Maternal effects and evolution at ecological time-scales

K. RÄSÄNEN*† and L. E. B. KRUUK‡

ETH-Zurich, Institute of Integrative Biology (IBZ) and EAWAG, Department of Aquatic Ecology, Ueberlandstrasse 133, CH-8600 Duebendorf, Switzerland; and ‡Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, UK

Summary

1. Genetic and environmental maternal effects can play an important role in the evolutionary dynamics of a population: they may have a substantial impact on the rate and direction of genetic change in response to selection, and they may generate immediate phenotypic change via phenotypic plasticity. Because of this potential to generate rapid phenotypic change in a population, maternal effects may be particularly important for evolution at ecological time-scales.

2. Despite an increased interest in the prevalence, composition and adaptive benefits of maternal effects, little is still known of their impact on ecological and evolutionary processes in natural populations. We consider here the insights that a quantitative genetic framework provides into the pathways by which maternal effects can influence trait evolution in wild populations. Widespread evidence for a genetic basis of a range of maternal effects traits reinforces the notion that they cannot be treated as purely environmental sources of variation. We also provide an overview of the impact of environmental conditions on the expression and impact of maternal effects, and describe empirical evidence for their impact on evolution at ecological time-scales.

3. We emphasize the need for empirical work to quantify the associations between maternal and offspring phenotype and genotype, and the suite of selection pressures generated by maternal effects, as well as the relationship between maternal effects and environmental variation. Future work should aim to identify the conditions under which maternal effects are likely to play a role in evolution, as well as explicitly test the contribution of maternal effects to evolutionary responses.

Key-words: environmental change, maternal genetic variance, microevolution, natural selection, phenotypic plasticity.

Introduction

Maternal effects occur when the phenotype of the mother affects the phenotype of her offspring in addition to the direct effects of the genes contributed by her. Maternal effects are ubiquitous in nature and have been demonstrated in a wide range of traits and taxa (Table 1; Mousseau & Fox 1998a). However, their role in the evolutionary dynamics of populations is still poorly established. On the one hand, they are still frequently viewed as environmentally determined sources of phenotypic variation with the potential to inflate estimates of the genetic basis of adaptive traits, and hence responses to selection (e.g. Falconer 1989; Rausher 1992); this reputation as a nuisance parameter has added to the impression of their being 'persistently unpopular' (Pigliucci 2001). On the other hand, theoretical models

show that maternal effects may have a substantial impact on the rate and direction of evolutionary change in response to directional selection (e.g. Riska 1989; Kirkpatrick & Lande 1989; Wade 1998). Moreover, maternal effects can also influence dispersal and gene flow (e.g. Donohue 1999; Hereford & Moriuchi 2005), the evolution of host–parasite interactions (Wade 1998), speciation (e.g. via host–race formation, Wade 1998; and cytoplasmic transfer of symbionts, such as *Wolbachia*, Charlat, Hurst & Merçot 2003) and population dynamics (Rossiter 1991; Ginzburg 1998; Benton *et al*. 2005; Plaistow, Lapsley & Benton 2006). However, although the role of maternal effects as a potentially powerful evolutionary force has recently received increased attention in empirical work (e.g. Rossiter 1996; Mousseau & Fox 1998a; Badyaev *et al*. 2002; Räsänen, Laurila & Merilä 2003b; Wilson *et al*. 2005a; Wilson, Kruuk & Coltman 2005b; Beckerman *et al*. 2006), there is still little correspondence between the theoretical and empirical studies. The aim of this paper is to evaluate

†Author to whom correspondence should be sent. E-mail: katja.rasanen@eawag.ch

Table 1. A selected set of empirical examples to illustrate the breath that maternal effects can take, focusing on studies that have also investigated effects of variable maternal and/or offspring environment on maternal effects (note that environmental induction does not preclude a genetic basis).

Species	Offspring trait	Maternal trait	Environment-dependent plasticity	Reference
Daphnia pulicaria	Propensity for resting stage production	Reproductive mode	Maternal and offspring environment	Alekseev & Lambert (2001)
Daphnia cucullata	Inducible defences	Inducible defences	Maternal and offspring environment	Agrawal, Laforsch & Tollrian (1999)
Daphnia magna	Parasite resistance	Per offspring investment	Maternal and offspring environment	Mitchell & Read (2005)
Soil mite (*Sancasania berlesei*)	Hatching time, Traits at maturation	Fecundity, age	Maternal and offspring environment	Beckerman *et al.* (2006)
Burrower bug (*Sehirus cinctus*)	Solicitation pheromones	Provisioning	Offspring environment	Kölliker *et al.* (2006)
Soap berry bug (*Jadera haematoloma*)	Morphology	Host plant choice	Offspring environment	Carroll *et al.* (2001)
Drosophila serrata	Survival	Age, grandmothers age	Offspring environment	Hercus & Hoffmann (2000)
Yellow dungfly (*Scatophaga stercoraria*)	Life-history traits	Mating pattern	Maternal environment	Tregenza *et al.* (2003)
Three species of poeciliid fishes	Offspring size and fat content	Offspring size and number	Maternal environment	Reznick, Callahan & Llauredo (1996)
Brown trout (*Salmo trutta*)	Survival, growth	Propagule size	Offspring environment	Einum & Fleming (1999, 2000)
Fire-bellied toad (*Bombina orientalis*)	Growth	Propagule size	Maternal and offspring environment	Kaplan & King (1997), Kaplan & Phillips (2006)
Moor frog (*Rana arvalis*)	Survival, growth	Egg capsule Propagule size	Offspring environment	Räsänen *et al.* (2003b, 2005)
House finch (*Carpodacus mexicanus*)	Survival, growth	Sex-biased laying sequence Onset of incubation	Maternal and offspring environment	Badyaev *et al.* (2002)
Field vole (*Microtus agrestis*)	Growth	Sex allocation	Maternal environment	Koskela *et al.* (2004)

the insights gained from the extensive body of work into the impact of maternal effects on rapid evolutionary change, occurring over 'ecological' time-scales such as years, decades or centuries (Thompson 1998; Hendry & Kinnison 1999; Hairston *et al.* 2005).

In essence, 'maternal effects' can be defined as *any* aspect of the mother's phenotype that affects her offspring's' phenotype. Consequently, not all maternal effects have adaptive benefits for offspring fitness. However, maternal effects will have evolutionary consequences whenever they alter phenotypes in a population. This could occur in two different, but not mutually exclusive, ways: first, through their impact on microevolution within a population via genetic change in response to natural selection, potentially generating rapid between-population divergence, and secondly, through their high levels of phenotypic plasticity, facilitating persistence of populations facing changing environments (Rossiter 1991; Mousseau & Fox 1998a). But how prevalent are such scenarios? Do maternal effects have a substantial impact on rates of evolutionary change, or do they ultimately only contribute statistical noise to our data?

