

SPRINGER BRIEFS IN EVOLUTIONARY BIOLOGY

Clara B. Jones

**Robustness,  
Plasticity,  
and Evolvability  
in Mammals**  
A Thermal  
Niche Approach

 Springer

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# Robustness, Plasticity, and Evolvability in Mammals

A Thermal Niche Approach

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# Preface

*“[E]ach activity performed by an individual can be thought of as incurring a certain probability of death and a certain probability of successful reproduction ... .”*

*McCleery (1978)*

*“On a priori grounds the causation responsible for ... elimination [mortality] must be ecological or genetic.”*

*Park and Lloyd (1955)*

Robustness (relative insensitivity to system perturbation), plasticity (relative sensitivity to system perturbation), resilience (“stress–strain curve”:  $X$ -axis = stress,  $Y$ -axis = response to stress = strain; pressure deviation = force/area), and elasticity (relative degree of resilience) have been fundamental concepts in applied physics at least since the eighteenth century (Malacarne 1783 in Rosenzweig 2007) and in the biological sciences at least since the early twentieth century when Cannon (1932; cf. JLF Bernard, “*thermodynamique*”) explicitly reconfigured the stabilizing bio-feedback construct (Schoener 2011; Bates and Cosentino 2011) as the mechanism, homeostasis (“homeorhetic” processes: Meiklejohn and Hartl 2002). Originally, use of the “homeostasis” concept among organismal and evolutionary biologists implied mechanistic “rheostat” processes used to characterize physical systems. Currently, emphasis is placed on the dynamic “balancing” of processes by negative and positive feedback mechanisms (“sensors”) responsive to sensory communication (signals, information) about deviations from “target set ‘points,’” including their thresholds, ranges, hierarchies, and probabilities of response. Many terms borrowed from physics have been “tweaked” by biologists, though mechanistic and reductionist approaches continue to define the scientific enterprise in the latter discipline.

Organismal processes, from molecular to higher levels, are effected by signal transmission (communication, “crosstalk”: Laughlin and Sejnowski 2003) from one system unit to others (cellular differentiation, development: Heidel et al. 2011; Hallgrímsson and Hall 2005; cultural processes: Centola et al. 2011), events that partially explain differential life-history (energy allocation) tactics and strategies

resulting from environmental information available to organisms (Kussel and Leibler 2005; Heidel et al. 2011). At every level of biological organization, feedback mechanisms are fundamental to resilience and elasticity since the former property describes post-perturbation return to energy balance while the latter property is the quantitative measure of resilience (Bates and Cosentino 2011). Under certain conditions, individuals may benefit from narrow “target set ‘points,’” and under other regimes, broad “target set ‘points,’” “mirroring” adaptive thermal tolerances maintained in dynamic equilibrium states by negative and positive feedback processes regulating an organism’s optimal energy allocations to structures and functions. From the most basic levels of vertebrate organization, each biological unit can be dissected and diagnosed as a model of regulatory feedback responsive to within and between component responses to molecular or other stressors and strains (perturbations), dynamically optimizing and maintaining nonlethal levels of function.

I was introduced to these formulations in the 1960s during discussions with a neighbor who exposed me to the terminology of biomechanics, preparing me to integrate physical constructs and the study of animals (including hominids). Classes in economics and ecology interrelated the aforementioned formulations with additional ones, in particular, stability (“free [available] energy” states), complexity (multicellular, multinodal), buffering (regulatory mechanisms protecting phenotypes from environmental and genetic perturbation), canalization (low variability of a reaction norm), modularity (neural assemblies, synchronization of neurons), “norms of reaction” (phenotypic variation as a function of environmental variation), and flexibility (reversible responses). Lectures addressed niche theory (formulations about fluctuations in limiting resources, particularly, food), intra- and interindividual competition, thermal and biophysical effects, as well as allocation strategies and differential reproductive success of individuals, mean fitness of populations, and evolvability (“evolvability of a trait = coefficients of additive genetic variance,  $CV_a$ , + square of trait mean,  $l_a^2$ ”; “evolutionary adaptability”). In the present treatment, evolvability will be defined as “the capacity to generate nonlethal heritable variation” (Kirschner and Gerhart 1998), an expression closely conforming to “thermal niche” effects.

