

REVIEW/SYNTHESE

Behavioural plasticity in variable environments**Petr E. Komers**

Abstract: The plasticity of behaviour consists of an array of behavioural responses to varying environmental conditions. It is widely predicted that the range of behavioural responses will increase with environmental variability. According to this prediction, the slopes of a response curve representing behavioural plasticity would be identical in environments with different variability. However, the range of behaviours can also increase with the slope of the curve, so that in a given range of environments, the plasticity of behaviour would vary. For example, where two environments are similar in terms of resource availability, the costs of exploiting the resource may differ. An improved ability to assess costs and benefits is predicted to increase behavioural plasticity because it decreases the costs and increases the benefits of alternative behaviours. Moreover, because trade-offs change with age and plasticity is related to trade-offs, plasticity should also change with age. While the ability of animals to adjust to current trade-offs is fundamental for behavioural ecology, demonstration of ranges, slopes, and shapes of plastic behavioural responses is virtually absent from the literature. Knowledge concerning the ability of animals to adjust to environmental fluctuations is important for making predictions about population viability, but empirical evidence is greatly needed to validate current generalizations.

Résumé : La plasticité du comportement repose sur un complexe de réactions à des conditions variables de l'environnement. Il est généralement supposé que l'éventail des réactions comportementales doit normalement s'élargir en fonction de la variabilité de l'environnement. Selon cette supposition, les pentes de la courbe des réactions qui représentent la plasticité du comportement seraient identiques dans des environnements à variabilités différentes. Cependant, l'éventail des comportements peut également augmenter selon la pente de la courbe et, conséquemment, dans un éventail donné d'environnements, la plasticité du comportement pourrait varier. Par exemple, lorsque deux milieux offrent la même disponibilité de ressources, les coûts liés à l'exploitation des ressources peuvent différer. L'amélioration de la capacité d'évaluer les coûts et les bénéfices doit, selon les prédictions, augmenter la plasticité comportementale, car elle réduit les coûts et augmente les bénéfices de comportements de rechange. De plus, comme les compromis changent avec l'âge et que la plasticité est liée aux compromis, la plasticité doit normalement changer avec l'âge. La capacité des animaux de s'adapter à des compromis est essentielle à l'écologie comportementale, mais la détermination des étendues, pentes et formes des réactions comportementales est une notion à peu près absente de la littérature. La connaissance de la capacité des animaux à s'adapter aux fluctuations de leur environnement est essentielle à la formulation de prédictions sur la viabilité des populations, mais des preuves empiriques sont nécessaires pour assurer la validité de généralisations courantes.

[Traduit par la Rédaction]

Introduction

Environmental variability is one of the factors that most strongly affects population growth and viability (Primack 1993; Caughley and Sinclair 1994; Lande 1994). Resource availability, predator pressure, or temperature may influence population growth by affecting litter size, juvenile or adult mortality, and reproduction rate, respectively (Reznick and Endler 1982; Reznick and Yang 1993; Sæther and Gordon 1994; Ahnesjö 1995; Smith and van Buskirk 1995). The various environmental factors fluctuate to different degrees, and it has been argued that the degree of environmental variability affects the degree to which the phenotype of each genotype can vary

and adopt phenotypic plasticity (Bradshaw 1965; Partridge and Harvey 1988; Thompson 1991; de Jong 1995).

Plasticity of behaviour is a special case of phenotypic plasticity, particularly because it involves an immediate and often reversible adaptive response to environmental cues (West-Eberhard 1989). The plasticity of behaviour is an array of behavioural responses to varying environmental conditions. The degree of behavioural plasticity, like that of any phenotypic plasticity, is expected to increase with environmental variability (Klopfer and MacArthur 1960; Morse 1980). In the following, I use "degree of behavioural plasticity" to represent a range of behaviours that I will discuss in relation to a range of environmental conditions.

The existence of behavioural alternatives is the basic assumption of game-theory models (Maynard Smith 1982; Parker 1984), and there is ample empirical support for these models, particularly in the context of reproduction and foraging ecology (Dunbar 1983; Krebs and Kacelnik 1991; Milinski and Parker 1991). Fewer studies have explored behavioural

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alternatives for avoiding predators (Lima and Dill 1990). Behavioural alternatives are traditionally interpreted as alternative behavioural strategies that often appear to be discontinuous behavioural options (Rubenstein 1980; Dunbar 1982; Caro and Bateson 1986). However, behavioural alternatives can be viewed as an array of available behavioural options (Vehrencamp and Bradbury 1984) that could be distributed along a continuum as a function of variation in the environment. In this case, i.e., where plasticity is continuous and reversible, behavioural plasticity represents a flexible reaction norm (for definitions see Stearns 1989).