Below, we first outline a quantitative genetic framework describing theoretical predictions of the impact of maternal effects on trait evolution, and review empirical estimates of the relevant parameters. We then consider the second process by which maternal effects may facilitate rapid phenotypic change, namely via phenotypic plasticity. We look for empirical evidence for the role of maternal effects in rapid evolution and in response to novel environmental challenges, and point out directions for future work. As the empirical literature reporting maternal effects is vast, and several excellent reviews exist both in plants and animals (e.g. Roach & Wulff 1987; Rossiter 1996; Bernardo 1996a; Mousseau & Fox 1998a; Reinhold 2002), we illustrate our points by focusing on empirical evidence from primarily nondomestic animal species and, where possible, natural populations. We end by emphasizing the directions future work should take to increase our understanding of the general role of maternal effects in evolutionary processes.

Potential effects on rates of evolution: a quantitative genetic framework

We consider first the impact of maternal effects on rates of evolutionary change within a population. In the absence of maternal effects, the response to directional selection on a single quantitative heritable trait is predicted by the breeder's equation:

$$R = V_A \beta$$

where R is the change in the mean value of the trait between generations, V_A is the additive genetic variance and β is the selection gradient on the trait, assuming for simplicity that no correlated traits are also under selection (Falconer & Mackay 1996). In practice, the

breeder's equation rarely generates accurate predictions of evolutionary change in response to natural selection in the wild (Merilä, Sheldon & Kruuk 2001), but it nevertheless provides a useful decomposition of evolutionary change into its dual components of heritable genetic variation and natural selection. With the incorporation of maternal effects, however, the expectations for evolutionary change become considerably more complex (Kirkpatrick & Lande 1989). If an offspring trait (for example, offspring growth rate) is influenced by a maternal trait (for example, lactation rate), the predicted response to selection in the offspring trait becomes:

$$R = (G_{oo} + \frac{m}{2}G_{mo})\beta_{o,t} + G_{mo}\beta_{m,t}$$
$$+ m(G_{mo} + \frac{m}{2}G_{mm})\beta_{o,t-1} + mG_{mm}\beta_{m,t-1} \qquad \text{eqn 1}$$
$$+ mP_{mo}(\beta_{o,t} - \beta_{o,t-1}) + mP_{mm}(\beta_{m,t} - \beta_{m,t-1})$$

where G_{oo} is the additive genetic variance in the offspring trait (the same as V_A above), G_{mm} is the additive genetic variance in the maternal trait, G_{mo} is the genetic covariance between the offspring trait and the maternal trait, m is a 'maternal effect coefficient' (a measure of the impact of the mother's phenotype on offspring phenotype), P_{mo} and P_{mm} are the respective phenotypic covariance and variance, $\beta_{o,t}$ is the selection gradient describing the partial regression of offspring fitness on offspring trait at time t and $\beta_{m,t}$ is the selection gradient linking offspring fitness and the maternal trait at time t (Kirkpatrick & Lande 1989, 1992).

The impact of maternal effects on a response to selection will therefore depend on the sign as well as the magnitude of all of the above parameters, with the result that maternal effects theoretically have substantial potential to alter evolutionary change. Moreover, as eqn 1 illustrates, selection pressures in the previous generation will affect maternally influenced characters in the current generation, generating an evolutionary time-lag (Kirkpatrick & Lande 1989): for example, if those individuals who are more likely to survive the juvenile stage then become mothers with high rates of maternal investment, selection at the juvenile stage in the mothers' generation will change the distribution of phenotypes in the offspring generation. Quantitative predictions of the evolutionary response with maternal effects in a natural system are therefore a tall order, and, understandably, studies of individual systems rarely deal with more than one of the above components at a time. Moreover, the above scenario considers a single offspring trait affected by a single maternal trait, whereas in reality suites of correlated traits are likely to be involved, necessitating yet more complex multivariate representations. It also only concerns quantitative (i.e. continuous) traits, assuming a polygenic inheritance, rather than discrete phenotypes (note, however, that the inheritance of discontinuous traits can be modelled by assuming an underlying continuous variable with 'threshold' values that determine the expression of different discrete phenotypes; Falconer & Mackay 1996). Despite these limitations, the general framework of eqn 1 is a useful illustration of the extra layers of complexity introduced by the existence of maternal effects. More importantly for the focus of this review: it shows how evolutionary genetic change can be accelerated, constrained or even reversed by maternal effects – specifically by their genetic basis, their impact on offspring phenotype and the selection pressures that operate through them. Below we consider empirical evidence relating to each of these aspects in turn.

GENETIC VARIANCE IN MATERNAL EFFECTS

There is substantial evidence for a heritable genetic basis to many maternal effects from both domestic livestock studies (e.g. Simm 1998) and plant breeding experiments (e.g. Platenkamp & Shaw 1993; Byers, Platenkamp & Shaw 1997; Thiede 1998). Studies of nondomestic animal species have more often treated maternal effects as environmental sources of variation, but evidence is now accumulating for a significant heritable genetic basis to a range of different maternal effect traits also in wild populations. Table 2 contains examples of these, and shows how, across a range of traits, taxa and alternative analytical approaches, there is frequently a substantial component of genetic variance in maternal effects.

The studies in Table 2 are partitioned into two groups. The first group (Table 2a) considers the heritable genetic basis of traits expressed in the mother that are known (or assumed) to generate maternal effects on the offspring. These will include traits such as maternal (or parental) provisioning (see also Kölliker 2005), timing of breeding, number of offspring, or (although not available here) lactation rate. The approach therefore corresponds to the framework of eqn 1 in considering a distinct offspring and maternal trait. The second group of studies (Table 2b) also provides evidence for 'maternal genetic effects', but here the maternal trait is not measured explicitly. Instead, it is assessed indirectly via its impact on offspring phenotype: the maternal trait is effectively 'maternal performance', whereas the offspring trait could be growth rate, size or survival (Riska, Rutledge & Atchley 1985). In this case, the analyses quantify the variance in the offspring trait between offspring of different mothers, and the extent to which this variance can be determined by relatedness (i.e. its genetic basis). Examples from wild species are scarcer here, because although many studies have documented the existence of a maternal effects component of variance (see discussions in Lynch & Walsh 1998; Merilä & Sheldon 2001; L.E.B. Kruuk & J.D. Hadfield, unpublished), far fewer have proceeded to separate the genetic from the environmental sources of variance between mothers. Note also that although consideration of just the offspring phenotype is conceptually (and practically) appealing, the approach can no longer be used for predictions of the between-generation

Table 2. Examples of traits with evidence of a genetic basis of maternal effects in wild animal populations (or from laboratory breeding experiments of wild stock). (a) Studies considering traits defined as mother's phenotype; (b) studies considering traits defined as offspring phenotype. Note that offspring size may be treated as either maternal or offspring phenotype: studies of the former are usually analyses of egg size, whereas the latter allow for the possibility of effects of the paternal genotype (and include ovoviviparous species). Proportion of variance is proportion of total phenotypic variance attributable to maternal genetic effects; for (a), this is the trait heritability. Domestic and semidomestic (e.g. laboratory lines of *Drosophila* or *Mus*) are excluded.

