ALTENBERG SEMINARS IN THEORETICAL BIOLOGY

Winter 2006/2007:
Phenotypic Plasticity

Hörsaal 1, Biozentrum, Althanstrasse 14, 6.15 p.m.

The Program at a glance:

8 November 2006
Sonia E. SULTAN(Wesleyan University, Middletown, CT, USA):
"Phenotypic Plasticity and Adaptive Interpretation: A Case Study in Annual Plants"

7 December 2006
Olof Leimar (Department of Zoology, Stockholm University):
"Unifying Genetic Polymorphism and Phenotypic Plasticity"

14 December 2006
Michael Kopp (Section Evolutionary Biology, University of Munich):
"Phenotypic Plasticity in Predator-Prey Interactions"

11 January 2007
Massimo Pigliucci (Dept. of Ecology & Evolution, SUNY-Stony Brook, NY, USA):
"What Do We Know About Phenotypic Plasticity?"

25 January 2007
Paul Brakefield (Institute of Biology, Leiden University):
"Evo-devo of Eyespots: Developmental Plasticity in Bicyclus Butterflies as a Response to Alternating Seasons"

The topic

Phenotypic Plasticity

In a letter to the Würzburg zoologist Karl SEMPER (1832-1893), the author of a groundbreaking book on animal ecology (SEMPER 1880/1881), Charles DARWIN (1881) speculated “whether a species very liable to repeated and great changes of conditions might not assume a fluctuating condition ready to be adapted to either condition (quoted in GORDON 1992: 255). The problem facing organisms that have to track changing environments repeatedly — say, seasonally — by genetic differentiation is comparable to that of “a military general always planning for the last war” (SHAPIRO 1984: 297), because the genetic composition of a population reflects the selective regime of the previous season. The evolution of phenotypic plasticity (PP), viz., “the property of a given genotype to produce different phenotypes in response to distinct environmental conditions” (PIGLIUCCI 2001: 1) allows to solve this problem (LEVINS 1968; SHAPIRO 1984; BRAKEFIELD and WIJNGAARDEN 2003; NIJHOUT 2003; SULTAN and STEARNS 2005).
Thus, seasonal polyphenism (e.g., in butterflies: BRAKEFIELD seminar), the adaptation of alternative phenotypes (‘morphs’) to the particular seasonal environment in which they spend all or most of their adult lives, can reduce the time lag (‘load’) of response under certain favorable conditions, viz., individuals equally competent to make correct developmental ‘decisions’ and ‘trustworthy’ environmental cues). When viewed as a source of variation within a generation, PP can be visualized by means of norms of reaction, i.e., functions describing the response of a genotype to a quantitative environmental manipulation. Using a reaction norm, the reactions of several genotypes to the same environmental manipulation can be compared. From an evolutionary point of view, PP is a consequence of a genotype coding not for a fixed phenotype, but for a reaction norm (SCHLICHTING and PIGLIUCCI 1998). It may thus be contrasted with canalization, by which a genotype yields similar phenotypes in different environments and developmental factors restrict variation in the final phenotype.

At the same time, PP allows to explain a number of mechanisms involved in the control of development and in the interactions between gene expression, epigenetic factors, and the environment during ontogeny (e.g., GERHARD and KIRSCHNER 1997). In developmental biology, PP — which developmental plasticity presupposes — helps us to understand how developmental pathways can be mediated in response to environmental stimuli and hence provide different phenotypic options (e.g., NIJHOUT 2003). In order to examine and measure PP at the level of individual organisms, it has to be defined as “any change in an organism’s characteristics in response to an environmental signal” (SCHLICHTING and SMITH 2002: 190). This definition and PIGLIUCCI‘s are mutually exclusive: When PP is defined in terms of a norm of reaction, it must be calculated by determining the mean phenotype manifested by a group of individuals of the same genotype at each level of the environmental manipulation, and hence cannot be measured on individual organisms. In addition to different time scales (across or within generations), the meaning of ‘PP’ may also differ depending on whether the variation is among or within populations, and on whether environmental change and organismal response are continuous or discrete, and reversible or irreversible (GORDON 1992). Nonetheless, many authors argue that PP should be “broadly construed to encompass a diversity of phenomena spanning several hierarchical levels of organization,” starting from underlying shared processes at the cellular level (SCHLICHTING and SMITH 2003). PIERSMA and DRENT (2003), among others, have begun to provide a common framework to bring the different categories of PP together, and articulate perspectives on adaptation that reversible types of plasticity might provide. We also note that not all PP is adaptive, as it sometimes may represent an inability to eliminate developmental instability (SCHLICHTING and SMITH 2002; BRAKEFIELD and WIJNGAARDEN 2003: 297).

