



ANNIVERSARY ESSAY

Behavioural processes affecting development: Tinbergen's fourth question comes of age

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Interest in relationships between behaviour and development has been spurred by research on related topics, including phenotypic plasticity, parental effects, extragenetic inheritance, individual differences and trait syndromes. Here, I consider several emerging areas of research in the interface between behaviour and development, with a focus on behavioural processes that are likely to affect the development and maintenance of interindividual variation in a wide array of morphological, physiological and behavioural traits. Using a norm of reaction approach, I introduce and illustrate the complexities of phenotypic development. Next, I consider the implications of environmental selection and niche construction for phenotypic development, and consider why these behavioural processes are likely to encourage the development and maintenance of repeatable, stable individual differences and trait syndromes. Parental effects involving behaviour also affect the development of a wide array of phenotypic traits; differential allocation is a currently underappreciated type of parental effect, by which males can affect the development of their offspring via nongenetic means, even if those males have no contact with their young. Behavioural parental effects also contribute to extragenetic inheritance, and recent studies suggest that this phenomenon may be more widespread than previously suspected. The effects of behavioural processes on phenotypic development have interesting implications for problems in related disciplines (e.g. ecology, evolution and conservation biology), providing additional impetus for future research on the effects of behavioural mechanisms on the development of behavioural and other traits.

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In the middle of the last century, [Tinbergen \(1963\)](#) was sufficiently interested in development to add this topic to his list of the 'four questions' of animal behaviour, having borrowed his other three questions (on immediate causation, survival value and evolution, respectively) from J. S. Huxley. Subsequently, research on developmental topics was temporarily eclipsed by the growth of sociobiology ([Wilson 1975](#)), behavioural ecology ([Krebs & Davies 1997](#)) and evolutionary psychology ([Buss 1999](#)), but the last few years have seen a resurgence of interest in relationships between behaviour and development ([Bateson 2001a](#); [Oyama et al. 2001](#); [Johnston & Edwards 2002](#)). In this essay, I suggest that we are poised for a surge in research on topics involving behaviour and development, impelled in part by the salience of these topics for related disciplines, including behavioural

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ecology, ecology and evolutionary biology. In particular, I suggest that behavioural processes may play a larger role than previously suspected in the development and maintenance of interindividual variation in a wide array of phenotypic traits, including morphological and physiological as well as behavioural traits.

Interest in behavioural processes affecting development has been encouraged by a renewed focus on developmental issues by ecologists and evolutionary biologists. One example is the literature on phenotypic plasticity and reaction norms, which considers the effects of experiential factors on the development of morphological and physiological traits (reviews in [West-Eberhard 1989](#); [Schlichting & Pigliucci 1998](#)). For instance, fish that eat hard prey items (e.g. snails) as juveniles develop much larger jaw muscles than otherwise equivalent juveniles provided with softer prey items ([Mittelbach et al. 1999](#)); similarly striking effects of early diet on the development of trophic structures have been reported for primates

(Corruccini & Beecher 1984), insects (Bernays 1986) and birds (Piersma et al. 1999). These and other recent studies of phenotypic plasticity have helped lay to rest the assumption that behavioural traits are necessarily more plastic than morphological traits, and have encouraged research on the ways that experiential factors influence the development of a wide range of morphological, physiological and behavioural traits (reviews in Gilbert 2001; Oyama et al. 2001).

Interest in relationships between behaviour and development has also been encouraged by the recent spate of studies on parental effects (also known as maternal effects), which consider situations in which phenotypic traits in parents affect patterns of development in their offspring (Mousseau & Fox 1998; McAdam et al. 2002; Sheldon 2002). Of course, many parental effects explicitly involve behavioural processes. In addition, parental effects can contribute to 'extragenetic inheritance': the transmission of phenotypic traits across generations via mechanisms that do not involve the transmission of genetic material (Jablonka 2001; Fleming et al. 2002).

Finally, interest in developmental processes that generate individual variation has been encouraged by a growing appreciation among behavioural and evolutionary biologists that selection often favours phenotypic diversity, rather than favouring a single phenotype that is optimal for every individual in a given population. It is easy to see that selection might favour the development of phenotypic polymorphisms when members of the same species live in different types of habitats, where they are subjected to different types of selective pressures (Hedrick 1986; Gillespie & Turelli 1989). For example, spiders that vigorously attack prey and conspecifics grow more rapidly than timid spiders in arid habitats with low prey availability, but timid spiders have the advantage in nearby riparian habitats, where bolder individuals suffer higher predation rates (Riechert & Hall 2000). However, selection can also favour phenotypic diversity even if every individual in the population lives in the same environment. For instance, animal behaviourists are familiar with the notion that alternative phenotypes can evolve as a result of negative frequency-dependent selection, which occurs when rare phenotypes are favoured by selection (Ayala & Campbell 1974; Maynard Smith 1982; Dugatkin & Reeve 1998). Thus, Sinervo & Lively (1996) suggested that three alternative reproductive morphs of lizards might be maintained by frequency-dependent selection, because individuals of each type perform best when the other morphs are more common. In addition, selection can favour the development and maintenance of phenotypic diversity when there are strong trade-offs among traits related to fitness, such that individuals with high values of particular fitness traits necessarily have lower values on other fitness traits (Whitlock 1996; Orzack & Tuljapurkar 2001). For instance, trade-offs between growth and mortality rates can produce situations in which individuals growing at a wide range of different rates end up with virtually the same fitness (Mangel & Stamps 2001).

This literature suggests that, from an evolutionary perspective, one should not necessarily expect natural or

sexual selection to favour a single developmental trajectory, which generates a single 'typical', 'normal', or 'optimal' phenotype that is best for every individual in the population. Instead, this literature suggests that we should be actively looking for behavioural processes that encourage the development and maintenance of interindividual differences in behavioural, physiological and morphological traits. As we will see below, certain types of behavioural processes are prime candidates for the development of predictable patterns of phenotypic diversity among the individuals in a given population.

Although the current essay focuses on the role of behavioural processes in the development of variation in phenotypic traits, a modest amount of 'background' material is required before we reach this point. I begin with definitions of some of the key terms in the paper, with an emphasis on topics (e.g. behavioural trait syndromes) that may be unfamiliar to some readers. Then, I use a norm of reaction approach to introduce and illustrate some of the complexities of interactions between genes and experiential factors on the development of behavioural and other traits. At that point, we can consider three behavioural processes with major potential effects on development: (1) environmental selection and modification, (2) parental effects (including differential allocation) and (3) extragenetic inheritance via behavioural processes. Finally, the last section considers some of the implications of these behavioural processes for problems in related disciplines, including ecology and evolution.

DEFINITIONS

To consider processes that affect development, we first need to consider the products of development (i.e. the morphological, physiological or behavioural traits that are generated via developmental processes). Here, 'trait' refers to any variable that can be measured for a given individual at a given point in time. Traits can be morphological (e.g. wing length), physiological (concentration of testosterone in the bloodstream) or behavioural (rate of production of an aggressive display). In this essay, I focus on behavioural traits that vary between individuals but are consistent (repeatable) within individuals over an appreciable period of their lifetimes; hereafter, I use the term 'individual differences' to refer to this situation (e.g. Wilson 1998).

When behavioural biologists measure different traits in the same individuals, they often observe correlations among different traits across individuals (Koolhaas et al. 1997; Wilson 1998; Gosling 2001; A. Sih, A. Bell, J. C. Johnson & R. E. Ziemba, unpublished data). In this essay, the term 'trait syndrome' refers to correlations among different traits across individuals in the same population; and recent studies indicate that behavioural trait syndromes are common in animals (Sih et al., unpublished data). One example is 'sociability' in primates, a trait syndrome that reflects positive correlations across individuals between different behavioural measures related to social interactions with conspecifics (e.g. see Capitanio

1999; Gosling 2001). In spiders, individuals that are quick to attack intruders (competitive behaviour) also have a shorter latency to emerge after a simulated predator attack (antipredator behaviour) and are more likely to engage in wasteful killing of prey (foraging behaviour) (Riechert & Hedrick 1993; Maupin & Riechert 2001). In great tits, *Parus major* (Verbeek et al. 1996), individuals that quickly (but superficially) explore novel environments attack conspecifics more quickly, are more likely to win aggressive interactions with opponents, are less likely to respond to changes in familiar environments and are more likely to follow a previously learned 'routine' when faced with environmental change than individuals that slowly and thoroughly explore novel environments. These differences in exploratory style and the traits correlated with them are consistent (repeatable) across time, and juvenile great tits have exploratory scores similar to those of their parents (Dingemanse et al., in press). As we will see, the existence of trait syndromes raises important questions about the processes that are responsible for generating and maintaining correlations among different traits across individuals.

