



ANNIVERSARY ESSAY

The case for developmental ecology

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We call for renewed emphasis on the tasks confronting animals as they develop and learn. We are extending the use of the term 'developmental ecology' employed by plant biologists who have studied how fitness can be influenced by the ecological context present during development (Watson et al. 2001, *Evolutionary Ecology*, **15**, 425–442). We seek an expanded venue for the term, arguing that for animal behaviourists to understand some of the traits so familiar in behavioural ecology, they must consider the fundamental phenomena of development. Not doing so runs the risk of misidentifying both the proximal and functional causes of traits. For example, without a developmental view, macrogeographical variation in species-typical behaviour may be viewed as evidence of genotypic differences when, in fact, the variation is being produced by developmental contexts. Detailed below are some general issues about how development can be studied if it is to contribute to our knowledge of the adaptive value of behavioural systems. We argue for a prospective and longitudinal orientation, with an emphasis on relatively continuous observation and measurement. Both behaviours and contexts that may only occur during ontogeny are examined, as well as the reproductive outcome of the traits of interest. We present examples from our work on courtship and communication in brown-headed cowbirds, *Molothrus ater*, to show that a prospective and ecological view of development reveals pronounced variation in patterns of reproductive behaviour that cannot be understood without taking into account developmental ecology.

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Behavioural ecology is now a dominant approach to the study of animal behaviour. It combines ethology, ecology, economics and natural selection as it evaluates the adaptive value of behavioural traits (Krebs & Davies 1997). Although ethology is part of the foundation of behavioural ecology, not all of its aims are equally represented in this approach to the study of behaviour. The focus is generally on adaptive function and, more recently, on proximal cause. Here we argue for the inclusion of development, a point of view that has been acknowledged by behavioural ecologists to have been downplayed despite its fundamental role in ethology (Tinbergen 1963; Krebs & Davies 1997). Our belief is that cause and function of behaviour cannot be understood without an analysis of ontogeny.

Developmental studies were a common part of ethology at the height of popularity of the nature–nurture paradigm, where the goal was generally to label a behaviour as innate or learned. In the aftermath of the debates begun by Lorenz (1965) and Lehrman (1971), nature/

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nurture was generally acknowledged to be a false dichotomy and the paradigm eventually lost heuristic value. The method used to establish innate origins, the use of animals reared in isolation, also lost its theoretical power as it was recognized that such a condition was not a developmental baseline, but an aberrant context (Slater 1985). More and more evidence accumulated about the presence of phenotypic plasticity in a wide variety of taxa, making it clear that ontogeny could produce multiple outcomes (West-Eberhard 1989). Despite these events, few new general theories of behavioural development emerged and the popularity of developmental studies in animal behaviour waned. At this point, the central driving theory in the study of behaviour was evolution, and the popular (neo-Darwinian) evolutionary theory had little to say about development (Raff 1996). Under this particulate model, the genes an individual was born with were the genes the individual would transmit at maturity. Thus, it seemed possible to view the time in between as not critical to an evolutionary analysis.

Currently, however, evolutionary biology has seen a surge of interest in synthesizing development with evolution, with the realization that development does

not change genes, but influences which genes are selected. New studies, books, and even journals, have emerged focusing on how developmental processes influence phenotypic form, maintain genetic and phenotypic variation, and respond to selection (Hall 1992; Raff 1996; Schlichting & Pigliucci 1998; Gilbert 2001; Wolf 2002). This new synthesis has led to a new reason for interest in development: studies of development can make direct contributions to understanding the adaptive role of flexible ontogenetic mechanisms in natural and sexual selection.