Trait and species	Population type	Test	Trait details	Proportion of variance	Reference
(a) Maternal trait					
Offspring number					
Milkweed bug (*Oncopeltus fasciatus*)	Wild stock crossed in lab	Breeding design	Fecundity over 5 days	0·00–0·31*	Groeters & Dingle (1987)
Dung beetle (*Onthophagus taurus*)	Laboratory colony	Breeding design	Number of brood masses	0·49	Hunt & Simmons (2002)
14 bird species	Wild populations	Various	Clutch size	0·14–0·61	Reviewed in Postma & van Noordwijk (2005)
Soay sheep (*Ovis aries*)	Wild population	Animal model	Litter size	0·21	D. Mifsud, unpubl. data
Red squirrel (*Tamiasciurus hudsonicus*)	Wild population	Animal model	Litter size	0·15	Réale *et al.* (2003a)
Breeding time					
Great tit (*Parus major*)	Wild population	Animal model	Lay date	0·19	Postma (2005)
Collared flycatcher (*Ficedula albicollis*)	Wild population	Animal model	Lay date	0·19	Sheldon, Kruuk & Merilä (2003)
Side-blotched lizard (*Uta stansburiana*)	Wild population	Parent–offspring regression	Lay date	1·00	Sinervo & Doughty (1996)
Red squirrel (*Tamiasciurus hudsonicus*)	Wild population	Animal model	Parturition date	0·16	Réale *et al.* (2003a)
Soay sheep (*Ovis aries*)	Wild population	Animal model	Parturition date	0·19	Kruuk & Hadfield, unpublished
Oviposition behaviour					
Bean weevil (*Callosobruchus maculatus*)	Wild stock crossed in lab	Breeding design	Egg-spacing behaviour	> 0	Messina (1993)
Parental care					
Burrower bug (*Sehirus cinctus*)	Laboratory	Breeding design	Maternal provisioning	Inferred from genetic correlation with offspring behaviour	Agrawal *et al.* (2001)
Great tit (*Parus major*)	Wild population	Cross-fostering	Maternal provisioning	Inferred from genetic correlation with offspring behaviour	Kölliker *et al.* (2000)
Long-tailed tit (*Aegithalos caudatus*)	Wild population	Animal model	Helping behaviour†	0·43	MacColl & Hatchwell (2003)
Offspring size					
Dung beetle (*Onthophagus taurus*)	Laboratory	Breeding design	Mass of brood	0·33	Hunt & Simmons (2002)
Seed beetle (*Stator limbatus*)	Laboratory	Breeding design	Egg size	0·22–0·91	Fox *et al.* (1999)
Side-blotched lizard (*Uta stansburiana*)	Wild population	Parent-offspring regression	Egg size	0·61	Sinervo & Doughty (1996)
Chinook salmon (*Oncorhynchus tsawytscha*)	Hatchery population	Mother–daughter regression	Egg mass	0·26–0·39	Heath *et al.* (2003)
(b) Offspring trait					
Size					
Burying beetles (*Nicrophorus pustulatus*)	Laboratory	Breeding design	Mass (at four different ages)	0·20–0·27	Rauter & Moore (2002)
Mosquito fish (*Gambusia affinis*)	Wild stock crossed in lab	Breeding design	Offspring mass	Differences between populations	Reznick (1981)
Guppy (*Poecilia reticulata*)	Wild stock crossed in lab	Breeding design	Offspring mass at birth	Differences between populations or strains	Reznick (1982); Shikano & Taniguchi (2005)
Zebra finch (*Taeniopygia guttata*)	Laboratory	Cross-fostering and animal model	Four sexual behaviour traits	0·00–0·15	Forstmeier, Coltman & Birkhead *et al.* (2004)
Bighorn sheep (*Ovis canadensis*)	Wild population	Animal model	Mass at age 0 Mass ages 1–5	0·175 0·02–0·06	Wilson *et al.* (2005b)
Soay sheep (*Ovis aries*)	Wild population	Animal model	Mass at birth Offspring birth date	0·12	Wilson *et al.* (2005a)
Red deer (*Cervus elaphus*)	Wild population	Animal model	Mass at birth	0·27	Kruuk & Hadfield, unpublished
Red squirrel (*Tamiasciurus hudsonicus*)	Wild population	Cross-fostering	Growth in body mass to 1 month	0·13	McAdam *et al.* (2002)
Development/longevity					
Burying beetles (*Nicrophorus pustulatus*)	Laboratory	Breeding design	Development rates: wandering phase	0·06–0·22	Rauter & Moore (2002)
Spruce budworm (*Choristoneura fumiferana*)			Larval development	Associated with X chromosome	Campbell (1962)
Bean weevil (*Callosobruchus maculatus*)	Laboratory	Breeding design	Male lifespan	Differences between lines	Fox, Czesak & Wallin 2004

*Two populations and two environmental regimes.
†In males.

response to selection as described in eqn 1, because of the failure to incorporate the time-lags implicit in the dynamics of response to selection with maternal effects (Kirkpatrick & Lande 1989).