Both discontinuous behavioural strategies and flexible reaction norms carry the implicit assumption that an array of responses with a particular distribution exists. The concept of an adaptive relationship between the degree of behavioural plasticity and ecological variability is not new. The assumption that behaviour should be more plastic where resources fluctuate was postulated decades ago (Klopfer and MacArthur 1960). Twenty years later, Morse (1980, p. 12) noted that "future studies" are required to support this assumption. Empirical studies demonstrating that the degree of behavioural plasticity varies among populations in response to different degrees of environmental variability are still rare, but they support the prediction (Carroll and Corneli 1995; Rodd and Sokolowski 1995).

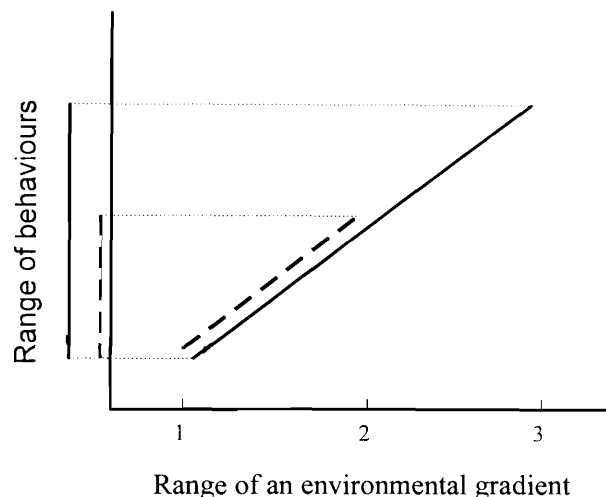
In this paper, I will review the existing empirical evidence for varying degrees of behavioural plasticity and discuss the possible benefits and costs in an evolutionary context. Owing to the small number of examples of variation in behavioural plasticity, I will occasionally use examples of morphological plasticity to make a point. I will then stress some of the difficulties in measuring behavioural plasticity, and attempt to infer testable predictions based on theory and available evidence.

Degree of plasticity: selected empirical examples

There is growing evidence that organisms can respond to environmental changes by producing adaptive phenotypes, and that the degree of plasticity, or the reaction norm, is under evolutionary pressure (for reviews see Stearns 1989; Thompson 1991). For example, tadpoles of amphibian species that breed in temporary ponds exhibited greater flexibility in the time to metamorphosis than species from permanent ponds (Wilbur 1987; Newman 1992). Also, in two closely related species of sticklebacks (*Gasterosteus* spp.), the one with the more variable diet showed greater morphological plasticity (Day et al. 1994). Finally, the development of "neck teeth" as an antipredator strategy in *Daphnia pulex* was phenotypically plastic in response to varying predation levels (Spitze 1992).

Evidence that plasticity of behaviour varies with the variation in environmental conditions is still scarce. A recent example shows that two populations of soapberry bugs (*Jadera haematoloma*) differed in their response to varying female availability: in response to changes in the sex ratio, males from a variable environment altered their behaviour more than males from a constant environment (Carroll and Corneli 1995). In another example, guppies (*Poecilia reticulata*) from two populations subject to different predator regimes exhibited different degrees of plasticity in sexual behaviour (Rodd and

Fig. 1. The range of behaviours (degree of behavioural plasticity) as a function of the range of an environmental gradient. The response curves have identical slopes. If the extreme points of an environmental gradient are represented by points 1 and 2, then, under identical slopes, the broken curve will translate into a smaller range of behaviours than the solid curve, for which the extremes of the environmental gradient are represented by points 1 and 3.



Sokolowski 1995). The degree of plasticity was demonstrably influenced by interaction between heritable factors, social environment, and age. It was inferred that male guppies which are under predation risk show less plasticity in their mating behaviour. In bison (*Bos bison*), some behaviours related to reproduction, such as approaching, consorting with, and mounting cows, are more plastic than fighting or the duration of consorting with each cow (Komers et al. 1994a, 1994b). This suggests that each behavioural trait may involve a specific degree of plasticity, depending on its costs and benefits.