But what if one's interest is only in behavioural outcomes and the final phenotypes on which selection operates? Is it necessary to delve into developmental underpinnings? We would answer in the affirmative because differences in reproductive success, and thus fitness, are products of differences in development. Without a focus on development, any observed variation in a behaviour either within or across populations may be automatically attributed to genotypic differences, when, in fact, it may be the consequence of common developmental processes. For example, over the last 25 years, our laboratory has studied the development of courtship behaviour in the three subspecies of the North American brown-headed cowbird, *Molothrus ater*. We have found substantial differences in all three subspecies. Specifically, we have found differences in the rate and timing of song development in the male as well as some variation in female song preferences particularly near subspecies' borders (King & West 1990). We have documented differences in patterns of courtship and song use across populations as well as differences in female responsiveness to song (West et al. 1998). These differences seem biologically significant in that attempts to hybridize distant populations from the different subspecies failed to produce significant numbers of viable offspring (unpublished data). Because these populations were geographically separated and morphologically distinct, we assumed the behavioural differences signalled genetically based macrogeographical variation (King & West 1990). In recent work, however, some of which is detailed below, we manipulated ecological variables and investigated the effects on phenotypic variation within a population. We found that all of the behavioural differences we documented in geographically distant populations can be induced within a single population in a single generation, even including reproductive incompatibilities (West et al. 2002; White et al. 2002b, c). Thus, without developmental approaches, phenotypic flexibility may go unnoticed or be unappreciated as a target of selection. Said another way, selection acts on traits that vary with developmental context and thus what is selected is the source of behavioural variation, the developmental process itself.

Developmental analyses of behaviour have not always been particularly useful in answering evolutionary questions because of limitations in the methods used, the absence of measures of functional outcome, a lack of focus on process, and little interest in ecological validity (but see Galef 1981; Gottlieb 1992; Hoffman et al. 1999). A common developmental practice, for example, is to target a mature behaviour of interest and essentially work

backwards, retrospectively tracing its ontogeny guided by notions of a predetermined final form. For example, those looking at the structure of bird song might identify adult stereotyped song and then find its roots in immature sounds (Marler & Peters 1982; King & West 1988). Questions may be asked about when these precursors appear and how they change over time relative to the final outcome. Studies focusing on sensitive periods for learning also tend to be retrospective, because they choose a final behaviour and ask at what point do different variables influence its appearance.

The retrospective approach is a necessary step to find order in the usually more variable activity of the young. But the retrospective method has important limitations. First, behavioural precursors of adult behaviour are generally assumed to be functionless because of their temporary and changing nature. For example, subsong or plastic song are often not assigned communicative value but categorized only as motor practice. The vocalizations undergo massive change as the animal matures and may never recur. So it may seem unnecessary to think that they are even indirectly related to fitness. These behavioural precursors, however, can provide the variation that can propel individuals down different developmental trajectories. In addition, the retrospective approach assumes what the function of the adult form of the behaviour should be but does not actually test the functional outcome directly. Assuming a single outcome obscures sensitivity to the variation in outcomes, which is critical to understanding what selection may be acting upon. In summary, if different developmental trajectories are not recognized, and their connection to differences in outcomes is missed, then it becomes impossible to determine with certainty what function the final behaviours serve.

Finally, developmental contexts may not be visible using a retrospective view. The specific environments in which behaviours develop are probably one of the most understudied parameters in animal behaviour (Kaufman 1975). Developmental environments contain some of the most important pieces of information about later outcomes. For example, the juvenile social structure contains detailed knowledge about what is available to be learned during development. Identification of juvenile social structure also reveals information about the timing of occurrence or absence of behavioural stimulation such as the quantity and quality of contact between adults and young. As Gould (1977) and others have argued, even small changes in the timing of developmental events can have evolutionary consequences through heterochrony (Moore 2001).

An alternative to a retrospective approach is a prospective one. The prospective approach makes few assumptions about the final form of a behaviour, but tracks organisms and their activities from their origins to their reproductive consequences. The prospective approach also does not assume that behavioural precursors are functionless. Instead, it considers that developing organisms may have capacities similar to adults, but because of a lack of experience, they do not have the same capabilities (Galef 1981). This method assumes multiple

outcomes in phenotypic form are possible within and across ecologies and attempts to describe the factors that contribute to variation. This approach also assumes that the contextual variables that structure development are not always obvious, because they are dynamically determined by the animals over time. Such a perspective means giving animals sufficient freedom to reveal the independent variables that matter to them as opposed to measuring how animals respond to a static experimental structure. The burden is on the investigator to know what some of the relevant ecological variables may be, based on the species' natural history (e.g. Payne & Payne 1993; Nordby et al. 1999, 2000). Thus, the prospective approach is heavily indebted to field and naturalistic studies to provide information about that history. Fieldwork is often constrained, however, in its ability to isolate developmental mechanisms, because of the difficulty in measuring and manipulating relevant variables.