The range of taxa and traits represented in Table 2 reflects the increasing awareness of the role of genetic variance in determining maternal effects, and argues against their treatment as purely environmental factors. By increasing the 'total heritability' (Wilham 1972) of a trait, the presence of maternal genetic variance will amplify any response to selection, thereby potentially greatly accelerating rates of microevolution within a population (eqn 1; Kirkpatrick & Lande 1989; see also Wade 1998). Furthermore, as eqn 1 also illustrates, the presence of genetic variance underlying a maternal trait may be sufficient to generate phenotypic change even in a nonheritable offspring trait, because any genetic change in the maternal trait will then affect the offspring's phenotypes.
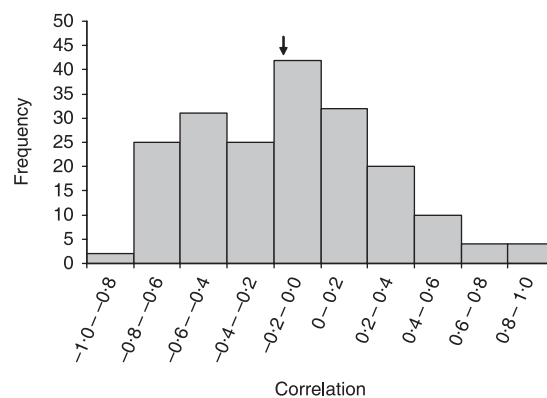

Fig. 1. Distribution of maternal-direct genetic correlations from studies of domestic cattle and sheep. $n = 267$ estimates, from studies of 209 populations. Traits considered are: body weight ($n = 195$); growth rate ($n = 27$); reproductive traits ($n = 17$); survival ($n = 9$); other ($n = 19$). The arrow shows the position of the mean value $= -0.167 \pm 0.026$ SE. (Data from Wilson & Réale 2006.)

GENETIC COVARIANCE BETWEEN MATERNAL AND OFFSPRING TRAIT

The evolutionary dynamics of a trait may also be dramatically affected by the association, or covariance, between genetic effects that determine the maternal phenotype and genetic effects that determine the offspring phenotype. A positive genetic covariance between an offspring and a maternal trait (or 'direct-maternal' genetic covariance) will accelerate any response to selection, whereas a sufficiently large negative genetic covariance will impede or could even reverse any response to selection (Kirkpatrick & Lande 1989; eqn 1). The latter scenario would occur, for example, if genes that produce a 'high-quality' maternal effect (e.g. high lactation rates) were, on average, associated with 'low-quality' direct effects (e.g. small body size) on offspring phenotype, and *vice versa*. (Consider for example the trade-off in selection for milk yield vs. body mass in cattle.) Genetic trade-offs such as this, whereby no single genotype can generate the optimal phenotype in both mother and offspring, will play an important role in the maintenance of genetic variation (Roff 1997, 2002).

The available empirical evidence shows a range of positive and negative covariance values, although again data from wild species are relatively rare. As in Table 2a, some studies consider two distinct maternal and offspring traits: for example, maternal provisioning and offspring elicitation of food show a positive genetic correlation (+0·68) in great tits (Kölliker *et al.* 2000), but a negative genetic correlation (−0·26) in burrower bugs (Agrawal, Brodie & Brown 2001). The alternative approach (cf. Table 2b) considers 'maternal performance' as assessed by the impact on a particular offspring trait, and estimates the genetic covariance with direct genetic effects (i.e. direct effects of the offspring's genotype on the trait). Using this approach, almost exclusively positive values (covariances ranging from −0·06 to +0·85) were found for body weight in mice (Riska *et al.* 1985),

and a direct-maternal genetic correlation of 1·25 (±0·08) was estimated for offspring body mass in red squirrels (McAdam *et al.* 2002). Negative, though nonsignificant, direct-maternal genetic correlation values for offspring birth weight and birth date were found in a feral population of Soay sheep (−0·41 ± 0·25 SE and −0·22 ± 0·23 SE; Wilson *et al.* 2005a). The best data come from studies of domestic ungulates (Wilson & Réale 2006): in sheep and cattle, the mean value of direct-maternal genetic correlation coefficients estimated for phenotypic traits is significantly less than zero (Fig. 1; data from Wilson & Réale 2006), although nearly a third of values (32·9%) are positive.

In conclusion, the available literature suggests that the association between direct and maternal genetic effects may be either positive or negative. A negative genetic covariance may play an important role in the maintenance of genetic variance, but will dampen or potentially even reverse any response to selection on the offspring trait. In contrast, a positive genetic covariance could rapidly accelerate rates of microevolution. However, to date, parameter estimates from wild species are regrettably still far too scarce to attempt to infer the conditions associated with values of different direction or magnitude.

THE MATERNAL EFFECT COEFFICIENT

The effect of a mother's *phenotype* (rather than just her genotype) on the offspring will also have evolutionary implications: consider, for example, the relationship between clutch size and offspring growth rates. In eqn 1, this impact is quantified by the maternal effect coefficient *m*, defined as the partial regression of offspring phenotype on maternal phenotype, holding the direct effects of the genes inherited from the mother constant (Kirkpatrick & Lande 1989; see Lynch & Walsh 1998 for methods of calculation). Positive values of *m* represent

the scenario in which, say, high rates of food provisioning by the mother or large maternal body size generate large offspring size: as examples of the latter, $m = 0.6$ for body weight in Darwin's finches, and $m = 0.3$ in great tits (Lande & Price 1989). However, as for the genetic covariance, maternal effects may be negatively associated with offspring phenotype. Negative values of m represent a scenario in which, for example, phenotypically large mothers produce large clutches in which individual offspring are relatively small (and hence themselves produce small clutches), thereby generating fluctuating maternal effects and impeding a response to selection. This scenario has been observed for body size in mice ($m = -0.13$, Falconer 1965), for juvenile growth rates in the red squirrel ($m = -0.29$, McAdam & Boutin 2003), for age at maturity in springtails ($m = $ approximately -0.5, Janssen *et al.* 1988) and for clutch size in the collared flycatcher ($m = -0.25$, Schluter & Gustafsson 1993). The maternal effects coefficient may also vary within a population, implying different evolutionary dynamics for different subsections. For example, in Chinook salmon, m ranged from positive to negative within a population depending on offspring age (Heath, Fox & Heath 1999). Thus, as for the genetic covariance, maternal effects coefficients indicate the potential for maternal effects to accelerate or slow down evolutionary change.[1] However, considerably more empirical estimates will be required for a comprehensive picture of their distribution in natural systems. Given their counterintuitive impact on rates of phenotypic change, it would be particularly interesting to be able to determine the prevalence and causes of fluctuating maternal effects.

SELECTION VIA MATERNAL EFFECTS

Substantial evidence testifies to the adaptive benefits of numerous forms of maternal effects for offspring fitness (Mousseau & Fox 1998a). The framework of eqn 1 shows how such positive effects ($\beta_m > 0$) should accelerate an evolutionary response to selection on offspring phenotype, given nonantagonistic phenotypic and genetic covariances. Moreover, it is important to realize that, when maternal effects affect offspring fitness (i.e. β_m is nonzero), an offspring trait may evolve even when it is not directly under selection itself (i.e.