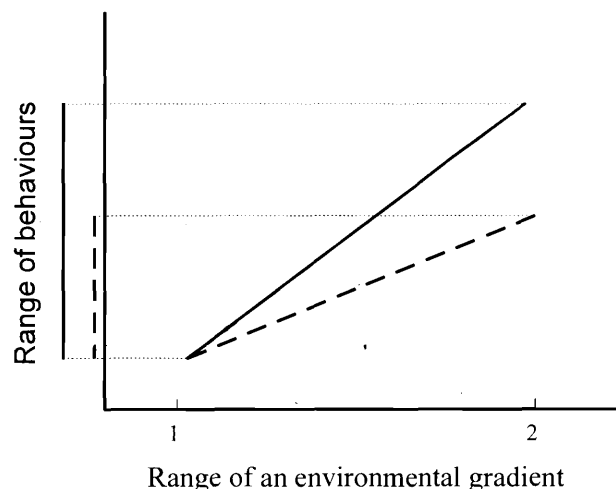
These examples illustrate that a relationship between phenotypic plasticity and environmental variability exists. The degree of plasticity can vary among species, populations, and behaviours of the same populations.

Behavioural plasticity as a response curve

One of the most powerful predictions in behavioural ecology is that animals adjust their behaviour to current trade-offs between some costs and benefits (Maynard Smith 1982; Parker 1984). Whether they are capable of adapting their behaviour, and the degree to which they can do it, presumably depend on whether they evolved in an environment in which the trade-offs vary. More specifically, it depends on whether a given behavioural trait is subject to variability in the trade-offs. A behavioural trait can be deemed invariant or stereotypical (Klopfer 1967; Morse 1980) if potential trade-offs are such that behavioural alternatives are not selected for.

The degree of behavioural plasticity is predicted to increase with environmental variability (Klopfer and MacArthur 1960; Morse 1980). Hence, the wider the range of environmental change, the higher the degree of behavioural plasticity (Fig. 1). This is true for behavioural traits with identical slopes of the response curves. The example of the soapberry bug appears to support this argument because when variability in female

Fig. 2. The range of behaviours (degree of behavioural plasticity) as a function of the range of an environmental gradient. The response curves have different slopes, but the range of the environmental gradient is the same for both. The steeper the slope, the larger the range of behaviours. A steeper slope can be interpreted as a greater change in behaviour, given the same change in the environment.



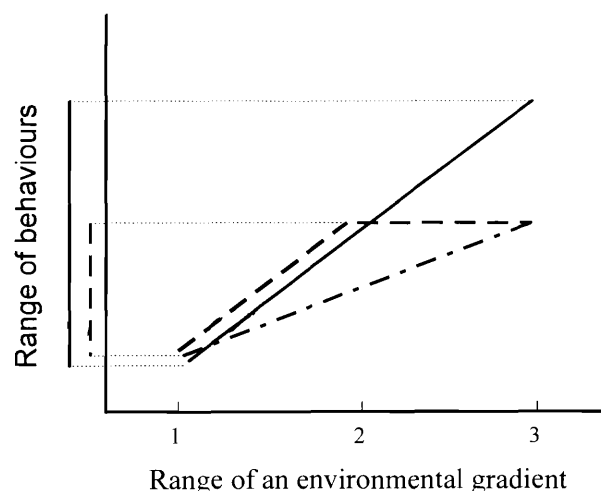
availability was greater, males showed greater plasticity in mating behaviour (Carroll and Corneli 1995).

However, the slopes of the reaction norms can differ among species or populations, which simply means that the trait with the steeper slope changes more in response to a given environmental change (Fig. 2). Differences in the slopes of behavioural responses could be due to the different costs and benefits of performing alternative behaviours. The costs and benefits, in turn, may be affected by the physiological and anatomical apparatus available to perform alternative behaviours, and hence present a phylogenetic constraint. The example of male guppies may be relevant here, because male guppies from a population under predation pressure show less plasticity in their mating behaviour than those in a population in which males were not exposed to predation (Rodd and Sokolowski 1995). In an experiment on pipefishes (*Syngnathus typhle*), males under higher predation pressure performed less courtship behaviour (Berglund 1993). This suggests that under risky conditions, certain behaviours are not performed and the range of behavioural options is reduced.

Interpretations of plasticities with either identical or differing slopes differ qualitatively. In the former, it is predominantly the range of environmental options that presents the opportunity for behavioural adjustments. In the latter, it is predominantly the result of trade-offs between the costs and benefits of plasticity. The arguments in favour of the two categories may not be exclusive, and a continuum between them may exist. However, I suggest that the two categories may form a useful conceptual framework for deriving generalizations concerning the evolution of behavioural plasticity.