Each functional unit of a biological system is characterized by an external surface or “phenotype” (“a periphery”). In the present review, “phenotype” refers to the whole organism’s (“individual’s”) sensory-motor surface area exposed to abiotic and biotic stimuli external (exogenous) to the surface area. Where phenotypes of endogenous properties are intended (events internal to the whole organism), the particular “phenotype” of interest will be indicated. In nonpathological (nontoxic, nondisease, noninfirm, abnormal) states, the phenotype’s reaction norms are expected to vary as a function of changes in thermal niches induced by environmental or other fluctuations, negatively impacting thermal tolerances and “free energy” states, often inducing compensatory responses (Ricklefs and Wikelski 2002; Vieira-Silva et al. 2011). Confronted with system perturbations deviating away from thresholds of nonlethal reaction norms, an individual’s “physiology/life-history nexus” (Denver 1997; Ricklefs and Wikelski 2002; Price 2006; Vieira-Silva et al. 2011; Dantzer and Swanson 2011; Dell et al. 2011; Nevo 2001; Hau 2007; Stearns

1992; Hallgrímsson and Hall 2005) may be activated to enhance or diminish system sensitivity to a new regime, thereby connecting individual phenotypes and inclusive fitness with thermal properties of habitats (Dell et al. 2011; Nevo 2001). Modified fitness landscapes, then, may favor increased or decreased robustness and plasticity at one or more level of biological organization. The “regulatory logic” of reprogramming mechanisms is expected to change inclusive fitness optima under changed regimes, given endogenous (Kitazoe et al. 2011; Heidel et al. 2011) and exogenous (Slobodkin and Rapoport 1974) constraints, perturbations, stressors, and other interruptions of (thermal shock, “knockdown” events) and disturbances (risks, uncertainties) to system processes (Weinreich et al. 2006).

Aggregate effects of organisms’ (synaptic) “decisions” partially determine shifting mean fitness of populations (Slobodkin and Rapoport 1974). In addition, individual tactics and strategies present as differential costs and benefits associated with modifications of reaction norms in response to altered patterns of environmental fluctuation. The persistence, reorganization, and collapse of biological systems depend upon differential energy inputs and outputs as well as scale, and lethal levels of imbalanced heat transfer may cause time-dependent, destabilizing cascades of system components (nodes, branches, circuits, networks, and modules) leading to system collapse (Bates and Cosentino 2011; Fig. 3.3).

Framing a selected review and discussion of robustness, plasticity, and evolvability in mammals was guided by the importance of these functional processes to differential reproduction of individuals and the production and maintenance of heritable variation in populations. The aforementioned topics are fundamental to the scientific study of basic and applied ecology and evolutionary biology (Schoener 2011; Ricklefs and Wikelski 2002) and are of current interest to many generalists and students, as well. Though this Springer Brief is not a specialized text and many of its examples and topics reflect my particular academic specializations, research, and interests, numerous references to the mainstream literature are provided to non-specialists as maps to the rapidly expanding databases. In addition, an efficient treatment of structural, mechanistic, and functional aspects of the topics was required that did not limit the study’s relevance to future speculations, insights, data, theories, and other quantitative treatments. Since I am not specialized in genetics and genomics, I was challenged to select citations and examples that were within my range of competence while, concurrently, retaining the specialist’s engagement. I relied heavily on recent review papers, in part, for purposes of bibliographic economy, in part, to provide accessible, synthetic treatments to readers at any level of mastery. On the whole, citations were selected for their general applicability and accessibility to investigations at all levels of mammalian organization, and, wherever possible, I relied on Hallgrímsson and Hall (2005) that is treated, herein, as a single reference volume. The number of references is restricted, except in cases of serious controversy or interpretation. Bates and Cosentino (2011); Wagner (2001); Stearns (1992); Roff (2002); Chapters 6, 10, 11, 15 in Pigliucci and Muller (2010); Seebacher et al. (2010); Nijhout (2003a, b); Stearns et al. (1991); Rutherford (2000); and Hallgrímsson and Hall (2005) provide comprehensive introductions to many of the concepts reviewed in the present text.