The prospective approach aims to identify sources of influence that animals use to modify or maintain their behaviour. The goal is to find the ontogenetic structures that shape, sustain or change the emergent behavioural form. One of those structures is the animal's species-typical ecology, its ontogenetic niche (West & King 1987; West et al. 1988). The ontogenetic niche encompasses the kinds of information that are potentially available to the developing organism. The animal, by virtue of its particular niche, inherits genes, conspecifics and habitats. Specifically, animals inherit provisions, nest sites, migration routes, territories or social rank, properties directly correlated with their genetic inheritance (West et al. 1988; Mousseau & Fox 1998; Wolf et al. 1999; Laland et al. 2000). It is as likely that songbirds inherit conspecifics that sing as it is that they will have a syrinx with which to sing. There is no shared denominator in the case of exogenetic inheritances; there is no common material comparable to DNA, making it more difficult to categorize exogenetic forms of heredity. But the diversity of form should not deter animal behaviourists from looking for the role of ontogenetic niches in defining developmental contexts. As we will show, knowledge of the ontogenetic niche can generate developmental predictions.

Studying development prospectively means a commitment to behaviour and context as the fundamental unit. Contexts, the immediate or proximate properties of an animal's overall niche, are multifaceted and can be dramatically affected by the specific individuals within them. So, just as there is a reaction norm for genotypes exposed to different environments, there is also a reaction norm for environments created by different individuals. This interaction means that behaviours are codefined by settings and individuals (Lewontin 1983; Moore 2001).

Studying behaviours and contexts requires new integrative concepts. An example of such an integrative structure is what we term a social gateway (White et al. 2002a), which is the pattern of recurring social interactions that channels sensory stimulation and subsequent responsiveness throughout a group. In a flock, for example, not all birds may have equal access to one another; a subordinate

individual may rarely be physically close to a dominant one. As a result, some animals are differentially exposed to models or competitors and are put in a position to learn more or less from conspecifics. The flock, or comparable social group, thus serves a sensory function, gating stimulation along different social pathways (Payne & Payne 1993; Nordby et al. 1999, 2000). Investigating the role of social context requires use of complex and public social ecologies, permitting animals to play multiple roles such as observers, models, competitors, or distracters. Such environments also allow animals to self-select patterns of stimulation while placing the burden on the investigator to see the environment from the animal's point of view.

A study with very young cowbirds demonstrates the early manifestation of niches and gateways (White et al. 2002a). Young cowbirds are first seen in groups in late summer (see Hauber et al. 2000). How sensitive are the immature birds to peers and to adults and how is such sensitivity displayed right after fledging? The species inhabits a wide range of habitats inheriting different niches: in some populations, adult cowbirds are still present, and in others, the adults have moved away. Thus, we chose to investigate the effects of the presence or absence of adults on newly fledged birds.

In three replications, we housed flocks of fledglings in two adjacent aviaries where they could see and hear each other. Adult conspecifics were alternately moved in and out of the two aviaries. To assess organization, we measured patterns of near-neighbour association and vocalizing among the young birds, many of whom were within a week or two of host independence. We found that young flock members, even at less than 40 days of age, showed clear and rapid responses to the presence of adults, even though the adults appeared to do little and did not generally interact with the fledglings. Young males housed with adults vocalized less than young males without adults. But juveniles with adults showed more social interaction with one another, although not with the adults themselves. The effects were remarkably easy to manipulate: if adults were removed or added from the juvenile flock, changes in vocalizing and social behaviour reversed quickly. Taken as a whole, the data showed that young cowbirds, newly independent, react differently to peers than to adults and react differently to peers as a function of adult presence. The reversibility of the effect shows that the young birds' behaviours are context dependent and highly adaptable.

The experiment demonstrates the operation of a social gateway. The young cowbirds, when housed without adults, could see and hear the adults and could observe the greater rate of social interaction between the adult-housed juveniles. Despite this physical proximity and exposure, we repeatedly obtained robust group differences between the two aviaries as a function of adult presence. These observations tell us that the flock is a perceptual, as well as a social, entity, affecting attentiveness to nearby and potentially accessible stimulation.