WEST-EBERHARD’s one sentence summary of her magnificent book, Developmental Plasticity and Evolution, aptly seizes the importance of PP for EvoDevo: “The universal environmental responsiveness of organisms, alongside genes, influences individual development and organic evolution, and this realization compels us to reexamine the major themes of evolutionary biology in a new light” (2003: vii). PP may concern morphology (e.g., DIGGLE 2002), life history (e.g., STEARNS and KOELLA 1986; BRAKEFIELD seminar), behavior, physiology (e.g., BLAUSTEIN and BELDEN

2003), etc.; it is “now known to be a source of enormous developmental, physiological, and life-history variation in a broad spectrum of organisms” (SULTAN seminar abstract). NIJHOUT (2003: 9) does not hesitate to call PP “the primitive character state for most if not all traits.” Instead of variation for plasticity being considered as a nuisance in evolutionary studies, it has become a main target of investigations that use an array of methods, including quantitative and molecular genetics, and several approaches that model the evolution of plastic responses. KOPP, and PIGLIUCCI in particular, will survey these recent developments, and assess in which areas progress has been made, and where additional effort is required.

SULTAN’s seminar will discuss methodological difficulties with conventional approaches to testing the adaptive value of traits that arise because of the environmental sensitivity of phenotypic expression, and focus on comparative plasticity experiments with annual plant species in the genus Polygonum as a pluralistic alternative.

LEIMAR will argue that, from the viewpoint of a developmental switch, genetic morph determination can function as adaptive developmental plasticity by providing developing individuals with information about the likely success of phenotypic alternatives. Just as adaptive PP is a developmental response to environmental cues that predict future selective conditions, genetic polymorphism may be viewed as a developmental response to genetic cues, in the form of selectively maintained gene frequency differences between population segments — a ‘conditional strategy’ in game-theoretic terms.

KOPP will give an overview of PP in predator-prey systems in which predation-related adaptations often involve costly investments, an issue that is currently at the forefront of research and that will also be discussed by PIGLIUCCI. This has led to the evolution of phenotypically plastic responses to specific prey or predators — ‘inducible defenses’; plastic adaptations of predators to prey are called ‘inducible offenses’. Theoretical models are needed to understand the evolution of both as well as of their ecological consequences.

BRAKEFIELD will report on the research of his team on Bicyclus butterflies in Africa, which exhibit seasonal polyphenism with alternating adult generations of wet and dry season forms. This divergence has led them to examine the bases of the PP in wing pattern in a model species, B. anynana, as well as the evolution of key life history traits including adult starvation resistance and longevity. A major goal of their framework is to gain a better understanding of the contributions of both developmental bias and natural selection to shaping the patterns among species in their occupancy of morphological space.

References

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GORDON DM (1992) Phenotypic plasticity. In: Keywords in Evolutionary Biology (KELLER EF, LLOYD EA, eds), 255-262. Harvard UP.

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NIJHOUT HF (2003) Development and evolution of adaptive polyphenisms. Evolution and Development 5: 9-18.

PIERSMA T, DRENT J (2003) Phenotypic flexibility and the evolution of organismal design. Trends in Ecology and Evolution 18: 228-233.

PIGLIUCCI M (2001) Phenotypic Plasticity: Beyond Nature and Nurture. Johns Hopkins UP.

SCHLICHTING CD, PIGLIUCCI M (1998) Phenotypic Evolution: A Reaction Norm Perspective. Freeman.

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SHAPIRO AM (1984) Experimental studies on the evolution of seasonal polyphenism. In: The Biology of Butterflies (VANE-WRIGHT RI, ACKERY PR, eds), 297-307. Academic Press.

STEARNS SC, KOELLA JC (1986) The evolution of phenotypic plasticity in life-history traits: Predictions of reaction norms for age and size at maturity. Evolution 40: 893-913.

