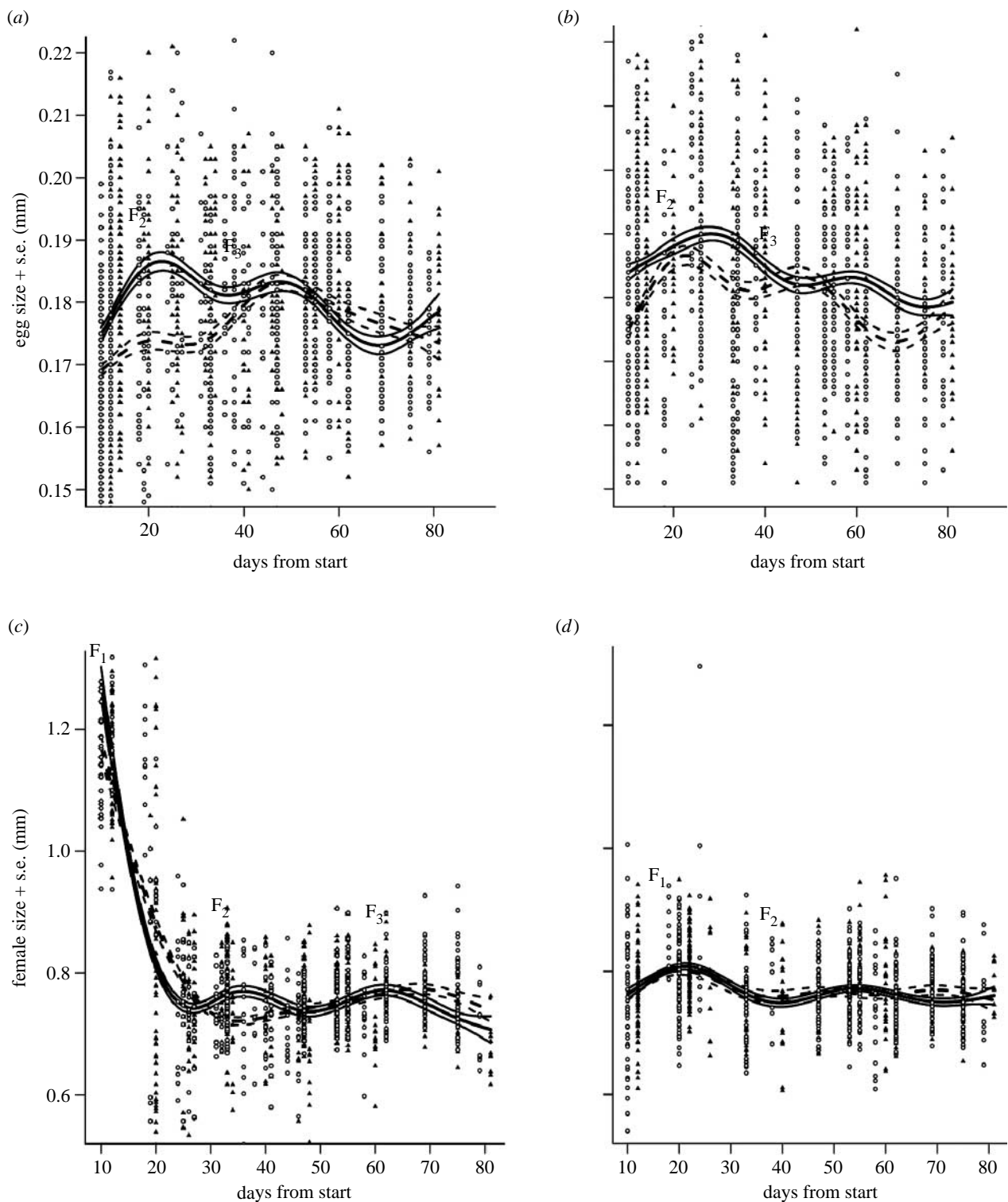


Figure 4. The effects of maternal age on the size dynamics of (a) eggs in populations initiated at low density (50 eggs); (b) eggs in populations initiated at high density (500 eggs); (c) females in populations initiated at low density; and (d) females in populations initiated at high density. The time series for egg and female size dynamics were described using GAMs (see §2 for further details). Populations initiated with eggs from 3 day old mothers are shown as dashed lines (size \pm s.e.), whereas populations initiated with eggs from 9 day old mothers are shown as solid lines (size \pm s.e.). The timing of the individual cohorts is marked on the figures as F_1 , F_2 and F_3 . The GAMs can be considered significantly different at any time point if the distance between the lines is approximately $3 \times$ greater than the s.e.

Bernardo 1996b; Rossiter 1998; Czesak & Fox 2003; Lardies *et al.* 2004; Marshall & Keough 2004; Räsänen *et al.* 2005; Plaistow *et al.* 2006; Marshall & Uller 2007; Räsänen & Kruuk 2007). Our results seem to contradict many previous studies, which typically conclude that the maternal effects influence offspring performance in

harsh environments but have little influence in benign environments (Mousseau & Fox 1998a; Räsänen & Kruuk 2007).