Another difficulty in interpreting response curves of behavioural plasticity is, of course, that they may not be linear. Two behavioural traits could have identical slopes over a limited range of an environmental gradient, but one could level off earlier than the other (Fig. 3). If we were to connect the extreme points of each with a straight line, the

Fig. 3. The range of behaviours (degree of behavioural plasticity) as a function of the range of an environmental gradient. As an extension of Fig. 1, the response curves may have identical slopes for a part of the environmental gradient, but the broken curve levels off after point 2. Measuring the behaviours at the extreme points of the environmental gradient (points 1 and 3) would reveal the total range of behaviours for both curves, but it may not reveal the correct range of the environmental gradient that is related to the range of behaviours.



slopes would appear to differ, which could affect the interpretation of the evolution of plasticity in the given traits. This argument may appear trivial, but we should be aware that in the absence of knowledge about the continuity of plastic responses, the possibility of such erroneous interpretations deserves mentioning. The examples of the soapberry bugs and the guppies both present essentially two points, which may or may not be the extremes of a continuum.

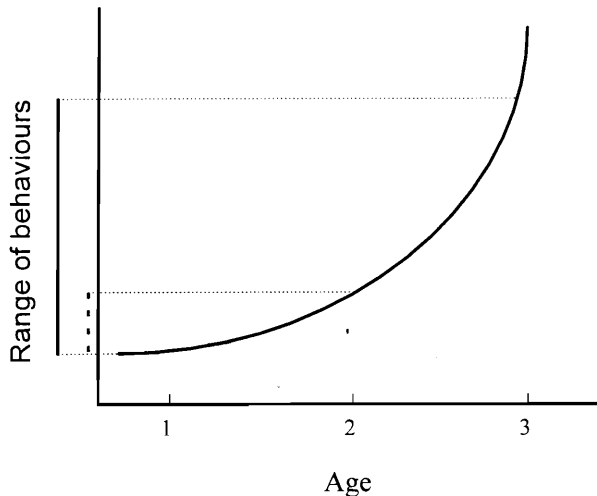
Finally, a nonlinear response curve could be the result of different degrees of plasticity at, say, different ages of individuals. In some cases, juveniles employ fewer behavioural strategies than adults (and vice versa; Caro and Bateson 1986). In such cases the slope could change, continuously or discretely, throughout an animal's lifetime (Fig. 4). This suggests that in addition to the range of an environmental gradient and the costs and benefits of alternative behaviours, the degree of plasticity can be affected by age. Age, however, may be related to changing trade-offs that are age-specific. The more general argument, then, is that factors related to changing trade-offs of behavioural alternatives may also be related to changes in the degree of behavioural plasticity.

That animals are able to alter their behaviour in response to varying stimuli which in turn relate to trade-offs does not require elaboration. What is virtually absent from the empirical literature, however, is a demonstration of the ranges, slopes, and shapes of plastic responses.

Forms of behavioural plasticity

At least three broad types of behavioural plasticity can be distinguished: differences in ontogenetic development, adjustments through learning, and the innate ability to respond to a variety of stimuli. Differences in the ontogeny of behavioural patterns may be due to varying social environments (Groothuis

Fig. 4. The range of behaviours (degree of behavioural plasticity) as a function of age. Trade-offs between the costs and benefits of alternative behaviours may change with age. In this theoretical presentation, the costs of some alternative behaviours may be high (or the benefits low) at a young age, resulting in a smaller degree of behavioural plasticity than at a later age.



1992; Miller 1994). The interpretation of plasticity in the ontogeny of behaviour is similar to that of morphological plasticity because it does not represent an immediate response and is not usually reversible (although irreversibility of age-specific behaviour is not universal; Robinson et al. 1992).

Learning, defined as the modification of behaviour by experience (Stephens 1991 and references therein), results in behavioural plasticity, with an immediate and reversible response. The evolution of learning is influenced by a balance between environmental change and environmental predictability, because within-generation predictability appears to be a factor that strongly promotes learning, as is environmental change between generations (Stephens 1991).