With respect to behavioural development, we rely on Tinbergen's original definition of ontogeny: a change in behaviour machinery during development. This definition emphasizes the physiological and morphological systems that are responsible for producing behavioural traits at any given point of time. Note that this definition is silent with respect to the duration or reversibility of changes in behaviour or behavioural machinery, reflecting an early appreciation among behaviourists that distinctions between long- versus short-term changes, or more versus less reversible changes in behaviour are arbitrary (see also Hinde 1970, page 5). Also, note that this definition is more general than 'maturation', or the achieving of 'adult' function. Changes in the machinery affecting behaviour do not cease when an animal matures, as evidenced by studies indicating that neural plasticity is characteristic of adults as well as juveniles (Stiles 2000). Nor do phenotypic traits expressed in juveniles simply reflect preparation or practice for adult function. Instead, they are shaped by selective forces that affect juveniles during the periods when those traits are expressed. For instance, Galef (1981) discusses the many specialized traits that young mammals use to extract resources from their mothers, and suggests that mammalian offspring might be more properly viewed as highly adapted parasites than as incompletely formed adults. Conversely, if a trait has the same form in juveniles and adults, there is no a priori reason to assume that the trait must have been shaped by selection acting on adults. Thus, water snakes, *Nerodia sipedon*, show colour polymorphisms that are expressed in neonates and continued into adulthood (King 1993). Field studies indicate that natural selection is currently operating on the distribution of colour patterns in neonates and juveniles, but not in adults, results that are consistent with the hypothesis that differential predation by visual predators on juveniles is responsible for the distribution of colour patterns in this species (King 1993).

GENES, EXPERIENCE AND THE DEVELOPMENT OF PHENOTYPIC DIVERSITY

To consider how behavioural processes contribute to the development and maintenance of phenotypic variation, we first need to consider how any experiential factor (not just those related to behaviour) affects the development of behavioural and other traits. One of the easiest ways to appreciate the complex ways that experiential factors interact with genetic factors to affect development is via reaction norms. The term 'reaction norm' refers to the set of phenotypes that can be produced by an individual genotype that is exposed to a range of different environmental conditions (Schlichting & Pigliucci 1998; Falk 2001). In turn, the term 'genotype' refers to all of the genes in a given individual, not just to a particular gene of interest. This is because the effects of a particular gene on development often vary as a function of other genes in that same individual, such that individuals with the same alleles at a given genetic locus, but with a different genetic background, develop differently under the same environmental conditions (e.g. Greenspan 2001).

Unfortunately, the perfect norm of reaction experiment is achievable only in science fiction: a series of 'parallel universes' in which the same individual experiences different sets of environmental conditions during its development. Given the impracticability of this experimental design, empirical studies of reaction norms typically rely on model systems in which the subjects destined to be raised in different environments are as genetically similar as possible (e.g. clones, parthenogenetically generated individuals, hybrid crosses of inbred strains, or very closely related individuals, such as full siblings). In this way, it is possible to raise different individuals with comparable genotypes in different environments at the same time.

Graphical depictions of reaction norms plot trait values against a range of environmental conditions for a number of different genotypes, each of which is represented by a different line.

A highly idealized set of reaction norms for three genotypes (individuals) from the same population is illustrated in Fig. 1. Assume that each of three genotypes is maintained from the time of conception to the time of measurement in several different environments, and that a behavioural trait (or an individual's score on a trait syndrome) is measured at the end of this period. Depending on the study, 'environment' might refer to a single experiential factor of interest (e.g. temperature, Imasheva et al. 1997), or it might refer to localities that differ from one another in a number of respects, only some of which are apparent to the experimenter (e.g. 'common garden' experiments, cf. Clausen et al. 1948). Similarly, 'phenotype' can refer to a single behavioural trait, or to a composite variable reflecting a cluster of correlated traits (e.g. an individual's score from a factor analysis).

Several general points can be illustrated using this idealized set of reaction norms. First, reaction norms span the entire range of environmental conditions in which the members of a population might be able to live and

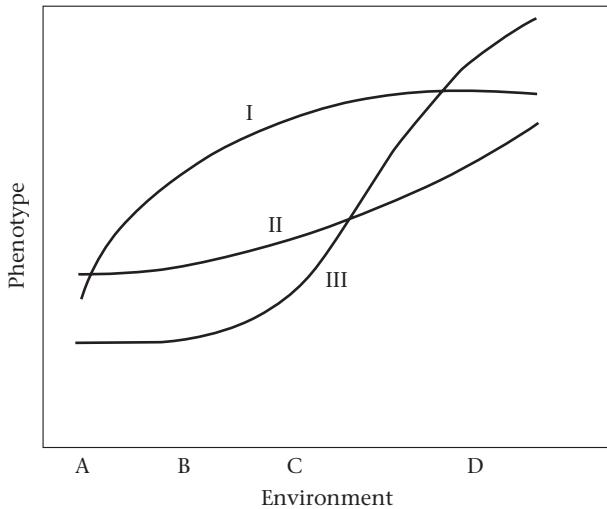


Figure 1. An idealized set of reaction norms for three different genotypes (I, II and III), which develop under a range of environmental conditions (A through D). Each individual's phenotype at a specified point in time results from interactions involving all of its genes (genotype) and the environmental conditions it experienced prior to that point in time. Variation among genotypes with respect to the intercept, slope and shape of their reaction norms makes it difficult to assign phenotypic variation to genetic or environmental influences.

reproduce, not just those in which they currently live (Schlichting & Pigliucci 1998). For instance, imagine that most members of a population currently live in one of two environments indicated by points B and C. Not unnaturally, a reaction norm study might focus on development in these two environments. However, in the past, the ancestors of this population lived in other types of environments (e.g. A), and as a result of global warming, members of this population will soon find themselves in a new type of environment, indicated by D. Hence, a reaction norm that considers experiential conditions beyond those currently experienced by the members of a population may uncover phenotypes that used to be common in their ancestors, and provide insights into new phenotypes that might be expressed by members of that population in the future.

Reaction norm diagrams also illustrate why it is so difficult to partition phenotypic variation into genetic and environmental components (Lewontin 1974; Gupta & Lewontin 1982; Bateson 2001b; Falk 2001). Reaction norms typically do not form a neat set of parallel straight lines. Instead, genotypes often vary with respect to the shape, intercept and slope of their reaction norms, so that all of these factors need to be specified when comparing reaction norms for different genotypes (Via et al. 1995; Schlichting & Pigliucci 1998). One consequence of inter-individual variation in the shape and position of reaction norms is that the proportion of phenotypic variance that can be attributed to genotype and to environment varies as a function of both the genotypes and the environments that are included in a given study. For instance, if genotypes I and III were raised in the environments

indicated by points B and C, most of the observed variance in the phenotypic trait would be attributable to variation between genotypes. In contrast, if genotypes I and II were raised in the environments at points A and D, most of the phenotypic variation in the same trait would be attributable to differences between environments A and D.

As a practical matter, variation among genotypes in the shape and position of their reaction norms greatly complicates efforts to identify genes that affect the development of behavioural and other traits. For example, behavioural geneticists using house mice, *Mus domesticus*, as a model system have crossed standard inbred lines to produce different genotypes, each of which has a stable genetic composition, making it possible to raise and test the same genotype under a range of environmental conditions (Wahlsten 2001). However, complicated interactions between genotype and environment are common, such that some genotypes respond more than others to particular features of the environments in which they are raised or tested. Thus, in an attempt to identify quantitative trait loci (QTLs) related to locomotion in mice, Flint et al. (1995) used an F2 hybrid cross from two strains (C57BL/6J × BALB/cJ) and tested their subjects in a circular, white, open field measuring 60 cm in diameter; these investigators reported QTLs for locomotor activity on chromosomes 1, 4, 12 and 15. In another study on the same question, Gershenfeld et al. (1997) used the F2 hybrid cross of C57BL/6J × A/J, tested them in a square, clear, open field measuring 42 × 42 cm, and reported QTLs for locomotor activity on chromosomes 1, 10 and 19. At this point, it is not clear whether the differences in the genetic loci associated with locomotor behaviour were a result of rearing mice in different laboratory environments, differences in the test apparatus, genetic differences between the crosses, or interactions between these factors (Wahlsten 2001).

Because this degree of variation in results is unacceptable for biologists interested in specifying the effects of genes on behavioural development, investigators typically handle the problem by concentrating on one (or a few) genotypes, which are maintained under rigidly controlled, standardized conditions in the laboratory (e.g. Gilbert & Jorgensen 1998; Schaffner 1998; Wahlsten 2001). In effect, such studies reduce the effects of environment and of genotype–environment interactions on development by focusing on a single genotype in a single environment (e.g. genotype I in condition C, Fig. 1). The difficulty, of course, is that even the most complete description of the genes involved in behavioural development for this individual in this environment might not tell us much about the genes related to the development of the same trait in other individuals in that same population, or about other genes that would have influenced the development of this trait, had the same individual been raised under a different set of conditions.