From a developmental perspective, these data show that the patterns of organization and vocalization of the young birds are already dependent on social

circumstances. These behaviours, social assortment and vocalizing, are ones that cowbirds use throughout ontogeny. The data also showed that different opportunities for social and vocal learning are created as a function of the nature of the young birds' surroundings (O'Loghlen & Rothstein 2002). In populations where adults are present, young birds may learn more about interaction but be delayed in the practice and performance of species-typical vocalizations. In areas without adults, singing may be a more frequent event. Most theories of bird song suggest that rudimentary sounds related to later song produced at this age are by-products of motor programming. But, if so, why the sensitivity to the presence of adults? The data suggest that vocalizing at this early age has significance as a means of communication within the juvenile flock. Birds may, therefore, begin their song ontogeny with a sensitivity to react to vocal and social cues, with a capacity similar to adults, but not with adults' capability, that is, they still have much to learn.

Although we focused on very young birds here, we have replicated the effect of social context affecting attentiveness three times with older birds, including adults. Thus, we have found a mechanism, the social gateway, that helps to organize and regulate plasticity. This finding also marks a change in the way one can view a developmental study, as noted earlier. The aim is not to document plasticity, which has now been done in so many taxa, but to find the ecological variables that create the social structures that define what is available to be learned. These structures can function to channel malleability into stable trajectories. An example of such an ecological variable would be the timing and extent of social contact with adult conspecifics (Nordby et al. 1999, 2000).

But what about longer-term effects and functional consequences of these different patterns of behaviour? The fledgling experiment might qualify as a sensitive-period phenomenon with differences disappearing as birds mature. This possibility raises the need to look at ontogeny for sufficient lengths of time to document the functional consequences of different patterns of social organization.

We chose to explore the longer-term development of young birds housed with and without adult males in large indoor-outdoor aviaries (White et al. 2002b). We configured two flocks of 20–25 birds each. Both flocks had juvenile males and both had females, but one flock also had adult males present (+ADM) whereas the other flock did not (–ADM). Juvenile males in the two conditions developed along different pathways and showed reliably different courtship and communication skills. As in the fledgling experiment, +ADM juveniles affiliated with other juvenile males and females more frequently than did the –ADM juveniles. +ADM juveniles also sang more to males and females. In the breeding season, the +ADM males were aggressive with other males and courted and copulated with females in patterns common for cowbirds in the midwestern U.S.A. In this condition, all females that copulated were monogamous. In contrast, –ADM juvenile males displayed very different social patterns. They rarely associated with females or each other, and

sang in long bouts of undirected soliloquies. In the breeding season, they showed no aggression towards other males, courted with minimal pursuit, and even after copulation, they did not guard females, allowing multiple males to copulate with their females. Females were promiscuous and laid fewer eggs than did the +ADM females. The +ADM and –ADM juveniles also developed structurally different songs at different rates. The –ADM juveniles advanced sooner to stereotyped song and developed songs that were more effective at eliciting females' copulatory responses than were the songs of the +ADM males. We followed the –ADM males for another year and found the –ADM phenotypes persisted even when we introduced new females. We have recently found that the now adult –ADM males could transmit their behaviour patterns to a new set of juveniles (unpublished data). Thus, this work shows that in the cowbird system, variation in developmental trajectories exists, trajectories are (culturally) heritable, and can have substantial effects on fitness.

The patterns of behaviour seen before the breeding season revealed the facultative nature of cowbird social development. Developmental trajectories were organized as a result of recurring social interactions. In addition to revealing mechanisms of social development, the different outcomes in mating strategies (social monogamy versus promiscuity) also had functional consequences. The conditions differed in the variance in mating success, copulation patterns and egg production. Thus, cowbirds in different developmental ecologies may experience differential variation in reproductive success and intensity of sexual selection (White et al. 2002b).

We have gone on to carry out many other aviary manipulations that are not described here (West et al. 2002; White et al. 2002c; King et al., *in press*). Some were done to replicate previous effects and some explored the effects of new social variables (see also Freeberg 1998; Freeberg et al. 1999). Traits yielding the highest degree of reproductive success differed depending on the context created by social organization during development. For example, in some contexts, males with the best-quality song (as measured by playback) were most successful, in other contexts, males with the best-quality songs were least successful (correlations between song quality and copulations varied from -0.89 to $+0.81$). These data suggest that the function of song in this species cannot be understood without understanding the ecology in which song is produced.