This argument is in harmony with a more recent finding that specialist strategies are favoured in constant environments and in environments that vary within generations, while generalists are favoured when between-generation variability is high (Gilchrist 1995). The latter argument also suggests that learning is not only a special type of phenotypic plasticity (Stephens 1991) but also a special type of behavioural plasticity, because learning is not a prerequisite for a plastic behavioural response. A range of innate behavioural options is sufficient for that purpose. It appears that learning is a superior tool for fine-tuning an animal to respond to environmental variations. However, the evolution of learning may be constrained by factors that are extrinsic or intrinsic to the animal, or both. By extrinsic factors I mean situations where information on potential trade-offs of behavioural options is not available, such as the presence of undetectable predators or parasites. By intrinsic factors I mean the capability of an animal to obtain, store, and process available information. The differentiation between the two types of behavioural plasticities, learning and innate behavioural options, deserves more attention in future studies that relate plasticity to variability of the environment.

Alternative discontinuous behavioural strategies have

received much attention in behavioural ecology (Rubenstein 1980; Dunbar 1983; Caro and Bateson 1986), but our understanding could be vastly improved by acquiring knowledge on the continuity of behavioural responses. It could be argued that behavioural plasticity based on learning is likely to be more continuous than a range of innate responses. This is because learning can be a function of age or of the duration of exposure to a stimulus, while innate behaviours can be understood as discrete responses to distinct categories of stimuli. Therefore, there is merit in research directed towards both discontinuous behaviour (Caro and Bateson 1986) and continuous responses (Alatalo et al. 1990; Gage 1995).

Behavioural plasticity is often inferred from intraspecific comparisons of social organization (see reviews in Thornhill and Alcock 1983; Lott 1984, 1991). Many examples exist in which populations of the same species differ in social structure. There are numerous correlates of the variation in social systems, including sex ratio, predation pressure, resource availability, and population density (Lott 1991). However, whether these correlates are determinants of the observed variations is not known in most cases. Moreover, populations may differ genetically rather than through adopting differing social behaviours. For example, it was only after an analysis of polymorphic loci that Kurt et al. (1993) concluded that forest-dwelling, territorial roe deer (*Capreolus capreolus*) did not differ genetically from those living in fields, often in groups.

In some cases individuals have been observed to switch from one behavioural strategy to another, but in many of these the changes seem to follow an age-specific, genetically determined schedule (Caro and Bateson 1986). No age effect, however, has been found in male fallow deer (*Dama dama*), which can adopt a variety of mating strategies, including territorial defense, harem defense, and males following female groups (Langbein and Thirgood 1989; Alvarez et al. 1990; Thirgood 1990). Individuals occasionally switch between strategies. A similar behavioural plasticity of individual males occurs in the pronghorn (*Antilocapra americana*; Copeland 1980; Byers and Kitchen 1988; Maher 1994). Strategies appear to vary in terms of their costs and benefits (Apollonio et al. 1992; Byers et al. 1994), but until energy and survival costs, as well as reproductive benefits, are determined, conclusions about costs and benefits remain tentative (Bell 1980; Caswell 1982). Such trade-offs could be estimated with greater accuracy if more empirical evidence was available on the range and continuity of behavioural options (Vehrencamp and Bradbury 1984) and the cost of their development and maintenance.

Genetic basis

The genetic basis for the existence of alternative strategies has been demonstrated (Gross 1985; Zimmerer and Kallman 1989). While strong evidence for the heritability of phenotypic plasticity now exists (Stearns 1989; Thompson 1991), the relationship between the plasticity of a trait and the trait mean is still a matter of debate (de Jong 1995; Schlichting and Pigliucci 1995). Whether plasticity itself is an evolved character that is under selection is difficult to demonstrate, and is the subject of differing assumptions and interpretations of mathematical models (Via and Lande 1985; Schlichting 1986; Scheiner 1993; Via 1993; de Jong 1995). A thorough discussion of the different models and their mathematical and

molecular underpinnings is far beyond the scope of this paper, and I refer to recent papers that offer such a discussion (de Jong 1995; Schlichting and Pigliucci 1995; Pigliucci 1996).

Here, I merely point out two important difficulties in the study of behavioural plasticity. First, the degree of plasticity may or may not be looked at as a trait in itself. Bradshaw (1965) discussed phenotypic plasticity as a trait, which de Jong (1995, p. 506) interpreted to mean "plasticity and trait mean are genetically correlated, not that separate genes for plasticity and trait mean exist." The important point here is that genetic variation for the purpose of phenotypic plasticity must exist for the degree of plasticity to evolve (Stearns 1989).

Second, not all phenotypic plasticity is genetically variable (Smith-Gill 1983; Partridge and Harvey 1988; West-Eberhard 1989). Some traits may vary in different environments, owing to developmental perturbations. These are countered by developmental-stability mechanisms that reduce phenotypic plasticity (Zakharov 1992; Clarke 1995).