SULTAN SE, STEARNS SC (2005) Environmentally contingent variation: Phenotypic plasticity and norms of reaction. In: Variation (Hallgrimsson B, Hall BK, eds), 303-332. Elsevier Academic Press.

WEST-EBERHARD MJ (2003) Developmental Plasticity and Evolution. Oxford UP.

Sonia E. SULTAN
Department of Biology
Wesleyan University
Middletown, CT, USA

Phenotypic Plasticity and Adaptive Interpretation: A Case Study in Annual Plants

9 November 2006

Abstract

Phenotypic plasticity is now known to be a source of enormous developmental, physiological, and life-history variation in a broad spectrum of organisms. The ecological and evolutionary consequences of this variation depend upon whether it constitutes adaptation at the individual level. Yet because of the environmental sensitivity of phenotypic expression, conventional approaches to testing the adaptive value of traits (including direct reciprocal experiments and statistical covariance estimates) can seldom be applied to plasticity patterns. Comparative plasticity experiments offer an alternative approach to this fundamental interpretive question. Studies of annual plant species in the genus Polygonum show that even closely related taxa may differ dramatically in patterns of environmental response, and exemplify how adaptive plasticity can be assessed for key functional traits. These data further show that plasticity for fitness itself is quite complex, since it involves both immediate and cross-generational components. These results argue for a more pluralistic approach in order to investigate plasticity as an alternative mode of adaptation.

Biographical note

Sonia SULTAN's primary research interests are (1) repertoires of phenotypic plasticity in plants ("plant ecological development"), and (2) the evolutionary and ecological consequences of plasticity as a source of both adaptive and maladaptive variation. After completing an undergraduate degree in the History and Philosophy of Science at Princeton University, SULTAN earned a PhD from Harvard University in 1990, working jointly with plant ecologist F. A. BAZZAZ and evolutionary biologist R. C. LEWONTIN on genotypic norms of reaction in natural plant populations. Her empirical and conceptual work on phenotypic plasticity has maintained this inter-disciplinary focus, drawing on ideas and approaches from population and quantitative genetics, ecophysiology, and population ecology. As a Post-Doctoral Fellow at the University of California's Center for Population Biology, SULTAN extended her experimental studies to include cross-generational plasticity, and developed the comparative approach used in much of her subsequent work. She has served on the editorial boards of Ecology, The American Naturalist, and (currently) New Phytologist, and co-hosted the first international symposium on plant ecological development at London's Royal Society in January. Since 1993 she has been a member of the Biology faculty at Wesleyan University, where she is now a tenured Associate Professor.

Selected publications

(2006) Adaptive consequences of species differences in plastic and constant developmental traits (with T GRIFFITH). Oikos 114: 5—14.

(2005) Seedling expression of cross-generational plasticity depends on reproductive architecture (with MR LUNDGREN). American Journal of Botany 92: 377—381.

(2005) Shade tolerance plasticity in response to neutral vs green shade cues in Polygonum species of contrasting ecological breadth (with T GRIFFITH). New Phytologist 166: 141—148.

(2005) Environmentally contingent variation: phenotypic plasticity and norms of reaction (with SC STEARNS). In Variation: A Central Concept in Biology (HALL B et al. eds), 303—332. Elsevier Academic Press.

(2005) Ecological Consequences of Phenotypic Plasticity (with BG MINER, SG MORGAN, DK PADILLA, and RA RELYEA). Trends in Ecology and Evolution 20: 685—692.

(2004) The double-edged sword of developmental plasticity: implications for human health and disease (with P BATESON, D BARKER, P GLUCKMAN, T KIRKWOOD, et al.). Nature 430: 419—22.

(2004) Promising research directions in plant phenotypic plasticity. Perspectives in Plant Ecology, Evolution and Systematics 6: 227—233.

(2004) Population differentiation and plastic responses to drought stress in the generalist annual Polygonum persicaria (with S HESCHEL, D SLOAN, and S GLOVER). International Journal of Plant Sciences. 165: 817—824.

(2003) Phenotypic plasticity in plants: A case study in ecological development. Evolution and Development 5: 25—33 (Special Issue: Ecological Developmental Biology).

(2003) The promise of ecological developmental biology. Molecular and Developmental Evolution 296B: 1—7.