Our work over the past two decades had been premised on the role of song as a stimulus for female mate choice. But we had taken a unitary view of song function: the better the song, the greater the chances of reproductive success. We must now qualify that statement to say that song bears the imprint of a male's social and vocal history: its efficacy and use during the breeding season depends on the kind of social organization experienced during that history. A playback test of vocal effectiveness can thus be misleading as to the honesty of song as a signal of a high-quality male, because it evaluates the signal in the absence of its context. The playback test, however, does differentiate

songs by structural properties and thus can be used as a clue that social development has measurable effects on the properties of vocal signals. We also know that song quality, as measured by playback, can change from year to year depending on a male's experience between breeding seasons, reinforcing the idea that song is a sensitive marker of changes in the nature of the local social ecology (West & King 1980; West et al. 1996; Nowicki et al. 2002).

Thus, the young cowbird develops critical reproductive skills opportunistically through recurring social interactions with others in its niche. That cowbirds will respond to a diversity of local differences is supported by findings showing strong cultural transmission of different phenotypes across generations in captive populations (Freeberg et al. 1999). The range of phenotypes transmitted underscores the facultative nature of the developmental system. The relation of such phenotypes to the social context during development cannot be seen using a retrospective view and thus may obscure the fact that selection is acting on the system of development itself (i.e. on the ability to deal with environmental contingencies that can alter developmental trajectories; see Schlichting & Pigliucci 1998).

An example of an environmental contingency is apparent in the differences during the year in the behaviour of song recipients in the \pm ADM aviaries. When $-$ ADM males sang to one another, the recipient generally left without returning a song. In the $+$ ADM aviary, males, especially adult males, stayed until the song overture, which led to sustained singing and aggressive interactions. $+$ ADM juveniles learned to sing with other males and as a result developed competitive and aggressive mating behaviour. $-$ ADM juveniles never learned to maintain male–male singing interactions but did engage in more undirected singing. This led these males to be less aggressive, but to develop more effective courtship song than the $+$ ADM males. The differences in the breeding behaviour of the two groups of juveniles emerged from their singing experience with other males during development.

Here we have focused on flock composition and social organization as developmental parameters, but migratory status and hatching time, which also affect contact with adults, have also proved to be heuristic in other avian species (Kroodsma & Pickert 1980; Nelson et al. 1995). These variables are of special interest because they affect the timing of developmental events. A way to think about evolution is that it necessarily incorporates changes in an animal's developmental system, changes that in part reflect selection on the timing of the developmental progression. We saw differences in the timing of song development, both its structure and use, come about as a function of social context from as early as it could be measured (White et al. 2002a). We also know from past work that female stimulation can modulate the rate of vocal development (Smith et al. 2000). Thus, another way to think about the timing differences is from the perspective of the context. An animal may be developmentally ready to learn new song material or improvise on material already acquired but not have close physical access to

adult models or tutors or other singers. The pattern of social organization, the gateway, can thus create differences in timing.

In summary, we hope to have shown that developmental approaches, when grounded in ecological perspectives, can contribute organizing variables to the study of behaviour. A specific kind of contribution such studies can make is to uncover how animals learn the pragmatics of employing species-typical behaviours such as vocalizing. In all of the studies we have done, male cowbirds vocalize, and although this capacity need not be learned, almost every other aspect of their song development is sensitive to the social context in which it occurs. The study of pragmatics, the use of communicative signals, has lagged behind the study of syntax or semantics with respect to the analysis of communication in many species, and the reason may be the lack of developmental analyses where behaviour and context are considered together.

Thus, we end by arguing the case for a developmental ecology to unite and inform the study of function, cause and phylogeny of behaviour. Developmental ecology is the study of the ontogenetic interactions between organisms, contexts and behaviours. But instead of merely stating or inferring that interactions occur, developmental ecology seeks to identify the specific nature and effects of the interactions. How? By manipulating ecologically based features of the proximate environment and observing how the effects change behavioural trajectories while they are still ongoing and by testing the reproductive significance of these trajectories (Freeberg et al. 1999). Observing and manipulating the ongoing processes of development is the hallmark of this approach and the feature that distinguishes it from other approaches to the study of behavioural change. The greater our sensitivity to behavioural reactions to developmental ecology, the more likely it is that the research will yield answers that are useful to understanding how selection acts on behaviour.

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