Part of this contradiction may be resolved because we are looking at the population context in this study. In food-rich and low-density environments, maternal

effects may readily translate into differences in body size because effectively all juveniles survive (more than 90% of F_1), so any maternal effects will be manifest in subsequent reproductive performance. In food-poor and high-density environments, juvenile survival is much lower (40% of the F_1 survive through to maturity), so maternal effects may affect survival and growth rate (figure 2f suggests that the HO and HY F_1 cohorts mature at slightly different rates approx. on day 15). In food-poor conditions, mites mature at a minimum size (Plaistow *et al.* 2004) and small females lay more uniform sized eggs (Plaistow *et al.* 2007). Thus, in food-rich environments, maternal effects on reproductive performance of offspring will be stronger and thereby more likely to impact upon the dynamics of the population. In food-poor environments, maternal effects will be manifested mostly in terms of juvenile survival. However, this will be hidden at the population level owing to the existence of a juvenile recruitment bottleneck created by the competitive superiority of adults. In essence, this means that the number of recruits to adulthood is limited, so greater juvenile survival means greater competition rather than higher recruitment rates; maternal effects on juvenile survival may affect the individuals that survive to recruit much more than the numbers recruiting and therefore have little impact on population growth rate.

There are at least two further reasons why the significance of maternal effects in benign environments may not previously have been fully appreciated. First, our interest in maternal effects as adaptations has consistently focused on offspring fitness rather than parental fitness (Marshall & Uller 2007; Plaistow *et al.* 2007). Therefore, most studies have concentrated on the 'offspring' environment and the effect that it has on the expression and adaptive significance of maternal effects acting on offspring traits such as growth, recruitment, age and size at maturity (Mousseau & Dingle 1991; Mousseau & Fox 1998a,b). Far fewer studies have considered how the environment influences variance in maternal effects between females (Räsänen & Kruuk 2007). In soil mites, adult traits such as fecundity and survival are most influenced by maternal effects in benign environments (Plaistow *et al.* 2006). Moreover, developing in a harsh environment reduces female body size and reduces the number and the sizes of eggs females lay (Plaistow *et al.* 2007). If this is true for other organisms too, harsh environments may reduce between-female variation in maternal effects, limiting the impact they can have on relative fitness and population dynamics.

The second reason maternal effects in benign environments may previously have been underestimated is that most studies have only measured transgenerational plasticity across a single generation, i.e. a maternal effect. Consequently, interactions between intergenerational effects in different environments, and the influence that this has on the strength and persistence of maternal effects, have generally not been measured (Räsänen & Kruuk 2007). Our results suggest that maternal effects will have a greater influence on the transient dynamics of populations that initially experience benign conditions for one or more generations. However, studies of

interactions between intergenerational effects in other species are required before we can generally understand their significance.

As well as influencing population dynamics, maternal effects can also influence evolutionary dynamics by altering the phenotypes of their offspring (Carroll *et al.* 2007; Räsänen & Kruuk 2007). Consequently, changes in the magnitude and persistence of maternal effects in different environments could greatly alter the evolutionary dynamics of a population. Our results suggest that micro-evolutionary change, local adaptation and population divergence will all be most affected by maternal effects in populations that frequently experience benign conditions. Given that such micro-evolutionary changes can occur within a few generations (see Carroll *et al.* (2007) for a review), it is even possible that some of the differences in the population dynamics observed in this study arose from micro-evolutionary processes, rather than phenotypic plasticity in the life history of individuals. However, this seems unlikely given that the animals used in this experiment were all highly inbred and a previous study of a similar nature revealed no difference in the body size of treatments once the population dynamics had converged (Benton *et al.* 2005).

While our data support the hypothesis that maternal effects can influence population dynamics, the oscillations we see in population dynamics are not the cyclicity predicted by simple models. This is because the oscillations decay over time; they are generational cycles and they have non-uniform periodicity in that the generation time is density-dependent (compare figure 2e,f; Benton *et al.* 2005, 2008). There are a number of probable explanations for why the cycles decay rather than persist. First, the mechanism by which delayed density dependence occurs is the mapping of maternal quality to offspring quality, and is much more complicated than assumed in the original maternal effects model (Plaistow *et al.* 2004, 2006, 2007). Second, the original maternal effects model does not consider an overlap between generations. In soil mites, the overlap between generations increases in low-food conditions resulting in cohort blurring and a loss of the cohort cycles that help to drive differences in the transient population dynamics of different populations (this study, Benton *et al.* 2005). Finally, as we show here, at a population level, the maternal effect can be 'swamped' by an immediate response of the offspring to their harsh environment. This is due to the context-dependence of the effect: in a recruitment-limited population, maternal effects on juvenile survival will not necessarily affect the number of subsequent offspring produced.

Maternal effects are complex. At the individual level, maternal effects impact different traits in context-dependent ways. There is no simple correlate of any univariate measure of maternal performance and offspring performance. Large females can lay small eggs (when young, or if starved) or large eggs (when they age). Large eggs can hatch into offspring who grow fast, or grow slowly. If the offspring grow slowly, they can increase survival or later fecundity depending on their food levels. This complexity suggests there is no single hypothesis of what maternal effects may do at the population level. We show here that perturbing population age structure (i.e. our initial conditions) may

dampen or accentuate the population level manifestation of maternal effects. We further show (here and in Benton *et al.* (2008)) that perturbations cause life-history changes, propagated by maternal effects across generations, which can be most evident at the population level some time later. As real populations exist in environments that fluctuate in resources and population density, stochastic or transient population dynamics are the norm. While we can be certain that maternal effects contribute to these by being a mechanism for delayed density dependence, it is one that is intermittent and highly complex. Simple discrete time analytical models will not capture this richness in response. If, like the mites, the life history of a focal species is determined by resources, the most productive modelling approach is likely to be a continuous-time physiologically structured model (Kooijmans 2000). This approach will allow an individual's life-history choices to reflect current and past patterns of resource availability (i.e. context dependence) and is able to model maternal effects as the direct transmission of resources from mother to offspring.

We are grateful to Jane D. Grant for counting and photographing animals during the population experiment. Tobias Uller, Eric Wapstra and three anonymous referees provided comments that improved an earlier version of this paper. The work was funded by NERC grant NX5023344/2 awarded to T.G.B.

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