[1]These examples consider a single trait maternally affecting itself, but a multivariate equivalent could be depicted by a matrix M with elements m_{ij} describing the impact of trait i on trait j (Kirkpatrick & Lande 1989). Note also that the absolute value of m should not exceed 1 (Kirkpatrick & Lande 1989), and $m = 1$ in the special case when the maternal trait being considered is maternal performance (following Wilham 1972; see (eqn 1) above). Although estimates of the maternal-direct genetic covariance can be derived using the maternal effects coefficient (Lande & Price 1989), the two parameters need not necessarily take the same sign (for example see model in Wolf & Brodie 1998) and may therefore impact on the evolutionary dynamics of a trait in different ways.

$\beta_o = 0$). However, as maternal effects encompass all aspects of the mother's phenotype that impact on offspring phenotype (additional to the direct effects of the genes it has inherited from her), selection acting via maternal effects may counteract rather than enhance selection via offspring fitness. Below we draw attention to the full spectrum of routes via which maternal effects may shape the overall selection regime.

Traditionally much work on the evolution of life histories has focused on the trade-offs faced by mothers between progeny quality and quantity (Roff 1992). Applying our framework to offspring size (the offspring trait) and offspring number (part of the mother's phenotype), larger offspring may have higher fitness (implying a positive β_o), but being part of a large clutch or litter may result in lower fitness of individual offspring (e.g. via increased competition, hence reduced growth rates and reduced survival; Beckerman *et al.* 2006), generating a negative β_m. Furthermore, in taxa with multiple breeding events, high investment by a mother in one breeding event can reduce her subsequent survival or fecundity. Such future costs of reproduction have been shown for example, in collared flycatchers (Gustafsson & Sutherland 1988) and in female red deer (Clutton-Brock, Guinness & Albon 1983; see review in Roff 2002). These costs constitute an additional route via which selection may act, not represented in eqn 1, namely a direct effect of the maternal trait on the fitness of the mother herself (Wolf *et al.* 2002). If this additional selection gradient is negative it too will constrain an evolutionary response in the offspring trait.

As a particular maternal effect trait, such as egg size or clutch size, may have different effects on offspring fitness than on maternal fitness, the evolution of maternal effects involves a balance between the two, with any trade-offs potentially contributing to the maintenance of genetic variance underlying the maternal trait. In an elegant example of just such a compromise, female oviposition preference in the walnut fly *Rhagoletis juglandis* does not maximize fitness of individual offspring, but appears to reflect an optimal strategy for female fitness (Nufio & Papaj 2004). Wilson *et al.* (2005c) also illustrate the potential for contrasting selection regimes via offspring vs. maternal fitness in Soay sheep: offspring birth weight and birth date are under positive directional selection via offspring fitness, but under stabilizing selection via maternal fitness. Incorporating such effects into a predictive quantitative genetic framework will require careful specification of a suitable selection model (Kirkpatrick & Lande 1989), with appropriate assignment of individual phenotype and fitness to mother vs. offspring (Wolf & Wade 2001). Identifying the true targets of selection rather than correlated traits may also be difficult.

In conclusion, despite the complexities associated with predicting rates of genetic change in traits associated with maternal effects, it is clear that: (1) the nature and direction of selection generated by maternal effects can have a critical impact on trait evolution; (2) this selection

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has the potential to reverse evolutionary change expected from considering selection on an offspring trait alone; and (3) studies of selection need to consider selection acting via the associations between phenotype and both offspring and maternal fitness.

Environmental dependency of maternal effects

Above we focused on maternal genetic effects (G_m) and the relationship between these and direct genetic effects ($G_m \times G_o$ interactions). However, maternal effects will have evolutionary consequences even when they initially do not alter the distribution of genotypes in a population, simply because they alter the phenotypes on which selection may act. Any investigation of the evolutionary impact of maternal effects therefore needs to consider their environmental dependency. Maternal effects frequently vary as a result of the environment experienced by the mother (E_m) and, whether genetic or environmental, their effects may also be heavily dependent on the environment experienced by the offspring (E_o) (Table 1). Hence, both $E_m \times E_o$ interactions and $G \times E$ interactions are a prominent feature of maternal effects (see Rossiter 1998 for a detailed description). Here we will focus on the role of environmental sources of variation in maternal effects via: (1) phenotypic plasticity; (2) between-individual variance in maternal effects; and (3) phenotypic variation between populations.

PHENOTYPIC PLASTICITY IN MATERNAL EFFECTS

Maternal phenotypic plasticity, maternally mediated changes of offspring phenotype in response to the environment, is well established in a range of systems, particularly for offspring size and timing of breeding (Pigliucci 2001). For example, egg size is often strongly influenced by environmental conditions experienced by the mother: a mother under nutrient stress may produce smaller eggs than one with unlimited resources. In *Bombina orientalis*, environmentally induced shifts in female body size are positively related to egg size, although the extent of egg size plasticity varies between females (Kaplan & King 1997). Likewise, in red deer *Cervus elaphus*, offspring birth weight increases with temperature during the last few months of gestation, presumably due to increased food availability, although the magnitude of an individual female's plasticity is itself dependent on the environmental conditions she experiences as a juvenile (Nussey *et al.* 2005). The environmental dependency of timing of breeding is also well established in a range of natural populations, most notably, though not exclusively, among avian taxa (e.g. Forchhammer, Post & Stenseth 1998; McCleery & Perrins 1998; Réale *et al.* 2003b; Both *et al.* 2004). In all these cases, plasticity in mothers' response to the environment will result in offspring phenotypes tracking changes in environmental conditions.

As any form of phenotypic plasticity, also maternal phenotypic plasticity can be noise produced by the environment, with the potential to initially have beneficial or nonbeneficial effects on offspring phenotype, or be truly adaptive (the result of past selection; Pigliucci 2001; Ghalambor *et al.*, in press). Maternal effects provide one of the strongest cases of adaptive plasticity: environmentally induced maternal effects often increase offspring fitness in heterogeneous environments (Bernardo 1996b; Galloway 2005). Environment-dependent benefits of maternal effects on offspring fitness create norms of reaction that can be moulded by natural selection (Mousseau & Dingle 1991; Rossiter 1998; Einum & Fleming 1999) and, when the cues are predictable, this can result in the evolution of *trans*-generational plasticity (Rossiter 1996; Mousseau & Fox 1998b). For instance, the adaptive benefits of a mothers' larger per offspring investment are often greater under stressful than under benign conditions (e.g. Gliwicz & Guisande 1992; Einum & Fleming 1999; Hereford & Moriuchi 2005; Mitchell & Read 2005; Räsänen, Laurila & Merilä 2005; but see Kaplan & Phillips 2006) favouring the evolution of larger eggs in stressful environments. In the same vein, benefits of maternal phenotypic plasticity can depend on offspring sex and environment. For example, the beneficial effects of large egg size on offspring body size could be more pronounced in female offspring when it influences their future fecundity (Falconer 1965) or in male offspring when it influences their attractiveness or competitive ability (Trivers & Willard 1973). In this vein, female field voles *Microtus agrestis* produce larger males when environmental conditions are good, whereas no such pattern is observed for female offspring (Koskela *et al.* 2004).