Costs

Surely, if plasticity was advantageous, it would evolve limitlessly, slowed only by potential developmental constraints (Partridge and Harvey 1988; Stearns 1989), unless some costs of plasticity restrained its evolution. Several potential costs of plasticity have been suggested, including reduced reproduction, reduced growth, errors in developing the appropriate response, and maintenance of the "machinery" that provides plasticity (Alcock 1989; Parejko and Dodson 1991; Newman 1992; Spitze 1992; Rodd and Sokolowski 1995). None has been conclusively demonstrated.

In *D. pulex*, neck teeth are a morphological structure that is developed as a defense against predators. The production of neck teeth is inducible by high predator levels (Parejko and Dodson 1991; Spitze 1992). However, development of neck teeth is associated with lower reproductive rates. Newman (1992) argued that this is not enough evidence in favour of the cost of plasticity, which would be demonstrated if, in the absence of predators, clones with plastic neck-tooth development had a lower reproduction rate than clones that are not plastic.

Some of the best correlational evidence thus far obtained was provided by Newman (1988), who studied the development rate of tadpoles of the spadefoot toad (*Scaphiopus couchii*). Those that showed the greatest plasticity in development were also the slowest to develop under equivalent conditions.

By intuition, we expect that the machinery which maintains behavioural plasticity must be complex and costly (Alcock 1989; Lott 1991). Sensory and physiological avenues must be available for assessing current trade-offs and acting on the result of the assessment. Recent studies have demonstrated that individuals develop new brain structures to perform new complex behaviours in response to changes in the social environment (Withers et al. 1993; Bamshad et al. 1994). A genetic basis for the development of these structures appears to exist (Robinson and Page 1995), but the costs of this development remain speculative.

The assessment procedure itself requires not only time, but also energy, and involves potential risks, such as exposure to predators. The example, given earlier, in which male guppies under higher predation pressure show less plasticity

(Rodd and Sokolowski 1995) may be a case in point. Thus, the cost may be solely due to performing some of the alternative behaviours. A complicating aspect is that the risk of making a wrong decision can be lowered by improving the accuracy of assessing trade-offs. If the male guppy can obtain and process information not only on the availability of females and male competitors but also on the current risk of predator attack, he can decrease the frequency of dangerous actions, as male pipefish do (Berglund 1993), without decreasing the degree of plasticity. However, if information on the current predation risk is not available, then behaviours that increase exposure to predators should be selected against in environments where the predation risk is usually high. In more general terms, an improved ability to assess trade-offs and implement appropriate behaviours should promote behavioural plasticity, because it decreases the frequency of costly (risky) behaviours. This line of thinking appears to be fundamental for understanding the co-evolution of assessment strategies and behavioural plasticity.

Some correlates of behavioural plasticity

Why are pronghorn so strikingly flexible in their mating system (Maher 1994) while other gregarious ungulates, such as bison, have never been observed to defend harems or territories, and males simply defend one receptive female at a time (Lott 1981; Komers et al. 1992)? In bison, variations in density, sex ratio, and age structure all exist in different populations (McHugh 1958; Lott 1981; Green 1992; Komers et al. 1992; Berger and Cunningham 1994), but the mating system does not seem to vary.

Although largely sympatric, the bison and pronghorn differ markedly in their use of habitat. The bison is a relatively unselective grassland-adapted species (Meagher 1973), while the pronghorn appears to be a more selective forager (Kitchen 1974) and its spatial and social organization varies with food distribution (Maher 1994). Occasional changes in the social structure of the pronghorn, such as the formation of large, wide-ranging herds alternating with small groups on small ranges, offer different opportunities for female monopolization and promote behavioural plasticity.

Similarly, the mating system of the monogamous Kirk's dikdik (*Madoqua kirki*), a dwarf antelope, is surprisingly inflexible and males do not seem to attempt to monopolize more than one female (Komers 1996). Monogamy also appears relatively invariant in gibbons (Brockelman and Srikosamatar 1984; Leighton 1987). The mating systems of these two monogamous species are in contrast to those of other species, such as prairie voles (*Microtus ochrogaster*) and black-lipped pikas (*Ochotona curzoniae*), in which the modal mating system is monogamy but deviates with population density and availability of competing males (Cockburn 1988; Smith and Wang 1991).