(2002) Metapopulation structure favors plasticity over local adaptation (with HS SPENCER). The American Naturalist 160: 271—283.

(2001) Phenotypic plasticity for fitness components in Polygonum species of contrasting ecological breadth. Ecology 82: 328—343.

(2000) Phenotypic plasticity for plant development, function and life-history. Trends in Plant Science 5: 537—542 (invited review article).

Olof LEIMAR
Department of Zoology
Stockholm University

Unifying Genetic Polymorphism and Phenotypic Plasticity

7 December 2006

Abstract

Organisms can have divergent paths of development, leading to alternative phenotypes or morphs. Examples include winged and wingless morphs in some groups of insects, defended and undefended morphs in certain prey species, and alternative male mating types, like large and small males in salmonid fishes. The developmental path can be set by environmental cues, or by the individual's genotype, or a combination of the two. The first of these possibilities represents phenotypic plasticity and the second is an example of genetic polymorphism. It has become traditional in evolutionary theory to treat these two cases as fundamentally distinct, although at the same time they have been much discussed as alternative evolutionary outcomes.

Genetic polymorphism and phenotypic plasticity have in common that they can be evolutionary responses to varied circumstances, which may provide a basis for conceptual unification. I will discuss the idea that, from the viewpoint of a developmental switch, genetic morph determination can function as adaptive developmental plasticity, by providing developing individuals with information about the likely success of phenotypic alternatives. Evolutionary analysis, in the form of analytical modeling and individual-based simulation, demonstrates that this perspective is logically feasible. I will argue that it is also helpful for understanding the evolution of variation in nature.

The unified perspective resolves a 50-year old debate in ecological genetics, with Theodosius Dobzhansky and R. A. Fisher as major participants, on whether genetic polymorphism can be regarded as an adaptation to variable circumstances. In the same way as adaptive phenotypic plasticity is a developmental response to environmental cues that predict coming selective conditions, genetic polymorphism can be seen as a developmental response to genetic cues, in the form of selectively maintained gene frequency differences between population segments. These genetic cues can also serve as statistical predictors of conditions. In this way, genetic polymorphism is interpreted as a conditional strategy. I will argue that such an interpretation is of basic conceptual importance for evolutionary theory.

Biographical note

Olof LEIMAR is a Professor of Zoology in the Ethology section of the Department of Zoology at Stockholm University. With an education in theoretical physics from the Royal Institute of Technology in Stockholm, he switched to biology and received his PhD at Stockholm University in 1988. After the PhD he obtained a researcher position in theoretical ethology, funded by the Swedish Research Council, and subsequently became a Lecturer and then Professor of Zoology at Stockholm University. His original field of interest in biology was evolutionary game theory and its application to fighting behaviour. In collaboration with Magnus Enquist from Stockholm University he developed the sequential assessment game, which has become one of the classical game-theory models of aggressive behavior. The evolution of cooperation is another of his scientific interests, in which he has collaborated with Peter Hammerstein from Humboldt University Berlin. In recent years he has devoted himself to the basic principles of the adaptation of an organism to its circumstances and to the role of genetic polymorphism as an adaptive developmental strategy.

Selected publications

(2006) A new perspective on developmental plasticity and the principles of adaptive morph determination (with P HAMMERSTEIN and TJM VAN DOOREN). American Naturalist 167: 367—376.

(2005) The evolution of phenotypic polymorphism: randomized strategies versus evolutionary branching. American Naturalist 165: 669—681.

(2001) Evolutionary change and Darwinian demons. Selection 2: 65—72.

(2001) Evolution of cooperation through indirect reciprocity (with P HAMMERSTEIN). Proceedings of the Royal Society B 268: 745—753.

(1996) Life-history analysis of the Trivers and Willard sex-ratio problem. Behavioral Ecology 7: 316—325.

(1996) The effect of flexible growth rates on optimal sizes and development times in a seasonal environment (with PA ABRAMS, S NYLIN and C WIKLUND). American Naturalist 147: 381—395.

(1993) The evolution of cooperation in mobile organisms (with M ENQUIST). Animal Behaviour 45: 747—757.

(1986) Evolutionary stability of aposematic coloration and prey unprofitability: a theoretical analysis (with M ENQUIST and BS TULLBERG). American Naturalist 128: 469—490.