Although little explored to date, recent work also highlights the complexity of maternal phenotypic plasticity that arises from interactions between the mother's environment and offspring's environment (i.e. $E_m \times E_o$). In the seed beetle *Stator limbatus* females raised at low temperature produce eggs that have reduced hatching at high temperature (Stillwell & Fox 2005). In *Daphnia magna*, mothers that are well provisioned during their own development produce offspring with high disease resistance when environment is poor during their production (Mitchell & Read 2005). These studies emphasize the need to study the complex set of environmental interactions to understand the dynamics of selection acting via maternal effects.

ENVIRONMENTAL EFFECTS ON VARIANCE IN MATERNAL EFFECTS

Most work that has attempted to study associations between environmental conditions and maternal effects has focused on the population level *average* of maternal effects. In contrast, much less is known about associations between environmental conditions and the *variance* between females within populations. Differences in the expression of maternal effects between individuals

may be increased or decreased by environmental stress. For instance, in the blue tit *Parus caeruleus*, the variance in offspring growth rates arising from shared environment effects between nests (which will be heavily determined by parental effects) increased with environmental stress arising from parasitism by blowfly larvae (Charmantier, Kruuk & Lambrechts 2004). In contrast, the maternal genetic component of variance in lamb birth weight in Soay sheep was reduced in poor environments (Wilson *et al*. 2006). In the common frog *Rana temporaria*, maternal effects tended to be more pronounced when resources were limited (Laugen *et al*. 2005). However, there was little evidence of differences between populations experiencing different food availability or different temperatures in maternal effects components of variance in tadpole growth rates (Laugen *et al*. 2005). Moreover, as strong selection on offspring or maternal traits may erode additive genetic variance in fitness related traits more effectively in some environments than others, environmentally determined maternal effects may become relatively more important in those environments (Charmantier & Garant 2005).

MATERNAL EFFECTS' CONTRIBUTION TO POPULATION DIVERGENCE

Phenotypic variation between populations in the wild may have a large environmental maternal effect component, the extent of which may differ between populations. However, differences between environments in the adaptive benefits of maternal effects should select for among-population variation in maternal effects when populations inhabit divergent selective environments. This expectation is further reinforced because epistatic interactions between mother and offspring ($G_m \times G_o$), as well as selection on maternal effects acting at the family level, can lead to rapid local adaptation and speciation (Wade 1998). Somewhat surprisingly, however, geographic variation in adaptive maternal effects has been little explored in empirical work. As an example, geographic variation was found in diapause in many insects (reviewed in Mousseau & Dingle 1991) and in environmental maternal effects in the plant *Diodia teres* (Hereford & Moriuchi 2005; see also Kaplan 1980; Badyaev *et al*. 2002; Laugen, Laurila & Merilä 2002; Räsänen *et al*. 2005). The need to understand the role of maternal effects in evolution at ecological time-scales is further emphasized by their potentially strong positive and negative effects on dispersal and gene flow (e.g. Donohue 1999; Hereford & Moriuchi 2005) and thereby on colonization of novel environments and the extent of phenotypic divergence between populations. Clearly, more studies on geographic variation in maternal effects would shed light on the ongoing processes of natural selection, as well as allow more accurate predictions on responses of local populations to environmental challenges.

In conclusion, environmental variation can strongly influence the expression as well as the adaptive benefits

of maternal effects and thereby the evolutionary trajectories of populations. This environmental dependency needs to be considered when attempting to infer the role of maternal effects in evolutionary processes within populations as well as their contribution to adaptive divergence between populations.

Evidence for rapid evolutionary change via maternal effects in natural populations

Many empirical examples show that adaptation to novel environmental challenges is possible at short time-scales (Reznick & Ghalambor 2001; Palumbi 2001). Studies conducted under artificial rearing conditions show that such rapid evolutionary responses can arise also via maternal effects. For example, in Chinook salmon *Oncorhynchus tshawytscha*, hatchery rearing relaxes natural selection for large eggs and results in a shift from viability to fecundity selection, with a resulting decline in egg size in less than 20 years (Heath *et al*. 2003). However, to what extent do maternal effects influence rapid evolutionary change in natural populations?

In the following we will highlight three natural empirical systems where maternal effects play a substantial role in responses to environmental variation. These systems were chosen because they are among the few examples that have established maternally mediated adaptive responses to environmental variation at ecological time-scales (within a few decades), present three different taxonomic groups (amphibians, birds, mammals) and illustrate different ways (contribution of maternal effects to phenotypic change over generations within a population, adaptation to environmental stress and species invasions via phenotypic plasticity, as well as divergence between populations) in which maternal effects may play a role in responses to environmental change.