Even as an idealized diagram, Fig. 1 is still a gross oversimplification because it assumes that genotypes are maintained in the same environments from the time of conception. There are at least two problems with this scenario. First, investigators virtually always initiate

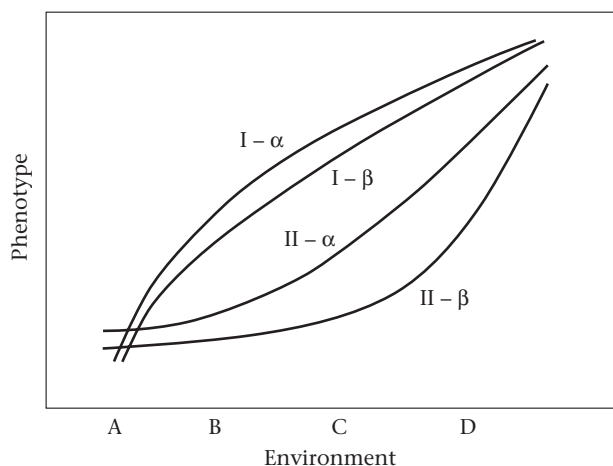


Figure 2. An idealized set of reaction norms illustrating the ways that early experience (α or β), later experience (environments A through D) and genotype can interact to influence the development of phenotypic traits. The shape and position of these curves illustrates a three-way interaction between the effects of genotype, early experience and later experience on development: for genotype II, early experience has a strong impact on phenotypic development in environment C, but a weaker effect on development in environment B, whereas for genotype I, early experience has a weak effect on development in both environments B and C.

experimental treatments well after the point of conception, after a variety of factors in the egg, the uterus, or the postnatal environment have had an opportunity to affect the developmental trajectories of the experimental subjects. Many of these factors are produced by the individual's parents (see parental effects, below), so at the very least, investigators must control for parental effects when studying the reaction norms of different genotypes raised in different environments (e.g. Holtmeier 2001; Laurila et al. 2002). Second, from a conceptual point of view, Fig. 1 glosses over the fact that the effects of experience on development often depend on the state of the individuals when that experience occurs, and, in turn, that an individual's state at any point in development is affected by interactions between its genotype and experiences prior to that point in time (Gottlieb 1992; McNamara & Houston 1996; Schlichting & Pigliucci 1998; Oyama et al. 2001). Indeed, even introductory students of animal behaviour are taught that the effects of experience on development depend on the period during development when the organism receives that experience, as reflected in the familiar concept of 'sensitive periods' (e.g. Alcock 1998).

The temporal contingencies that affect behavioural development are difficult to capture in a simple diagram, but Fig. 2 may provide a useful starting point for thinking about them. Assume that individuals are placed into the environments of interest at a convenient point in early development (e.g. at hatching), and that each individual's state at hatching is determined by its genes, factors its mother placed into its egg, and all of the other environmental factors that impinge on an individual from conception to hatching. For simplicity, assume that there are only two sets of conditions that individuals

experience prior to hatching (α or β), and that we are interested in the reaction norms for two genotypes (I and II). After hatching, individuals with different genotypes and early experience are reared in a range of environments, after which their phenotypes are measured, as in Fig. 1. In this graph, a two-way interaction between early experience and later experience on the development of the phenotypic trait is indicated by the fact that for each genotype, the effect of the second environment (e.g. B versus C) on the development of the phenotype varies as a function of previous experience (α or β). A three-way interaction between genotype, early experience and later experience on development is indicated by the fact that the interaction between early experience and later experience varies as a function of genotype: in genotype II, early experience has a much stronger effect on the relationship between later experience and phenotypic development than is the case for genotype I. Although still highly oversimplified, Fig. 2 illustrates why it is so important to keep an individual's prior history in mind when designing and interpreting studies of the development of behavioural and other traits.

In summary, diagrams of reaction norms can be quite useful for illustrating some of the complexities of development that have been obvious to animal behaviourists for many years (e.g. see Lehrman 1953), but are sometimes difficult to grasp when presented in a descriptive format. In addition, a norm of reaction approach provides a useful point of departure for a discussion of behavioural processes that are likely to influence the production and maintenance of phenotypic variation within populations, a topic I explore in greater depth below.

DEVELOPMENT AND MAINTENANCE OF INDIVIDUAL DIFFERENCES AND TRAIT SYNDROMES

Selection and Modification of the Environment

The classic norm of reaction approach implicitly assumes that experience affects the individual but that the reverse is not the case: the individual does not influence its own experience. However, any animal behaviourist is aware that animals are not merely passive organisms at the mercy of external environmental forces. Instead, animals frequently select their own environments, or modify their environments through their own actions (Waddington 1959; Lewontin 1983; Bateson 1988; Olding-Smee 1988; Laland et al. 2001). Of course, environmental selection and environmental modification are both explicitly behavioural processes. As we will see below, both of these processes can profoundly affect the patterns of phenotypic variation that we observe in natural populations.

Over the years, behavioural ecologists have documented many situations in which individuals select the environments that they will experience in the future. Thus, dispersers in heterogeneous landscapes select the habitats in which they will spend their lives (Stamps 2001), and within those habitats, individuals choose

particular microhabitats in which to conduct particular activities, including foraging, mating and raising offspring. An example are cryptic species in which individuals improve their degree of crypsis by selecting microhabitats based on their visual characteristics (Broadman et al. 1974; Gillis 1982; Steen et al. 1992).

In many animals, the social environment is at least as important as the physical environment: the group, mate or neighbourhood with which an individual lives will affect its social behaviour over extended periods. Individuals in nature often have a choice of social situations available to them, as a result of which, the social environment experienced by a particular individual can be at least partially determined by choices made by that individual. In socially monogamous birds, animals select the partner with whom they will interact for subsequent months to years (Gowaty & Mock 1985; Black 1996), and in group-living animals, natal dispersers select a new group in which they are likely to remain for the rest of their lives (Brown & Brown 1996; Kunkele & Von Holst 1996). Even in territorial species, dispersers often have a choice of neighbourhoods that differ with respect to the density or type of residents living within them (Stamps 2001; Doligez et al. 2002).

Selection of an environment is not the only process by which individuals can affect the environment in which they develop: animals can also modify the environment(s) in which they will live. Traditional studies of niche construction have focused on modifications of the physical environment; examples include beaver dams, termite mounds, or spider webs (review in Laland et al. 2001). Less widely appreciated is the extent to which animals control their social environment through their own behaviour, a situation we might term 'social construction'. Social construction occurs when an individual affects its future social environment, by initiating particular types of social interactions with conspecifics with whom it might interact in the future.

For instance, consider a situation in which an individual remains in a particular area, and vigorously attacks conspecifics whenever it encounters them. If the members of this species tend to avoid areas where they have been attacked (i.e. 'punished'), then an individual who attacks conspecifics will eventually construct a social environment that features low spatial overlap and low encounter rates with those conspecifics. In other words, using aggressive behaviour, the individual has constructed a territory (Stamps & Krishnan 1999, 2001; Switzer et al. 2001). Other examples of social construction include the use of aggressive behaviour to affect the rates and types of subsequent agonistic interactions with group members, through the establishment of dominance relationships (Drews 1993; Pagel & Dawkins 1997), or the use of affiliative behaviour to increase the likelihood of engaging in a range of positive interactions with particular individuals in the future (Capitani 1999).

The ability of animals to select or modify their environments has implications for the development and maintenance of phenotypic diversity in natural populations. Returning to Fig. 1, imagine that genotype I prefers

environment C, while genotype II prefers environment B. In that case, most individuals would express one of two alternative phenotypes: one a result of the combination of genotype I and environment C, and the other a result of the combination of genotype II and environment B. Note that this bimodal distribution of phenotypes requires that individuals be able to select their own environments; it would not develop if those same genotypes were randomly assigned to environments (as is typically the case in norm of reaction experiments).

Indeed, variation among genotypes in environmental selection or construction is not required, behavioural processes alone could encourage the development and maintenance of alternative phenotypes within the same population. The development of stable individual differences and trait syndromes is expected whenever the following conditions are satisfied: (1) a population lives in a heterogeneous environment, (2) each individual selects an environment that it can use for an extended period, (3) experience in a particular type of environment affects development in a way that improves subsequent performance in that type of environment, and (4) individuals prefer to remain in or return to environments in which they perform at relatively high levels. If these four conditions are satisfied, an initial choice of environment (perhaps made on a purely random basis) will encourage the development and maintenance of adaptive trait syndromes involving a suite of behavioural, physiological and morphological traits.