(1983) Evolution of fighting behaviour: decision rules and assessment of relative strength (with M ENQUIST). Journal of Theoretical Biology 102: 387—410.

Michael Kopp
Section Evolutionary Biology
University of Munich

Phenotypic Plasticity in Predator-Prey Interactions

14 December 2006

Abstract

Most species are either predators or prey (or both), and they have evolved numerous adaptations to these life-styles. Frequently, predation-related adaptations involve costly investments, which should be made only when they are truly needed. This has led to the evolution of phenotypically plastic responses to specific prey or predators. Plastic responses of prey to predators are known as inducible defenses. Examples include morphological, behavioral, biochemical and life-history changes and have been found in organisms ranging from protozoans to higher plants and vertebrates. Similarly, plastic adaptations of predators to prey may be called inducible offenses. Often, these include the development of carnivorous or cannibalistic giant forms. Theoretical models are needed for understanding both the evolution of inducible defenses and offenses and their ecological consequences. I will give an overview of phenotypic plasticity in predator-prey systems and highlight some recent developments.

Biographical note

Michael KOPP is a theoretical evolutionary biologist broadly interested in adaptation under complex selection regimes. His work has focused on predator-prey interactions, environmental variability, phenotypic plasticity, coevolution, frequency-dependent selection, and speciation. After graduating in biology from the Ludwig-Maximilian-University Munich in 1998 he did a PhD on phenotypic plasticity in predator-prey systems at the Max-Planck-Institute of Limnology in Plön, Germany. From 2003 to 2004, he worked at the University of Tennessee in Knoxville, USA, and since September 2004, he is a postdoctoral research associate at the University of Munich.

Selected publications

(2006) The evolution of genetic architecture under frequency-dependent disruptive selection (with J HERMISSON). Evolution 60: 1537—1550.

(2006) Multilocus genetics and the coevolution of quantitative traits (with S GAVRILETS). Evolution 60: 1321—1336.

(2006) The effect of an inducible defense in the Nicholson-Bailey model (with W GABRIEL). Theoretical Population Biology 70: 43—55.

(2003) Reciprocal phenotypic plasticity in a predator-prey system: inducible offences against inducible defences? (with R TOLLRIAN). Ecology Letters 6: 742—748.

(2003) Trophic size polyphenism in Lembadion bullinum: costs and benefits of an inducible offense (with R TOLLRIAN). Ecology 84: 641—651.

(2001) Exact compensation of stream drift as an evolutionarily stable strategy (with JM JESCHKE and W GABRIEL). Oikos 92: 522—530.

Massimo Pigliucci
Dept. of Ecology & Evolution
SUNY-Stony Brook, NY, USA

What Do We Know About Phenotypic Plasticity?

11 January 2007

Abstract

The study of phenotypic plasticity has progressed significantly over the past few decades. We have moved from variation for plasticity being considered as a nuisance in evolutionary studies to it being the primary target of investigations that use an array of methods, including quantitative and molecular genetics, as well as of several approaches that model the evolution of plastic responses. In this talk, I consider some of the major aspects of research on phenotypic plasticity, assessing where progress has been made and where additional effort is required. I suggest that some areas of research, such as the study of the quantitative genetic underpinning of plasticity, have been either settled in broad outline or superseded by new approaches and questions. Other issues, such as the costs of plasticity, are currently at the forefront of research in this field, and are likely to be areas of major future development.

Biographical note

Massimo PIGLIUCCI is Professor in the Department of Ecology & Evolution at SUNY-Stony Brook (Long Island, NY). His research is on the evolution of genotype-environment interactions and on the role of constraints in evolutionary biology. He also has an interest in epistemology and philosophy of science.
He received his Doctorate in Genetics at the University of Ferrara in Italy, his PhD in Botany from the University of Connecticut, and a PhD in Philosophy of Science at the University of Tennessee. He has published 68 technical papers and three books on evolutionary biology.
Dr. PIGLIUCCI has won the Dobzhansky Prize from the Society for the Study of Evolution. In 2004 he has been elected fellow of the American Association for the Advancement of Science “for fundamental studies of genotype by environmental interactions and for public defense of evolutionary biology from pseudoscientific attack.” He is also an editor for the Quarterly Review of Biology and for Biology & Philosophy.