CONTRIBUTION OF MATERNAL EFFECTS TO BETWEEN-GENERATION CHANGE IN THE RED SQUIRREL

A study of North American red squirrels *Tamiasciurus hudsonicus* in Canada provides a rare test of some of the predictions of the quantitative genetic framework outlined above, and evidence for the impact of maternal effects on the rate of evolution within a wild population. Juvenile growth (body mass between birth and emergence from the natal nest) is a heritable trait. However, it also has a significant maternal genetic component of variance and a positive direct-maternal genetic covariance (McAdam *et al*. 2002; see also Table 2 and above), suggesting the potential for maternal effects to accelerate a response to the observed selection on juvenile growth rate (McAdam & Boutin 2003). In accordance with this expectation, between-generation rates of change were substantially greater than expected in the absence of maternal effects on growth. Second, the study was also able to detect the evolutionary time-lags characteristic
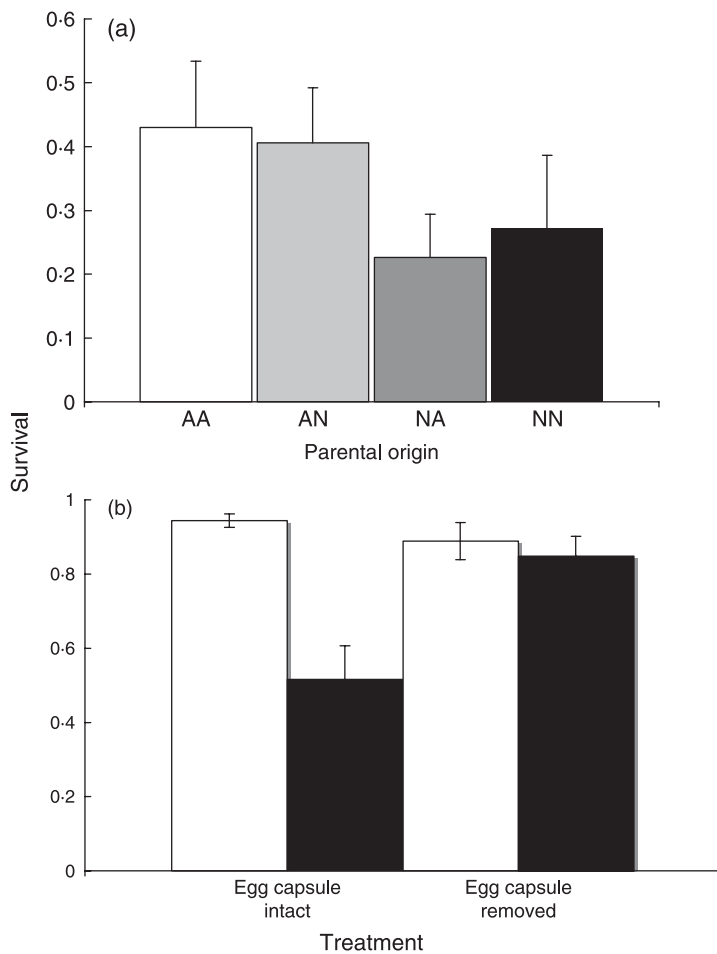
Fig. 2. The proportion (mean ± SE) of *Rana arvalis* embryos that survived until hatching at pH 4·0. (a) Embryos from reciprocal crosses between two populations. Codes on *x*-axis refer to the different crossing combinations: A = acid origin, N = neutral origin, maternal origin indicated by the first of the two letters. (b) Embryos from an acid- (white bars) and a neutral-origin (black bars) population with and without enzymatic removal of the egg capsule. For sake of clarity only pH 4·0 is presented. Survival at pH 7·5 is 91–97% in all cases and does not differ among groups. (See Räsänen *et al.* 2003b for details.)

of evolution through maternal effects (see above): observed rates of change were determined by the magnitude of selection experienced by both the current and the previous generation (McAdam & Boutin 2004). The research illustrates the potential for studies of natural systems to quantify the contribution of maternal effects to rapid evolutionary change within populations.

ADAPTATION TO HUMAN INDUCED
ENVIRONMENTAL STRESS IN THE MOOR FROG

Recent studies of the moor frog *Rana arvalis* show that maternal effects can contribute to adaptation to human-induced environmental change, such as increased levels of acidification. Acid conditions exert strong selective pressures on amphibians, in particular via reduced embryonic survival as well as larval growth and development rates (Pierce 1985; Räsänen, Laurila & Merilä 2003a). Swedish populations of *R. arvalis* appear to have overcome these challenges via adaptive maternal

effects and are able to successfully breed at sites where pH is as low as 3·8.

Consistent with local adaptation, acid-origin embryos have a two- to threefold higher survival at pH 4·0 than neutral-origin embryos (Räsänen *et al.* 2003a). Reciprocal crosses between a neutral-origin and an acid-origin population further showed that this adaptation is maternally mediated (Fig. 2a, Räsänen *et al.* 2003b; see also Merilä *et al.* 2004), likely arising from geographic variation in the chemical composition of egg capsules (Fig. 2b, Räsänen *et al.* 2003b). Moreover, under acid conditions, initially large acid-origin offspring (from large eggs) develop faster and metamorphose at a larger size for a given development rate (Räsänen *et al.* 2005). This fitness benefit also appears to have shaped female life histories: acid-origin females invest in fewer but larger eggs than neutral-origin females (Räsänen *et al.* 2005; Söderman 2006).

The adaptation has presumably occurred within 40 generations (100 years, Räsänen *et al.* 2003a), fitting a scenario of rapid response via maternal effects. The species' long generation time (maturation at 2–3 years) has so far precluded establishing whether these maternal effects are a result of changes in the genetic composition between the populations or species level phenotypic plasticity. Whichever the case, however, maternal effects have facilitated population persistence in face of environmental stress in this system. Such maternally mediated selective factors may become important via several novel environmental stressors: for example, chemical pollutants, pathogens and immune factors are often transmitted from the mother to the offspring – potentially imposing strong selection at very short time-scales.

COLONIZATION OF NOVEL ENVIRONMENTS
IN THE HOUSE FINCH

Extensive studies on the house finch *Carpodacus mexicanus* have highlighted how phenotypic plasticity in maternal effects can have population level consequences by enabling colonization of new environments. Two recently established populations occur at climatic extremes of the species' range. In Montana (where breeding started in late 1970s as an expansion of native range), suboptimally cold temperatures are common early in the season, whereas in Alabama (where breeding started in 1983 as a follow-up to introductions by humans) suboptimally hot temperatures are common late in the season (Badyaev *et al.* 2002, 2003). Juvenile survival in these populations is sex and hatching order dependent, but the pattern differs among populations (Badyaev *et al.* 2002). Subsequently, the optimal and observed onset of incubation, as well as laying order in relation to offspring sex, differ between the populations (Fig. 3a; Badyaev *et al.* 2003). These strategies modify offspring growth rates and parallel survival selection observed in adult birds, and have led to a rapid divergence of sexual size dimorphism in these populations
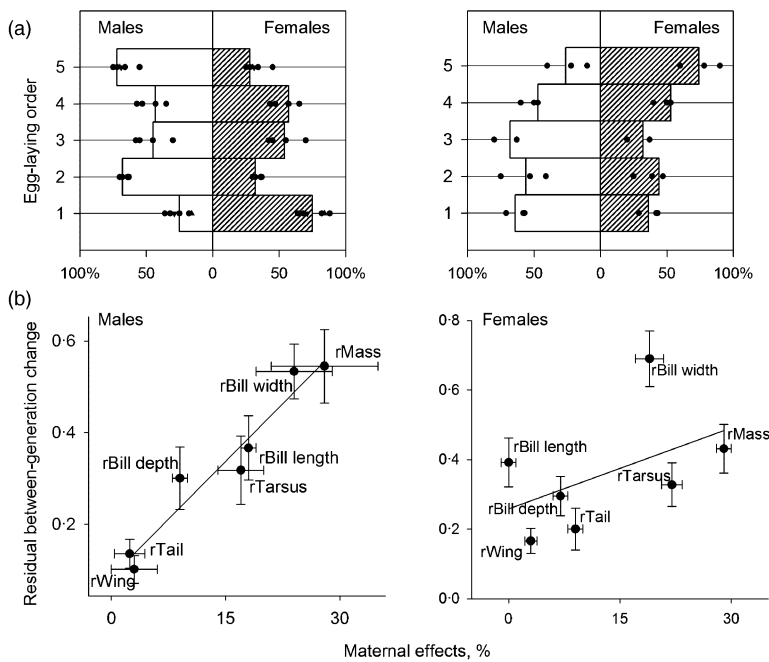
Fig. 3. (a) The ratio of sons and daughters in relation to the egg laying sequence in two populations (Montana and Alabama) of *Carpodacus mexicanus*. The bars represent the means from four (left: Montana) and three (right: Alabama) years of observations (indicated by filled circles). (b) Between-generation change in residual shape traits (mean ± 1 SE) in relation to the relative contribution of maternal effects (%) to the phenotypic within-generation variance in residual shape traits in the Montana population (see Badyaev *et al.* 2002 and Badyaev 2005 for details, respectively).