I am unaware of any empirical study that directly bears on this point, but juvenile fish might be suitable candidates for such a study. Many fish live in habitats that are heterogeneous at the spatial scale of a home range or territory. For instance, juvenile brook charr, *Salvelinus fontinalis*, can spend their time in fast- or in slow-moving water, and fish living in these two types of microenvironments within the same stream significantly differ with respect to a number of traits, including site fidelity, aggressive rates, foraging styles, diet, body shape and caudal fin height (Grant & Noakes 1988; McLaughlin & Grant 1994). Current evidence suggests that the differences between the juveniles inhabiting fast- and slow-flowing water could be a result of phenotypic plasticity (e.g. significant differences in caudal fin heights can be generated by raising randomly selected charr in different flow regimes; Imre et al., in press), and in other fish, foraging on a particular type of prey has been shown to improve subsequent performance with that type of prey, for example, because particular diets induce changes in musculature or skeletal components of the feeding apparatus (Wainwright et al. 1991; Day & McPhail 1996), or because the ability of individuals to recognize, attack and handle particular types of prey improves as a function of previous experience with that type of prey (Kieffer & Colgan 1991; Skulason et al. 1993). Hence, current evidence implies that even if two young brook charr were identical when they first selected a location in which to live, behavioural processes would encourage the development of predictable clusters of correlated traits for individuals that selected fast- versus slow-moving water.

Parental Effects and the Development of Individual Differences and Trait Syndromes

Every animal develops in an environment that is influenced, in one way or the other, by its parents (Rossiter 1996). Social learning is obviously one process by which the behaviour of parents affects the development of traits in their offspring, but there are many others. For instance, a mother lizard's choice of incubation temperature for her eggs can affect the antipredator behaviour of her hatchlings (Downes & Shine 1999), or the amount of food dung beetle parents provide to their offspring can affect the body size of their offspring (Hunt & Simmons 2000).

Even in species with extensive amounts of parental care, important parental effects may occur via behavioural mechanisms that do not involve social learning. A particularly salient example is provided by Meaney (2001) and his colleagues, who studied how variation in 'maternal style' in rats affects the development of a cluster of correlated behavioural and physiological traits in their pups. Some mothers lick and groom offspring at high rates, and adopt a nursing posture that allows pups easy access to the nipples, and other mothers lick and groom at lower rates, and adopt a more restrictive posture while nursing. In turn, maternal behaviour has profound effects on the development of a suite of correlated traits in their young, effects that appear to be mediated by changes in the development of corticotropin-releasing factor (CRF) systems. For instance, cross-fostering studies indicate that pups reared by high-licking mothers are less fearful and less responsive to stress at adulthood, and have reduced resistance to certain pathogens, than pups reared by low-licking mothers. Hence, in this case, differences in maternal behaviour during the first week after birth contribute to the development of central CRF systems that affect a suite of behavioural and physiological traits throughout life.

Differential allocation is another parental effect with the potential to affect the development of an impressive list of phenotypic traits. Differential allocation occurs when the allocation of resources to offspring by one parent varies as a function of phenotypic traits in the mate (Burley 1986). Thus, differential allocation explicitly involves behavioural processes, in that stimuli from one parent influences parental effects mediated by the other parent. Burley (1988) provided the first evidence for this hypothesis, by experimentally manipulating the attractiveness of male and female zebra finches, *Taeniopygia guttata*, using coloured leg-bands, and showing that the mates of individuals with attractive bands invested more time caring for their offspring than did the mates of individuals with unattractive bands. Subsequent studies have shown that female zebra finches sequentially mated to males with attractive and unattractive bands alter the amount of testosterone in their eggs, as a function of male band colour (Gil et al. 1999; but see Petrie et al. 2001). In turn, exposure to testosterone deposited in avian eggs affects the begging rates, aggression and growth rates of the nestlings that hatch from those eggs (Schwabl 1993, 1996; Eising et al. 2001; C. M. Eising & T. G. Groothuis, unpublished data). Taken

together, this literature suggests that stimuli from a male bird could influence the development of a suite of behavioural and physiological traits in his offspring, via the effects of those stimuli on hormones placed into the eggs by his mate.

In recent years, differential allocation has been reported in a wide range of taxa, suggesting that this phenomenon may be quite common in animals (review in Sheldon 2000; see also Kolm 2002; Nilsson et al. 2002; Saino et al. 2002). This indicates that a hitherto unsuspected behavioural process may provide yet another way that traits in parents can influence the development of their offspring. In particular, differential allocation provides a nongenetic route by which phenotypic traits in fathers can influence the development of their offspring, even in species in which fathers have no contact with those offspring.

Extragenetic Inheritance and the Development of Individual Differences and Trait Syndromes

Any discussion of parental effects leads directly to a closely related topic: extragenetic inheritance. Extragenetic inheritance occurs when there is a correlation between phenotypic traits in parents and offspring for reasons other than the transmission of genetic material between parents and their offspring. The fact that extragenetic inheritance is defined in negative terms reflects the prevalent assumption that the inheritance of phenotypic traits is virtually always due to the inheritance of genetic material (Jablonka 2001). This emphasis on genes as the primary, if not the only, mode of inheritance has broadened over the years to encompass other processes affecting development. For instance, parental effects can be subsumed within the genetic-primary paradigm by including genes that affect traits in the parents (Rossiter 1996; Mousseau & Fox 1998; Wolf 2000); genes are still assumed to govern inheritance, but now we consider two sets of genes, those in parents, and those in offspring, and estimate the effects of the former on the latter (Kirkpatrick & Lande 1989; Oklejewicz et al. 2001). Reaction norms can also be accommodated under the same paradigm, by assuming that reaction norms, and the plasticity they generate, have a genetic basis (Schlichting & Smith 2002).

Over the years, animal behaviourists have provided several clear counterexamples of extragenetic inheritance in animals. Familiar cases include the cultural transmission of songs in birds (e.g. Grant & Grant 1996; MacDougall-Shackleton & MacDougall-Shackleton 2001), or the transmission of food preferences from mothers to their offspring (Galef & Whiskin 1997). Even so, many biologists still seem to view examples of extragenetic inheritance via behavioural processes as interesting curiosities, exceptions to the general rule that modes of inheritance are almost always genetic.

One possible reason for the widespread dismissal of behavioural extragenetic inheritance is the equally widespread assumption that social learning is the mechanism responsible for most, if not all, extragenetic inheritance in animals (Cavalli-Sforza & Feldman 1981; Boyd &

Richerson 1985, 1996; Takahasi 1999; Jablonka 2001). However, only a limited number of species and situations satisfy the conditions required for the transmission of behavioural traits via social learning (Caro & Hauser 1992; Brooks 1998; Galef 2001), and empirical support for cultural inheritance in animals is sparse (Boyd & Richerson 1996; Sterelny 2001).

Recently, however, it has become apparent that social learning is only one of several behavioural processes that can encourage correlations between traits in parents and their offspring. Generally speaking, two components are required for any type of extragenetic inheritance. First, extragenetic inheritance requires parental effects: some physiological, behavioural or morphological trait X in parents that directly affects the development of trait Y in their offspring. Second, mechanisms must exist in the offspring that increase the likelihood that individuals that develop trait Y early in life will express trait X later in life, when they themselves mature and become parents. This second mechanism is required to ensure that the parental trait(s) that shape offspring developmental trajectories reliably reappear in successive generations.

Cultural transmission provides a simplified version of this scenario, because in this situation, X and Y are the same trait. The same is true when parents directly pass substances to their young during the period of parental care (e.g. when the transfer of odours in maternal milk affects the food odours preferred by young after they begin to forage on their own; Galef & Sherry 1973; Provenza & Balf 1987). In these situations, the critical question is why individuals that learned motor patterns or preferences for particular stimuli from their parents early in life would continue to express these same behaviour patterns much later in life, when they have offspring of their own. One possible answer to this question is that the behaviour X learned from its parents will be maintained into adulthood when the rewards that are contingent upon the production of behaviour X as an adult are higher than the rewards that are contingent upon the production of alternative forms of behaviour (Galef 1996; Galef & Whiskin 1997).

Recently, a small but growing group of investigators has begun to investigate examples of extragenetic inheritance that do not rely on social learning. One particularly interesting example follows from the studies discussed earlier of the effects of maternal behaviour (licking, nursing posture) on the development of a trait syndrome involving stress reactivity of young rodents. An important addition to this story is that the behaviour of mothers affects the development of maternal behaviour in their daughters (Meaney 2001; Fleming et al. 2002). Cross-fostering studies show that females raised by high-licking mothers develop into high-licking mothers themselves, and vice versa (i.e. the maternal behaviour of a female is similar to that of her foster mother, not to that of her biological mother). In this case, a trait syndrome is maternally inherited by nongenetic means: high-licking, low-reactivity mothers produce low-reactivity offspring of both sexes, and their low-reactivity daughters lick their own offspring at high rates after they mature, producing grandchildren with low reactivity.

