

manipulation are developed, there is every reason to expect ample reward for research effort.

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*Maternal Effects as Adaptations*. Edited by TIMOTHY A. MOUSSEAU & CHARLES W. FOX. New York: Oxford University Press (1998). Pp. xiv+375. Price \$65.00.

Twenty years after the spandrels of San Marco, it is possible again to talk about adaptation (and adaptationism), albeit in a clearly more sophisticated way than previously (e.g. Rose & Lauder 1996). The volume edited by Mousseau & Fox is concerned with maternal adaptations, those mechanisms that mothers employ to enhance the fitness of their offspring; with maternal effects, parents contribute more than genes to the next generation. These mechanisms can accelerate, deter or sometimes reverse other responses to selection and can have profound effects of population dynamics and our understanding of evolutionary processes. Indeed, simply recognizing that maternal effects exist means that we need to consider selective events across two generations. More specifically, a maternal effect occurs if the phenotype of an individual is determined not only by its own genotype and environment, but also by the phenotype or environment of the mother. In the preface, Mousseau & Fox note that in the past maternal effects were usually treated as environmental noise! But variation is not noise, and this volume is an excellent exposition of the role of maternal effects in maintaining phenotypic variation.

The volume is organized into four parts: (1) recent theoretical developments; (2) assessment and measurement of maternal effects; (3) reviews of maternal effects across taxa; and (4) case studies of the adaptive significance of maternal effects. Each part begins with a precis by the editors, providing an overview and organizational framework for the papers that follow.

The theoretical section includes papers on the evolutionary genetics of maternal effects, the interaction of social selection, sexual selection and maternal effects, the role of maternal effects in population dynamics, and the discussion of oviposition behaviour as maternal effects. There are a number of important messages from these chapters. When maternal effects are present, evolutionary processes cannot be partitioned into

selection within versus between generations. The evolution of maternal effects involves selection among families. Maternal effects, relating offspring quality to per capita reproduction, can lead to oscillations in population dynamics (one of my favourite chapters, in part because of the simplicity of the model and the profundity of the consequences). Maternal behaviour that affects the environment of the offspring, such as egg-laying behaviour in parasitoids or butterflies, is as much a maternal effect as egg size or yolk allocation.

The second part of the book contains three excellent chapters that provide a guide for future empirical studies on the adaptive significance of maternal effects. The quantitative measurement and assessment of maternal effects present challenges in statistical analysis and experimental design. To some extent, recognition of maternal effects requires a change in the way that we think about parental contributions to offspring. That is, maternal effects are explicitly cross-generational and for design and analysis of experiments need to be viewed as an environmental (rather than a genetic) component of offspring fitness, even if the source of the component arises solely from the parent's genetic expression.

The last two parts of the book examine the specifics of maternal effects. The survey in the third part of the book is exciting, partly because it focuses on so many interesting organisms and partly because we see the ubiquity of maternal effects. These have been observed in a variety of plants, many species of birds, over 70 species of insects, and 20 species of fish, along with (of course) mammals. My own favourite topics, the oviposition behaviour of insects and life history variation in fish, are well represented. In both cases, we see the 'classical' maternal effect that there is a generally positive correlation between maternal size, egg size and offspring size and a generally positive correlation between egg size and survival. In birds, maternal effects can provide an explanation for the observation of a decline in clutch size as laying date increases. The case studies in the last part of the book include the maternal control of diapause in the flesh fly *Sarcophaga bullata*, maternal effects in side-blotched lizards, *Uta stansburiana*, environmental sex determination in the diamond back turtle, *Malaclemys terrapin* (where a mother places her egg determines whether that offspring will be female or male, possibly the ultimate maternal effect), and density-mediated maternal effects in the wild radish, *Raphanus sativus*.

Like wealth, maternal effects are inherited but not heritable; but also like wealth, they can be very important to the success of offspring. They affect the development, behaviour and life history of individuals, the interactions between individuals, and the population dynamics of species. They blur the distinction between genetic and environmental components of phenotypic variation and present a range of challenges from conceptual formulation to experimental design and assessment. But, to paraphrase Feller (1971), challenges are not overcome by ignoring them. This excellent volume will allow us both to face the challenges raised by maternal effects and to overcome these challenges, into an even more advanced understanding of adaptation.

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