First, although there is accumulating evidence for a genetic basis in maternal effects, one of the major tasks of empirical studies is still to establish their genetic basis and, in particular, the covariance of any such basis with other genetic effects as well as with the environment. Measuring all of the parameters that describe the genetic basis of maternal effects and the selection pressures associated with them in a natural population in the wild would be a daunting endeavour, and it may be unlikely that eqn 1 will provide a close correspondence with observed phenotypic change in a trait in a wild population. The complexities are further increased by time-lags in response to selection introduced by maternal effects (Kirkpatrick & Lande 1989), and by the fact that selection acting among families as well as at an individual level permits components of epistatic genetic variance (between offspring and maternal traits) to contribute to the evolutionary response (Wade 1998).

Nevertheless, empirical estimates of these components will provide valuable insights into the potential impact that maternal effects have on rates of genetic change in a population, and their relative importance for evolution at ecological time-scales. The study of red squirrels (McAdam & Boutin 2004) described above provides an important illustration of the insights into a system's evolutionary dynamics offered by Kirkpatrick and Lande's quantitative genetic framework. Hopefully similar insights will be possible in systems where estimates are available for the contribution of maternal effects to both phenotypic variance and selection patterns, such as the feral population of Soay sheep on St Kilda, Scotland (Wilson *et al.* 2005a,c, 2006). Empirical estimates of the relevant parameters are still scarce for nondomestic species, and generalizations as to the conditions under which maternal effects may accelerate rather than constrain microevolution are currently difficult. Hopefully an increasing interest in the evolutionary ecology and quantitative genetics of maternal effects will encourage future research in these areas, and hence facilitate tests of explanations for the diversity of values observed.

As evidenced above, the impact of maternal effects may vary greatly between environments and between different populations: in some cases, they will presumably accelerate evolutionary change, and in others they will constrain it. The strong environmental dependency in both the expression of maternal effects and their adaptive benefits calls for more studies that establish the extent to which maternal effects differ among environments and among populations. Such studies will increase our ability to infer their impact on the evolutionary trajectories of populations in response to novel selective factors. When logistical constraints prevent this, such as would be common in studies of natural populations of organisms with long generation times, the availability of long-term data on environmental factors is extremely valuable. Several studies of wild populations in natural environments, particularly those using long-term records of individually monitored

(Badyaev *et al.* 2002, 2003). The strong maternal effects are influenced by differential sensitivity of males and females to adaptations of the maternal generation (Badyaev 2005), and the sex-specific clustering of oocytes in the ovary (Badyaev, Oh & Mui 2006). Analyses over multiple generations in the Montana population further show that, in males, the traits that evolved most rapidly are those that have the greatest maternal and environmental effects (Fig. 3b, Badyaev 2005).

The extent to which differences among these populations are genetically determined remains to be seen. Nevertheless, this system provides a rare empirical example of how plasticity in maternal effects can contribute to rapid colonization of new environments and species invasion. Such maternally mediated responses of contemporary populations may become a critical feature, for instance, under climate change as mothers in many species determine sex ratio and incubation conditions of offspring.

Synopsis and recommendations for future work

In the final remarks of their '*Maternal Effects as Adaptations*' book, Mousseau & Fox (1998a) concluded that many aspects of the contribution of maternal effects to evolution are poorly understood. Based on our brief review, it appears that despite increased attention in empirical work in recent years, many of the same gaps still remain.

animals, already contain information on sufficiently many generations across different environmental conditions to illustrate the relationship between maternal effects and natural environmental heterogeneity (for example, Clutton-Brock *et al.* 1983; Schluter & Gustafsson 1993; McCleery & Perrins 1998; McAdam & Boutin 2004; Nussey *et al.* 2005; Wilson *et al.* 2005a,b), and can be used for tests of the contribution of maternal effects to phenotypic change.

The empirical examples we present provide evidence for the role of maternal effects in evolution at ecological time-scales. The most daunting task, however, may lie in establishing how commonly and under which conditions maternal effects make a difference to the rate and direction of evolution. An attempt to infer their general role in evolution was made in a recent review of behavioural and morphological data, including studies of mammals, birds and some insects (Reinhold 2002). These data suggest that only mammals have strong and general maternal effects, possibly due to differences in the length of the parental care period. However, considering the numerous empirical studies from a range of taxa presented here (Tables 1 and 2), as well as the many theoretical predictions, maternal effects may play a role more often than is currently acknowledged in many systems. Future work should try to identify the conditions under which maternal effects are likely to have a significant (negative or positive) contribution to evolutionary processes within natural populations as well as contribute to adaptive divergence between populations. As with many areas of evolutionary biology, although the goal may be a better understanding of the natural world, much of the empirical data available to date still comes from work on domestic/agricultural populations, and useful insights can be gained by considering these data in the light of evolutionary questions (e.g. Wilson & Réale 2006). In the absence of rigorous studies on natural populations, targeted selection experiments could also allow researchers to explicitly test how evolutionary responses may be affected by the presence of maternal effects. At the very least, studies of the genetic basis and adaptive benefits of maternal effects must play an important part in reaching an understanding of the evolutionary dynamics of populations. The ongoing environmental challenges have already stimulated much work on attempting to establish the genetic basis of fitness related traits. What we now need is that these studies also fully acknowledge the potential importance of maternal effects.

Acknowledgements

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