Although thus far, most studies of extragenetic inheritance of maternal behaviour have focused on rodents and primates (Berman 1990; Fairbanks 1996; Maestriperi 1999; Fleming et al. 2002), researchers working with other taxa are also beginning to study this phenomenon. For instance, in dung beetles, maternal provisioning behaviour (amount of dung in the brood mass) affects the growth trajectories and final sizes of both male and female offspring, and, in turn, large adult females produce large brood masses for their offspring. As a result, females that provision their young with large brood masses produce daughters that are also likely to provision their offspring with large brood masses (Hunt & Simmons 2002).

Even if behavioural modes of extragenetic inheritance turn out to be common in mammals, birds and other species with extensive parental care, this would leave the genetic-primary paradigm intact for biologists studying taxa in which neither parent cares for the offspring. Unless mechanisms for extragenetic inheritance exist in species lacking parental care, extragenetic inheritance is likely to remain a curiosity, of little relevance to the inheritance of phenotypic traits for most of the animals on earth.

However, virtually all animals engage in one type of parental behaviour that has the potential to profoundly affect the development of phenotypic traits in their offspring: females select a location for their eggs. By selecting a natal habitat for their eggs, females provide their offspring with a broad range of environmental conditions that affect embryos during the period between laying and hatching. In addition, in many species, offspring remain near their natal location for an extended period after hatching; in this situation, maternal choice of oviposition site determines the environment that will be experienced by offspring over an extended period of juvenile development (West & King 1987).

Because the burgeoning literature on parental effects clearly shows that a mother's choice of a natal habitat can greatly impact the development of her offspring, the critical question is whether extragenetic mechanisms exist that encourage a correlation between the habitat preferences of parents and their offspring. This question has a long and illustrious history. In 1864, Walsh proposed that insects become conditioned to the host in which they develop, a process that would encourage adult females to deposit her eggs on the same host that was selected by her mother. In the entomological literature, this idea evolved into the Hopkins' host-selection principle, which, in its broadest sense, predicts that insects will develop a preference for the host species on which they developed (Jaenike 1983). At the same time, biologists working with vertebrates became interested in a similar phenomenon they termed 'habitat imprinting', in which an individual's experience with a particular type of habitat early in life increases that individual's level of preference for the same type of habitat later in life (Hilden 1965; Klopfer & Ganzhorn 1985). Currently, these and related phenomenon are subsumed under the general term of 'preference induction', which refers to situations in which experience (not necessarily restricted

to learning) in a natal habitat encourages an individual to select the same type of habitat for reproduction later in life (J. N. Davis, J. A. Stamps & T. P. Coombes-Hahn, unpublished data).

To date, empirical support for preference induction has been obtained for animals from a wide range of taxa, including mammals (Wecker 1963), birds (Teuschl et al. 1998), fish (Arvedlund & Nielsen 1996), amphibians (Hepper & Waldman 1992) and insects (Anderson & Hilker 1995; Djieto-Lordon & Dejean 1999; Barron 2001). In addition, interest in this phenomenon is growing, in part because of the obvious relevance of preference induction to problems in population and conservation biology (Stamps 2001; Davis et al., unpublished data). At this point, the available evidence suggests that preference induction is likely to contribute to extragenetic inheritance in many animals, including many species in which neither parent provides any care to their young after the eggs are laid. Given the potential importance of preference induction for the extragenetic inheritance of a wide range of traits, this phenomenon clearly warrants additional attention from animal behaviourists.

IMPLICATIONS FOR PROBLEMS IN ECOLOGY AND EVOLUTIONARY BIOLOGY

A norm of reaction approach implies that any dramatic change in environmental factors during development is likely to generate equally dramatic changes in behavioural traits and trait syndromes, and that these changes can be expressed within a very short period (as little as a single generation). In turn, if animals are exposed to novel conditions during development, they may display 'behavioural neophenotypes': behavioural traits or trait syndromes never before observed for the members of their species (Kuo 1976; Gottlieb 1992, 2002). Behavioural neophenotypes are expected when individuals find themselves in a new habitat that differs in a number of respects from other habitats used by that species, and that is suitable for at least modest levels of survival and reproduction. Most captive environments satisfy these criteria, and behavioural neophenotypes are routinely generated in the laboratory (e.g. see West et al. 1994). In nature, behavioural neophenotypes are expected in any situation in which the members of a population find themselves in a new habitat that differs in a number of respects from their previous habitats. For instance, invasion biology considers situations in which the members of a species establish themselves in new localities, where they experience a different set of selective pressures than those experienced by their ancestors in the habitat of origin (Vermeij 1996; Kolar & Lodge 2001). A norm of reaction approach suggests that novel behavioural phenotypes, or novel clusters of traits involving behaviour could emerge within a generation or two after the invaders arrived at the new habitat. Thus, new behaviour observed in animals colonizing new habitats (e.g. Holway & Suarez 1999) need not necessarily reflect genetic changes as a consequence of founder effects or strong directional selection in those new habitats.

Similarly, many applied biologists, including conservation biologists and integrated pest managers, seek to establish populations in new habitats using individuals raised in captivity or in other types of natural habitats. A norm of reaction approach argues that if animals develop for extended periods in one type of environment and are then transferred to another type of environment, they may have difficulty making the transition, because so much of their morphology, physiology and behaviour has already been shaped by factors experienced in their previous environment. Conservation biologists are already aware of this problem (e.g. as evidenced by attempts to 'train' captive-raised animals to recognize predators before releasing them in their new habitats; Griffin et al. 2000). However, a norm of reaction approach suggests that instead of trying to change the behavioural phenotypes of subadults or adults prior to release, it might be more practical to provide them with protection, food and other forms of support in the new habitat (i.e. soft release; Letty et al. 2000). Assuming that these individuals are able to survive and reproduce in the new habitat, their offspring would be exposed throughout ontogeny to experiential factors that are likely to encourage the development of phenotypes appropriate to the new habitat. Captive-release programmes for golden lion tamarins, *Leontopithecus rosalia*, illustrate the utility of this approach: efforts to provide 'training' to captive-raised animals prior to release had no appreciable effect on success rates, but the wild offspring born to captive-raised individuals were far more efficient than their parents at surviving and reproducing in their new habitats (Beck et al., in press).

Behavioural processes can also encourage the development and maintenance of stable, predictable patterns of individual differences in behaviour, and stable, predictable clusters of correlated traits. Thus, variation in maternal styles among rodents generates a trait syndrome featuring a variety of correlated behavioural and physiological traits in their offspring, and selection of a foraging habitat may encourage the development of a complex syndrome involving behavioural and morphological traits in brook charr. These and related studies suggest that biologists should not assume that stable, repeatable individual differences in phenotypic traits, or predictable correlations among phenotypic traits, are necessarily the product of underlying genetic variation between those individuals.

Biologists should also be cautious when extrapolating from developmental patterns in the laboratory to developmental patterns in nature, because the subjects of most laboratory studies are severely restricted with respect to their ability to select or modify their physical or social environments. If the development and maintenance of individual differences and trait syndromes requires that individuals be able to select or modify the environments that will shape their own development, then phenotypes in the laboratory will diverge rather dramatically from those in the field. This may help to explain situations in which trait syndromes reliably appear under natural conditions, but disappear when animals are confined. For instance, in pumpkinseed sunfish, *Lepomis gibbosus*,

stable individual differences in behavioural traits reflecting 'shyness' and 'boldness' were observed when individuals were living in seminatural enclosures, but these differences gradually disappeared when those individuals were transferred to the laboratory (Wilson et al. 1993). Hence, predictable patterns of phenotypic diversity and stable behavioural polymorphisms may be more common in nature than in captivity, because their development requires a degree of free choice and free expression that is typically denied to animals housed in captive environments.

Differential allocation is another behavioural process with important implications for evolutionary biology. Currently, most scientists assume that in species lacking male parental care, correlations between the phenotypes of fathers and the phenotypes of their offspring must be the result of the transfer of genetic material from fathers to offspring. Differential allocation provides an alternate, extragenetic route by which fathers can influence the development of traits in their offspring. As we have seen, differential allocation is a type of indirect parental effect, by which sensory stimuli from fathers influence the development of their offspring via the effects of these stimuli on maternal traits affecting offspring development.

The emerging literature on differential allocation suggests that this phenomenon may be widespread in nature. If this is the case, then research programmes and paradigms that ignore this phenomenon may need to be revised. For instance, standard techniques for estimating heritability using a paternal half-sibling design are based on the assumption that correlations between phenotypic traits in fathers and offspring can be attributed to genes transferred from fathers to offspring (Falconer & Mackay 1996). However, if differential allocation is occurring, this technique will produce inflated estimates of the contributions of genes to inheritance. Similarly, in species that lack male parental care, a positive correlation between attractive traits in fathers and viability traits in their offspring is usually construed as supporting the hypothesis that the attractive male traits are correlated with 'good genes' (Sheldon 2000). However, in any species in which a female receives sensory stimuli from her mate before investing in her young, differential allocation by mothers may also encourage positive correlations between attractive traits in fathers and viability traits in their offspring. The implications of differential allocation for genetics, evolutionary biology and behavioural ecology are just beginning to be appreciated. This is clearly one behavioural process with the potential to affect the ways that scientists in related disciplines conduct their research.