Throughout, optimality terminology is employed as the *lingua franca* in physics, economics, ecology, and behavior (Slobodkin and Rapoport 1974; Giraldeau and Caraco 2000; Bates and Cosentino 2011; Wilkie and Godoy 2001). Even though “shifting optima” models are considered by some scientists to be more useful descriptions of populations in fluctuating regimes or in populations where “arms races” (coevolution: different mutations in more than one species acted on by selection, yielding similar phenotypes; Sect. 4.3, Box 3.1) strongly influence mean fitness of populations, these quantitative approaches are not as advanced as ESS treatments assuming frequency dependence. Furthermore, neuroscience research provides strong evidence for the importance of optimization processes in complex (multi-nodal) nervous systems (Vickery et al. 2011). Working definitions are provided parenthetically directly after a word or term’s first usage unless wide agreement obtains in the nonspecialized biological literature for its use. Parenthetical citations are intentionally limited in number and format, with preliminaries (e.g., “also see,” etc.) omitted for economy as well as visual appeal.

Common but slippery terms are differentiated, in particular, “adaptive” (a trait beneficial to a phenotype) from “adaptation” (an evolutionarily selected trait) and “variation” (realized differences within a population) from “variability” (whether or not character traits vary) after Gotthard and Nylin (1995) and Pigliucci (2008), respectively. Although the majority of extant mammals are eutherians, I have attempted to address monotremes and marsupials adequately. Where theoretical or empirical research on mammals was unavailable for critical issues (Frazier et al. 2006; Meyer et al. 2011; Tills et al. 2011), other taxa are referenced if the results involve extremely conservative traits (Meyer et al. 2011; Eschbach et al. 2011) or, less frequently, if the questions investigated appeared to apply to mammalian mechanisms without conserved features having been demonstrated (Coutinho-Abreu et al. 2011). Further, consistent with life table sums (Stearns 1992, Jones 1997a), female responses and parameters are emphasized throughout this review since male inclusive fitness is ultimately limited by the opposite sex (Emlen and Oring 1977; Trivers 1972, Wittenberger 1980) and by time (Schoener 1971), the only “truly fixed” parameter (Ricklefs and Wikelski 2002).

It is a pleasure to contribute to the SpringerBrief series, a format designed to fill an open niche for compact texts delivering efficient access to accurate information and productive ideas with the potential to promote learning and generate creative exploration. I am indebted to my Springer contacts, Melissa Higgs, Assistant Editor, Life Sciences/Biomedicine, responsible for copyediting my MS, and, especially, Janet Slobodien, Editor, Ecology and Evolutionary Biology, for her unparalleled, ongoing, patience and insight regarding all aspects of the project. I am honored that Stephen C. Stearns agreed to critically read my manuscript, and I benefited immensely from his comments. My assistants, Monica E. McGarrity (graphics), Jason Epperson (technical), and Anne R. Dachowski (bibliography), provided requisite skills and good humor. Tristan Burgess, Colin Chapman, Natalie Dawson, Carrie DeJaco, Ted Fleming, Brittany Grayson, Kayla Griffith, Frank Grutzner, James E. Mazur, Gary Mohr, Rick Murphy, Adam Reitzel, Elliot Tucker-Drob,

Polly Wiessner, and Gabriel Zunino generously responded to various inquiries related to mammalian ecology, evolution, diversity, and behavior.

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# Contents

<b>1 Introduction: What Paths to Inclusive Fitness of Individuals and Mean Fitness of Mammal Populations?</b> .....	1
1.1 Mean Reaction Norms: “Mirroring” Spatiotemporal Variations in Microhabitat from Molecular to Phenotypic Levels of Organization.....	3
<b>2 Mammals: From Humble Vertebrate Beginnings to Global Terrestrial Dominance</b> .....	7
2.1 Robustness Matters: Appearance and Early Evolution of Mammals.....	8
2.2 Order Monotremata: Good Work Ethic, Abundant Food, Lots of Luck .....	15
2.3 Subclass Theria (Infraclasses Metatheria and Eutheria): “Tinkering” with Contents of a Generalized “toolkit”.....	17
2.4 The Mammalian Placenta: The “Intimate Connection” Between Female Reproductive Physiology, Offspring Heat Regulation, and Life-History Strategies .....	20
<b>3 Variability of Mammalian Thermal Niches: Differential Effects of Local and Global environmental Heterogeneity</b> .....	21
3.1 Are There General Laws of Mammalian Thermal Niches and of Thermal Tolerance Evolvability?.....	23
3.2 Is Genetic Heterogeneity an Advantage in Fine-Grained Conditions? .....	27
3.2.1 Howler Monkeys as Assays for Studies of Genotypic and Genomic Responses to Environmental Heterogeneity .....	29