Conceivably, it can be inferred that dikdik and gibbons live in relatively stable environments and that variations in the environment are not sufficient to alter the trade-offs between the benefits of searching for additional females and remaining with the first one. By contrast, in the temperate environment of prairie voles and black-lipped pikas, population fluctuations frequently offer opportunities that may render occasional monopolization of more than one female profitable.

I chose these examples because they illustrate several important aspects of the study of behavioural plasticity. First, demon-

strating the existence and degree of behavioural plasticity is an area of current and future research. Second, the observed plasticity in behaviour, or at least in social systems, appears to follow the predictions of the theory of the evolution of phenotypic plasticity (Stearns 1989, 1992). Third, to my knowledge, almost no information exists on the heritability or genetic variability of the plasticity of behaviours. Notable exceptions include the mating behaviour of guppies and soapberry bugs (Carroll and Corneli 1995; Rodd and Sokolowski 1995). Fourth, while the social systems of many species have been described in some detail, there is little information on the actual behaviours that are involved in alternations of mating systems.

Finally, these examples also illustrate that it is possible to measure the variability of behavioural responses by comparing populations or species from environments with differing ranges of fluctuations, or by comparing the responses of individuals from different age-classes to a given range of an environmental gradient.

Testable predictions and the measurement of behavioural plasticity

Probably the most comprehensive prediction of the theory of the evolution of behavioural plasticity is that the degree of plasticity is expected to be higher when the variability of the environment is greater (Bradshaw 1965; Morse 1980; Carroll and Corneli 1995; Fig. 1). The "environment," of course, includes a wide diversity of potential factors of a demographic, resource, predatory, and abiotic nature. To formulate testable predictions we need to identify a specific environmental factor that is expected to affect the plasticity of a specific character. Hence, the environmental factor and the relevant character must be appropriately matched.

Exemplary studies in which this has been done are few; they include the inducible neck teeth of *D. pulex* (Parejko and Dodson 1991; Spitze 1992), the development rate of tadpoles (Newman 1992), and the mate-guarding behaviour of soapberry bugs (Carroll and Corneli 1995).

The number of competing species

Individual birds from islands with few other bird species were more behaviourally plastic than individuals from islands with many species (Crowell 1962; Klopfer 1967; Sheppard et al. 1968). This seems to support the view that competition between species results in a narrower niche, because some parts of the diet are not available, owing to exploitation by a competitor (Pianka 1988). This is in contrast to birds in mixed-species flocks, which forage more diversely when together with birds of a dominant species than when separate from them (Morse 1980). To understand this apparent contradiction, it may be useful to distinguish between competition where a part of the diet is removed and competition where the frequency of the most preferred diet is decreased, resulting in a more even distribution of forage items. In the former case, plasticity should be reduced, in the latter it should be favoured.

Density

Fluctuations in density often involve changes in demography (Caughley and Sinclair 1994). Demographic changes result

in differences in the social environment that may affect the availability of mates and the level of intrasexual competition (Cockburn 1988). It can be expected that behavioural plasticity would be greatest not only in species with large fluctuations in population density (Cockburn 1988; Clutton-Brock et al. 1991; Grenfell et al. 1992), but also in species that follow *r*- as opposed to *K*-strategies (Partridge and Harvey 1988; Pianka 1988). Colonizing events are characterized by small founding populations in which demographic stochasticity is relevant (Caughley and Sinclair 1994). This may represent a source of environmental variability in *r*-selected species. Little is known about the relationship between *r*- and *K*-strategies and the degree of behavioural plasticity.

Other factors

The above examples illustrate instances where behavioural plasticity can be expected to vary in response to environmental variability. Other examples may be added without difficulty, including longevity, mobility, and gregariousness (Levins 1968; Morse 1980; Lott 1991), each potentially presenting a different source of environmental variability that could affect the degree of behavioural plasticity. Moreover, the area of potential costs, which may select against the employment of some alternative behaviours and result in different slopes of the response curves (Fig. 2), is almost unexplored.

I argued above that predation risk may represent such a cost, the implications of which have been pointed out by Lima and Dill (1990) and Abrams (1993). Exposure to dangerous competitors represents another form of potential costs. There is solid theoretical and empirical evidence that juvenile animals employ different behaviours from adults, and it has been argued that the difference may be related to an increase in reproductive effort, which is expected to occur with age (Caro and Bateson 1986; Pianka 1988). Whether age-specific behaviours are subject to different degrees of plasticity at different ages is a matter for future studies. The hypothesis can be formulated that if trade-offs change with age and if behavioural plasticity is related to trade-offs, then the degree of behavioural plasticity will also change with age.