Finally, the recent literature suggests that extragenetic inheritance via behavioural processes may be more common, and may involve a much wider range of phenotypic traits, than previously suspected. As we have seen, social learning is only one of several behavioural mechanisms that may contribute to the extragenetic inheritance of morphological, physiological and behavioural traits. One general way that females can affect the development of many traits in their young is by selecting a site for their

eggs, and there is growing evidence in a wide range of taxa for preference induction, the inheritance of habitat preferences by extragenetic means. In retrospect, it seems surprising that animal behaviourists have not devoted more attention to processes that are likely to encourage the extragenetic inheritance of habitat preferences, given the potential importance of such processes for the development and evolution of such a wide array of other phenotypic traits.

In conclusion, studies of behavioural processes that affect development are not only interesting in their own right, but this line of inquiry may shed light on questions and issues of concern to scientists working in related disciplines. At this point, animal behaviourists have just begun to study several behavioural processes with large potential effects on the development of individual differences and trait syndromes. Hence, if the recent past is any indication, Tinbergen's fourth question should attract attention from animal behaviourists for many years to come.

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References

- Alcock, J. 1998. *Animal Behavior: an Evolutionary Approach*. 6th Edn. Sunderland, Massachusetts: Sinauer.
- Anderson, P. & Hilker, M. 1995. Larval diet influence on oviposition behaviour in *Spodoptera littoralis*. *Entomologia Experimentalis et Applicata*, **74**, 71–82.
- Arvedlund, M. & Nielsen, L. E. 1996. Do the anemonefish *Amphiprion ocellaris* (Pisces: Pomacentridae) imprint themselves on their host anemone *Heteractis magnifica* (Anthozoa: Actinidae)? *Ethology*, **102**, 197–211.
- Ayala, F. J. & Campbell, C. A. 1974. Frequency dependent selection. *Annual Review of Ecology and Systematics*, **5**, 115–138.
- Barron, A. 2001. The life and death of Hopkins' host-selection principle. *Journal of Insect Behaviour*, **14**, 725–737.
- Bateson, P. 1988. The active role of behaviour in evolution. In: *Evolutionary Processes and Metaphors* (Ed. by M. W. Ho & S. Fox), pp. 191–207. Chichester: J. Wiley.
- Bateson, P. 2001a. Where does our behaviour come from? *Journal of Biosciences*, **26**, 561–570.
- Bateson, P. 2001b. Behavioural development and Darwinian evolution. In: *Cycles of Contingency* (Ed. by S. Oyama, P. Griffiths & R. E. Gray), pp. 149–166. Cambridge, Massachusetts: MIT Press.
- Beck, B. B., Castro, M. I., Stoinski, T. S. & Ballou, J. In press. The effects of pre-release environments on survivorship in golden lion tamarins. In: *The Lion Tamarins: Twenty-Five Years of Research and Conservation* (Ed. by D. G. Kleiman & A. Rylands). Washington, D.C.: Smithsonian Institution Press.
- Berman, C. M. 1990. Intergenerational transmission of maternal rejection rates among free-ranging rhesus monkeys on Cayo Santiago. *Animal Behaviour*, **44**, 247–258.

- Bernays, E. A. 1986. Diet-induced head allometry among foliage-chewing insects and its importance for gramnivores. *Science*, **231**, 495–497.
- Black, J. M. 1996. *Partnerships in Birds, the Study of Monogamy*. New York: Oxford University Press.
- Boyd, R. & Richerson, P. J. 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.
- Boyd, R. & Richerson, P. J. 1996. Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy*, **88**, 77–93.
- Broadman, M., Askew, R. R. & Cook, L. M. 1974. Experiments on resting site selection by nocturnal moths. *Journal of Zoology*, **172**, 343–355.
- Brooks, R. 1998. The importance of mate copying and cultural inheritance of mating preferences. *Trends in Evolution and Ecology*, **13**, 45–46.
- Brown, C. R. & Brown, M. B. 1996. *Coloniality in the Cliff Swallow*. Chicago: University of Chicago Press.
- Burley, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *American Naturalist*, **127**, 415–445.
- Burley, N. 1988. The differential allocation hypothesis: an experimental test. *American Naturalist*, **132**, 611–628.
- Buss, D. M. 1999. *Evolutionary Psychology: the New Science of the Mind*. Boston: Allyn & Bacon.
- Capitanio, J. P. 1999. Personality dimensions in adult male rhesus macaques: prediction of behaviours across time and situation. *American Journal of Primatology*, **47**, 299–320.
- Caro, T. M. & Hauser, M. D. 1992. Is there teaching in nonhuman animals? *Quarterly Review of Biology*, **67**, 151–174.
- Cavalli-Sforza, L. L. & Feldman, M. W. 1981. *Cultural Transmission and Evolution*. Princeton, New Jersey: Princeton University Press.
- Clausen, J. D., Keck, D. & Hiesey, W. M. 1948. *Experimental Studies on the Nature of Plant Species. III. Environmental Responses of Climatic Races of Achillea*. Washington, D.C.: Carnegie Institution, Publication 581.
- Corruccini, R. S. & Beecher, R. M. 1984. Occlusofacial morphological integration lowered in baboons raised on soft diet. *Journal of Craniofacial Genetics and Development Biology*, **4**, 135–142.
- Day, T. & McPhail, J. D. 1996. The effect of behavioural and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosteus* sp.). *Oecologia*, **108**, 380–388.
- Dingemans, N. J., Both, C., Drent, P. J. & van Oers, K. 2003. Repeatability and heritability of exploratory behaviour in great tits. *Animal Behaviour*, **64**, 929–937.
- Djipto-Lordon, C. & Dejean, A. 1999. Tropical arboreal ant mosaics: innate attraction and imprinting determine nest site selection in dominant ants. *Behavioral Ecology and Sociobiology*, **45**, 219–225.
- Doligez, B., Danchin, E. & Clobert, J. 2002. Public information and breeding habitat selection in a wild bird population. *Science*, **297**, 1168–1170.
- Downes, S. J. & Shine, R. 1999. Do incubation-induced changes in a lizard's phenotype influence its vulnerability to predators? *Oecologia*, **120**, 9–18.
- Drews, C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour*, **125**, 283–313.
- Dugaktin, L. A. & Reeve, H. K. 1998. *Game Theory and Animal Behaviour*. New York: Oxford University Press.
- Eising, C. M., Eikenaar, C., Schwabl, H. & Groothuis, T. G. 2001. Maternal androgens in black-headed gull (*Larus ridibundus*) eggs: consequences for chick development. *Proceedings of the Royal Society of London, Series B*, **268**, 839–846.
- Fairbanks, L. M. 1996. Individual differences in maternal style. *Advances in the Study of Behaviour*, **25**, 579–611.
- Falconer, D. S. & Mackay, T. F. 1996. *Introduction to Quantitative Genetics*. Essex: Longman.
- Falk, R. 2001. Can the norm of reaction save the gene concept? In: *Thinking About Evolution, Historical, Philosophical and Political Perspectives* (Ed. by R. S. Singh, C. B. Krimbas, D. B. Paul & J. Beatty), pp. 119–140. Cambridge: Cambridge University Press.
- Fleming, A. S., Kraemer, G. W., Gonzalez, A., Lovic, V., Rees, S. & Melo, A. 2002. Mothering begets mothering: the transmission of behaviour and its neurobiology across generations. *Pharmacology, Biochemistry and Behaviour*, **73**, 61–75.
- Flint, J., Corley, R., DeFries, J. C., Fulker, D. W., Gray, J. A., Miller, S. & Collins, A. C. 1995. A simple genetic basis for a complex psychological trait in laboratory mice. *Science*, **269**, 1432–1435.
- Galef, B. G. 1981. The ecology of weaning: parasitism and the achievement of independence by altricial mammals. In: *Parental Care in Mammals* (Ed. by D. Gubernick & P. H. Klopfer), pp. 211–241. New York: Plenum.
- Galef, B. G. 1996. The adaptive value of social learning: a reply. *Animal Behaviour*, **52**, 641–644.
- Galef, B. G. 2001. Where's the beef? Evidence of culture, imitation and teaching, in cetaceans? *Behavioural and Brain Sciences*, **24**, 335.
- Galef, B. G. & Sherry, D. F. 1973. Mother's milk: a medium for transmission of cues reflecting the flavour of mother's diet. *Journal of Comparative Physiological Psychology*, **83**, 374–378.
- Galef, B. G. & Whiskin, E. E. 1997. Effects of social and asocial learning on longevity of food-preference traditions. *Animal Behaviour*, **53**, 1313–1322.
- Gershenfeld, H. K., Neumann, P. E., Mathis, C., Crawley, J. N., Li, X. & Paul, S. M. 1997. Mapping quantitative trait loci for open-field behaviour in mice. *Behaviour Genetics*, **27**, 201–210.
- Gil, D., Graves, J., Hazon, N. & Wells, A. 1999. Male attractiveness and differential testosterone investment in zebra finch eggs. *Science*, **286**, 126–128.
- Gilbert, S. F. 2001. Ecological developmental biology: developmental biology meets the real world. *Developmental Biology*, **233**, 1–12.
- Gilbert, S. F. & Jorgensen, E. M. 1998. Wormholes: a commentary on K. F. Schaffner's *Genes, Behaviour and Developmental Emergentism*. *Philosophy of Science*, **65**, 259–266.
- Gillespie, J. H. & Turelli, M. 1989. Genotype-environment interactions and the maintenance of polygenic variation. *Genetics*, **121**, 129–138.
- Gillis, J. E. 1982. Substrate colour-matching cues in the cryptic grasshopper *Circotettix rabula rabula* (Rehn and Hebard). *Animal Behaviour*, **30**, 113–116.
- Gosling, S. 2001. From mice to men: what can we learn about personality from animal research. *Psychological Bulletin*, **127**, 45–86.
- Gottlieb, G. 1992. *Individual Development and Evolution: the Genesis of Novel Behaviour*. New York: Oxford University Press.
- Gottlieb, G. 2002. Developmental-behavioural initiation of evolutionary change. *Psychological Review*, **109**, 211–218.
- Gowaty, P. A. & Mock, D. W. 1985. *Avian Monogamy*. Washington, D.C.: American Ornithologists' Union.
- Grant, B. R. & Grant, P. R. 1996. Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution*, **50**, 2471–2487.
- Grant, J. W. A. & Noakes, D. L. G. 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, *Salvelinus fontinalis* (Pisces, Salmonidae). *Behavioral Ecology and Sociobiology*, **22**, 435–445.
- Greenspan, R. J. 2001. The flexible genome. *Nature Reviews Genetics*, **2**, 383–387.
- Griffin, A., Blumstein, D. & Evans, C. 2000. Training captive-bred or translocated animals to avoid predators. *Conservation Biology*, **14**, 1317–1326.