Selected publications

(2006) Genetic variance-covariance matrices: a critique of the evolutionary quantitative genetics program. Biology & Philosophy 21: 1—23.

(2005) Evolution of phenotypic plasticity: where are we going now? Trends in Ecology & Evolution 20: 481—486.

(2005) Effects of gibberellin mutations on tolerance to apical meristem damage in Arabidopsis thaliana. (with J BANTA). Heredity 94: 229—236.

(2005) Morphological responses to simulated wind in the genus Brassica (Brassicaceae): Allopolyploids and their parental species (with C MURREN). American Journal of Botany 92: 810—818.

(2004) Phenotypic Integration: the Evolution of Complex Phenotypes (ed, with K PRESTON). Oxford University Press.

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Paul Brakefield
Institute of Biology
University of Leiden
The Netherlands

Evo-devo of Eyespots: Developmental Plasticity in Bicyclus Butterflies as a Response to Alternating Seasons

25 January 2007

Abstract

Invertebrates faced with the challenge of persisting through alternating wet and dry seasons in the tropics have frequently evolved developmental plasticity as an adaptive response to the temporal variation in the environment. Bicyclus butterflies in Africa exhibit seasonal polyphenism with alternating adult generations of a wet season form and a dry season form. These differ in the pattern of wing eyespots but also show numerous other adaptations, either to a favourable (wet) season in terms of resources or to one (dry) that is more stressful. This divergence has led us to examine not only the bases of the phenotypic plasticity in wing pattern in a model species, B. anynana, but also the evolution of key life history traits including adult starvation resistance and longevity. This has been done both in terms of the processes of development that generate phenotypic variation and in the ecological context of adaptive responses to variation in the occurrence of environmental stress. With this work on Bicyclus we seek to link studies from the expression of developmental genes through to variation in fitness in natural environments. A major goal of this framework is to better understand the contributions of both developmental bias and natural selection to shaping the patterns among species in their occupancy of morphological space.

Biographical note

Paul BRAKEFIELD has held the Chair in Evolutionary Biology at the Institute of Biology (IBL) in Leiden since 1987. He is also now Vice Director of the IBL. He is President of the European Society of Evolutionary Biology and of the Tropical Biology Association. His research has become focused on a new laboratory model organism, the African butterfly Bicyclus anynana. It is multidisciplinary in nature and has, in particular, established strong components in evolutionary developmental biology or 'EvoDevo'. He is concerned to explore adaptive evolution in both morphological and life history traits, and is also becoming increasingly interested in making links from adaptation to the processes of speciation in the lineage of species of Bicyclus and related genera. He is on the editorial board of a number of Journals that span the fields of evolutionary biology, entomology and EvoDevo.

Selected publications

(2006) Consequences of artificial selection on pre-adult development for adult lifespan under benign conditions in the butterfly Bicyclus anynana (with J PIJPE, K FISCHER, and BJ ZWAAN). Mechanisms of Ageing and Development 127(10): 802—807.

(2006) Multitrait evolution in lines of Drosophila melanogaster selected for increased starvation resistance: the role of metabolic rate and implications for the evolution of longevity (with EA BALDAL and BJ ZWAAN). Evolution - International Journal of Organic Evolution 60(7): 1435—1444.

(2006) Evo-devo and constraints on selection. Trends in Ecology & Evolution 21(7): 362—368.

(2005) Generating phenotypic variation: prospects from "evo-devo" research on Bicyclus anynana wing patterns (with P BELDADE and AD LONG). Evolution and Development 7(2): 101—107.

(2005) The evolutionary genetics of egg size plasticity in a butterfly (with MJ STEIGENGA, BJ ZWAAN, and K FISCHER). Journal of Evolutionary Biology 18(2): 281—289.

(2005) Natural selection and developmental constraints in the evolution of allometries (with WA FRANKINO, BJ ZWAAN, and DL STERN). Science 307(5710): 718—720.

(2005) Evolutionary developmental biology: how and why to spot fly wings (with V FRENCH). Nature 433(7025): 466—467.

(2003) The power of evo-devo to explore evolutionary constraints: experiments with butterfly eyespots. Zoology (Jena) 106(4): 283—290.