Findings not supporting the prediction

In some cases, observations do not seem to support the predicted relationship between environmental variability and plasticity. De Jong (1989) stated that local populations subject to little environmental variation show more plasticity than expected when brought into the laboratory. Klopfer (1967) also found that hand-reared tropical birds showed a higher degree of plasticity than predicted. What remains to be determined, however, is whether all relevant environmental factors are invariant, and if so, whether the species or population existed in a more variable environment beforehand.

Consequences and implications of plasticity

In the preceding sections I presented the mostly theoretical basis of our knowledge about the relationship between environmental variability and the degree of behavioural plasticity. In the following section, I shall concentrate on applied aspects of behavioural plasticity. These are particularly, but not exclusively, relevant to conservation biology, a field of rapid

current development in both theory and practice. For example, if the demography of an ungulate population is changed by removing older males (be it by humans or by some selective predator), then the population is not expected to be affected in its viability because young males are known to reproduce if given the opportunity. However, on closer observation, several consequences of this plasticity can be identified.

First, because the sex ratio favours females, a higher proportion of individuals in the population produce young. Consequently, the rate of increase should be higher (Caughley and Sinclair 1994). Second, because young males do not simply take over the role of mature males but omit certain behaviours (Komers et al. 1994a, 1994b), the distribution of matings may be altered, with a larger proportion of the remaining males contributing. In a bison population from which mature males were removed, a significantly higher proportion of the remaining males consorted with females (Komers 1992). This potentially increases the number of males passing on their genes, hence increasing the effective population size (Soulé 1987; Primack 1993). Third, because young males in a population lacking mature males disturb the females (Clutton-Brock et al. 1982; Komers et al. 1994a), females may incur increased energy costs during the reproductive period. Bison females in a population lacking mature males suffered decreased feeding and resting times during the rut compared with females under control conditions (Komers 1992).

Whether these factors in combination actually increase or decrease population growth remains a matter for further investigation. The important point here is that the degree of plasticity changes our predictions about population dynamics because the limits of behavioural plasticity may have surprising consequences.

Similarly, knowledge of the degree of behavioural plasticity may improve the accuracy of our predictions of resource consumption and niche breadth (Morse 1980) or the effects of predation pressure (Lima and Dill 1990; Abrams 1993). Moreover, the plasticity of dispersal behaviour may determine dispersal rates of animals (Fahrig and Merriam 1994). This is particularly important in conservation biology, where the connectedness of fragmented habitat patches is of central interest (Bennett et al. 1994; Dunning et al. 1995). A special problem of behavioural plasticity has recently been pointed out: the range of what animals can perceive may have important implications for behavioural decision-making in the context of landscape ecology (Lima and Zollner 1996).

Conclusions

While there is now growing evidence for the heritable nature of morphological plasticity, empirical evidence for an evolutionary relationship between behavioural plasticity and environmental variability is still rare. From some of the pioneering studies of behavioural plasticity it is evident that relating the degree of environmental variability to the degree of behavioural plasticity is feasible, and that given adequate knowledge of ecological variation, testable predictions regarding behavioural plasticity can be formulated. An important and testable hypothesis is that if trade-offs change with age and if behavioural plasticity is related to trade-offs, the degree of behavioural plasticity will also change with age. This hypothesis implies

that focusing exclusively on the relationship between behavioural plasticity and environmental variability would underscore the extent of the problem because variability in behavioural plasticity can be also related to the costs and benefits of alternative behaviours.

I suggested that the ability to assess trade-offs and implement appropriate behaviours should promote behavioural plasticity because it decreases the frequency of costly behaviours. This ability is presumably associated with the information available in the environment and the capacity of an animal to obtain, store, and process the information. Behavioural plasticity, then, should increase with learning capacity. However, learning is not a prerequisite for behavioural plasticity, because a variable response can be produced by an array of innate behavioural responses. These arguments appear to be fundamental to an understanding of the co-evolution of assessment strategies and behavioural plasticity.

Theory and the small body of empirical evidence suggest that the degree of behavioural plasticity is heritable and that it can vary among species, populations, and behaviours within a population. It may therefore be misleading to declare a species to be more or less plastic without identifying the behavioural trait in question. The study of behavioural plasticity may be particularly relevant in applications of conservation biology where questions are raised concerning the adaptability of species to environments imposed on them by human activities (Caughley 1994).

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