- Gupta, A. P. & Lewontin, R. C.** 1982. A study of reaction norms in natural populations of *Drosophila pseudoobscura*. *Evolution*, **36**, 934–948.
- Hedrick, P. W.** 1986. Genetic polymorphism in heterogeneous environments: a decade later. *Annual Review of Ecology and Systematics*, **17**, 535–566.
- Hepper, P. G. & Waldman, B.** 1992. Embryonic olfactory learning in frogs. *Quarterly Journal of Experimental Psychology B, Comparative and Physiological Psychology*, **44**, 179–197.
- Hilden, O.** 1965. Habitat selection in birds: a review. *Annales Zoologici Fennici*, **2**, 53–75.
- Hinde, R. A.** 1970. *Animal Behaviour*. New York: McGraw-Hill.
- Holtmeier, C. L.** 2001. Heterochrony, maternal effects and phenotypic variation among sympatric pupfishes. *Evolution*, **55**, 330–338.
- Holway, D. A. & Suarez, A. V.** 1999. Animal behaviour: an essential component of invasion biology. *Trends in Ecology and Evolution*, **14**, 328–330.
- Hunt, J. & Simmons, L. W.** 2000. Maternal and paternal effects on offspring phenotype in the dung beetle *Onthophagus taurus*. **54**, 936–941.
- Hunt, J. & Simmons, L. W.** 2002. The genetics of maternal care: direct and indirect genetic effects on phenotype in the dung beetle *Onthophagus taurus*. *Proceedings of the National Academy of Sciences, U.S.A.*, **99**, 6828–6832.
- Imasheva, A. G., Loeschcke, L. A., Zhivotovsky, L. A. & Lazenby, O. E.** 1997. Effects of extreme temperatures on phenotypic variation and developmental stability in *Drosophila melanogaster* and *Drosophila buzzatii*. *Biological Journal of the Linnean Society*, **61**, 117–126.
- Imre, I., McLaughlin, R. L. & Noakes, D. L. G.** In press. Phenotypic plasticity in brook charr *Salvelinus fontinalis*: changes in caudal fin induced by water flow. *Journal of Fish Biology*.
- Jablonska, E.** 2001. The systems of inheritance. In: *Cycles of Contingency* (Ed. by S. Oyama, P. Griffiths & R. E. Gray), pp. 99–116. Cambridge, Massachusetts: MIT Press.
- Jaenike, J.** 1983. Induction of host preference in *Drosophila melanogaster*. *Oecologia*, **58**, 320–325.
- Johnston, T. D. & Edwards, L.** 2002. Genes, interactions, and the development of behaviour. *Psychological Review*, **109**, 26–34.
- Kieffer, J. D. & Colgan, P. W.** 1991. Individual variation in learning by foraging pumpkinseed sunfish, *Lepomis gibbosus*: the influence of habitat. *Animal Behaviour*, **41**, 603–611.
- King, R. B.** 1993. Color-pattern variation in Lake Erie water snakes: prediction and measurement of natural selection. *Evolution*, **47**, 1819–1833.
- Kirkpatrick, M. & Lande, R.** 1989. The evolution of maternal characters. *Evolution*, **43**, 485–503.
- Klopfer, P. H. & Ganzhorn, J. U.** 1985. Habitat Selection: behavioural aspects. In: *Habitat Selection in Birds* (Ed. by M. L. Cody), pp. 435–453. Orlando, Florida: Academic Press.
- Kolar, C. S. & Lodge, D.** 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, **16**, 199–204.
- Kolm, N.** 2002. Male size determines reproductive output in a paternal mouthbrooding fish. *Animal Behaviour*, **63**, 727–733.
- Koolhaas, J. M., de Boer, S. F. & Bohus, B.** 1997. Motivational systems or motivational states: behavioural and physiological evidence. *Applied Animal Behaviour Science*, **53**, 131–143.
- Krebs, J. R. & Davies, N. B.** 1997. *Behavioural Ecology: an Evolutionary Approach*. Cambridge, Massachusetts: Blackwell Scientific.
- Kunkele, J. & Von Holst, D.** 1996. Natal dispersal in the European wild rabbit. *Animal Behaviour*, **51**, 1047–1059.
- Kuo, Z. Y.** 1976. *The Dynamics of Behaviour Development: an Epigenetic View*. New York: Plenum.
- Laland, K. N., Odling-Smee, F. J. & Feldman, M. W.** 2001. Niche construction, ecological inheritance, and cycles of contingency in evolution. In: *Cycles of Contingency* (Ed. by S. Oyama, P. E. Griffiths & R. D. Gray), pp. 117–126. Cambridge, Massachusetts: MIT Press.
- Laurila, A., Karttunen, S. & Merila, J.** 2002. Adaptive phenotypic plasticity and the genetics of larval life histories in two *Rana temporaria* populations. *Evolution*, **56**, 617–627.
- Lehrman, D. S.** 1953. A critique of Konrad Lorenz's theory of instinctive behaviour. *Quarterly Review of Biology*, **28**, 337–363.
- Letty, J., Marchandeu, S., Clobert, J. & Aubineau, J.** 2000. Improving translocation success: an experimental study of anti-stress treatment and release method for wild rabbits. *Animal Conservation*, **3**, 211–219.
- Lewontin, R. C.** 1974. The analysis of variance and the analysis of causes. *American Journal of Human Genetics*, **26**, 400–411.
- Lewontin, R. C.** 1983. Gene, organism and environment. In: *Evolution: from Molecules to Men* (Ed. by D. S. Bendall), pp. 273–285. Cambridge: Cambridge University Press.
- MacDougall-Shackleton, E. A. & MacDougall-Shackleton, S. A.** 2001. Cultural and genetic evolution in mountain white-crowned sparrows: song dialects are associated with population structure. *Evolution*, **55**, 2568–2575.
- McAdam, A. G., Boutin, S., Reale, D. & Berteaux, D.** 2002. Maternal effects and the potential for evolution in a natural population. *Evolution*, **56**, 846–851.
- McLaughlin, R. L. & Grant, J. W. A.** 1994. Morphological and behavioural differences among recently emerged brook charr, *Salvelinus fontinalis*, foraging in slow- and fast-running water. *Environmental Biology of Fishes*, **39**, 289–300.
- McNamara, J. M. & Houston, A. I.** 1996. State-dependent life histories. *Nature*, **380**, 215–221.
- Maestriperi, D.** 1999. The biology of human parenting: insights from nonhuman primates. *Neuroscience and Biobehavioural Review*, **23**, 411–422.
- Mangel, M. & Stamps, J.** 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research*, **3**, 583–593.
- Maupin, J. L. & Riechert, S. E.** 2001. Superfluous killing in spiders: a consequence of adaptation to food-limited environments? *Behavioral Ecology*, **12**, 569–576.
- Maynard Smith, M.** 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Meaney, M. J.** 2001. Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annual Review of Neuroscience*, **24**, 1161–1192.
- Mittelbach, G. C., Osenberg, C. W. & Wainwright, P. C.** 1999. Variation in feeding morphology between pumpkinfish populations: phenotypic plasticity or evolution? *Evolutionary Ecology Research*, **1**, 111–128.
- Mousseau, T. A. & Fox, C. W.** 1998. *Maternal Effects as Adaptations*. New York: Oxford University Press.
- Nilsson, T., Fricke, C. & Arnqvist, G.** 2002. Patterns of divergence in the effects of mating on female reproductive performance in flour beetles. *Evolution*, **56**, 111–120.
- Oklejewicz, M., Pen, I., Durieux, G. C. R. & Daan, S.** 2001. Maternal and pup genotype contribution to growth in wild-type and tau mutant Syrian hamsters. *Behavior Genetics*, **31**, 383–391.
- Olding-Smee, R. J.** 1988. Niche-constructing phenotypes. In: *The Role of Behaviour in Evolution* (Ed. by H. C. Plotkin), pp. 73–132. Cambridge, Massachusetts: MIT Press.
- Orzack, S. H. & Tuljapurkar, S.** 2001. Reproductive effort in variable environments, or environmental variation is for the birds. *Ecology*, **82**, 2659–2665.
- Oyama, S., Griffiths, P. & Gray, R. E.** 2001. *Cycles of Contingency*. Cambridge, Massachusetts: MIT Press.

- Pagel, M. & Dawkins, M. S.** 1997. Peck orders and group size in laying hens: 'futures contracts' for non-aggression. *Behavioural Processes*, **40**, 13–25.
- Petrie, M., Schwabl, H., Brande-Lavridsen, N. & Burke, T.** 2001. Sex differences in avian yolk hormone levels. *Nature*, **412**, 498–499.
- Piersma, T., Dietz, M. W., Dekinga, A., Nebel, S., van Gils, J., Battley, P. F. & Spaans, B.** 1999. Reversible size-changes in stomachs of shorebirds: when, to what extent, and why? *Acta Ornithologica*, **34**, 175–181.
- Provenza, F. D. & Balf, D. F.** 1987. Diet learning by domestic ruminants: theory, evidence and practical implications. *Applied Animal Behavioural Science*, **18**, 221–232.
- Riechert, S. E. & Hedrick, A. V.** 1993. A test of correlations among fitness-related behavioural traits in the spider, *Agelenopsis aperta* (Araneae, Agelinadae). *Animal Behaviour*, **46**, 669–675.
- Riechert, S. E. & Hall, R. A.** 2000. Local population success in heterogeneous habitats: reciprocal transplant experiments completed on a desert spider. *Journal of Evolutionary Biology*, **13**, 541–550.
- Rossiter, M.** 1996. Incidence and consequences of inherited environmental effects. *Annual Review of Ecology and Systematics*, **27**, 451–476.
- Saino, N., Ferrari, R. P., Martinelli, R., Romano, M., Rubolini, D. & Møller, A. P.** 2002. Early maternal effects mediated by immunity depend on sexual ornamentation of the male partner. *Proceedings of the Royal Society of London, Series B*, **269**, 1005–1009.
- Schaffner, K. F.** 1998. Genes, behaviour, and the developmental emergentism: one process, indivisible? *Philosophy of Science*, **65**, 209–252.
- Schlichting, C. & Pigliucci, M.** 1998. *Phenotypic Evolution: a Reaction Norm Perspective*. Sunderland, Massachusetts: Sinauer.
- Schlichting, C. D. & Smith, H.** 2002. Phenotypic plasticity: linking molecular mechanisms with evolutionary outcomes. *Evolutionary Ecology*, **16**, 189–211.
- Schwabl, H.** 1993. Yolk is a source of maternal testosterone for developing birds. *Proceedings of the National Academy of Sciences, U.S.A.*, **90**, 11446–11450.
- Schwabl, H.** 1996. Maternal testosterone in the avian egg enhances postnatal growth. *Comparative Biochemistry and Physiology*, **114**, 271–276.
- Sheldon, B. C.** 2000. Differential allocation: tests, mechanisms and implications. *Trends in Ecology and Evolution*, **15**, 397–402.
- Sheldon, B. C.** 2002. Adaptive maternal effects and rapid population differentiation. *Trends in Ecology and Evolution*, **17**, 247–249.
- Sinervo, B. & Lively, C. M.** 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, **380**, 240–243.
- Skulason, S., Snorrason, S., Ota, D. & Noakes, D. L. G.** 1993. Genetically based differences in foraging behaviour among sympatric morphs of arctic charr (Pisces: Salmonidae). *Animal Behaviour*, **45**, 1175–1192.
- Stamps, J. A.** 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 230–242. Oxford: Oxford University Press.
- Stamps, J. A. & Krishnan, V. V.** 1999. A learning-based model of territory establishment. *Quarterly Review of Biology*, **74**, 291–318.
- Stamps, J. A. & Krishnan, V. V.** 2001. How territorial animals compete for divisible space: a learning-based model with unequal competitors. *American Naturalist*, **157**, 154–169.
- Steen, J. B., Erikstad, K. E. & Hoidal, K.** 1992. Cryptic behaviour in moulting hen willow ptarmigan *Lagopus lagopus* during snow melt. *Ornis Scandinavica*, **23**, 101–104.
- Sterelny, K.** 2001. Niche construction, developmental systems and the extended replicator. In: *Cycles of Contingency* (Ed. by S. Oyama, P. Griffiths & R. E. Gray), pp. 333–350. Cambridge, Massachusetts: MIT Press.
- Stiles, J.** 2000. Neural plasticity and cognitive development. *Developmental Neuropsychology*, **18**, 237–272.
- Switzer, P. V., Stamps, J. A. & Mangel, M.** 2001. When should a territory resident attack? *Animal Behaviour*, **62**, 749–759.
- Takahasi, K.** 1999. Theoretical aspects of the mode of transmission of cultural inheritance. *Theoretical Population Biology*, **55**, 208–225.
- Teuschl, Y., Taborsky, B. & Taborsky, M.** 1998. How do cuckoos find their hosts? The role of habitat imprinting. *Animal Behaviour*, **56**, 1425–1433.
- Tinbergen, N.** 1963. On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, **20**, 410–433.
- Verbeek, M. E., Boon, A. & Drent, P. J.** 1996. Exploration, aggressive behaviour and dominance in pairwise confrontations of juvenile male great tits. *Behaviour*, **133**, 945–963.
- Vermeij, G. J.** 1996. An agenda for invasion biology. *Biological Conservation*, **78**, 3–9.
- Via, S., Gomulkiewicz, R., de Jong, G., Scheiner, S. M., Schlichting, C. D. & van Tienderen, P. H.** 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology and Evolution*, **10**, 212–216.
- Waddington, C. H.** 1959. Evolutionary systems: animal and human. *Nature*, **183**, 1634–1638.
- Wahlsten, D.** 2001. Standardizing tests of mouse behaviour: reasons, recommendations and reality. *Physiology & Behavior*, **73**, 695–704.
- Wainwright, P. C., Osenberg, S. W. & Mittelbach, G.** 1991. Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): effects of environment on ontogeny. *Functional Ecology*, **5**, 40–45.
- Walsh, B. D.** 1864. On phytophagic varieties and phytophagic species. *Proceedings of the Entomological Society of Philadelphia*, **3**, 403–430.
- Wecker, S. C.** 1963. The role of early experience in habitat selection by the prairie deer mouse, *Peromyscus maniculatus bairdi*. *Ecological Monographs*, **33**, 307–325.
- West, M. J. & King, A. P.** 1987. Settling nature and nurture into an ontogenetic niche. *Developmental Psychobiology*, **20**, 549–562.
- West, M. J., King, A. P. & Freeberg, T. M.** 1994. The nature and nature of neo-phenotypes: a case study. In: *Behavioural Mechanisms in Evolutionary Ecology* (Ed. by L. A. Real), pp. 238–257. Chicago: Chicago University Press.
- West-Eberhard, M. J.** 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics*, **20**, 249–278.
- Whitlock, M. C.** 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *American Naturalist*, **148**, S65–S77.
- Wilson, D. S.** 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London, Series B*, **353**, 199–205.
- Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L.** 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.
- Wilson, E. D.** 1975. *Sociobiology: the New Synthesis*. Cambridge, Massachusetts: Belknap Press.
- Wolf, J. B.** 2000. Gene interactions from maternal effects. *Evolution*, **54**, 1882–1898.