

# Glossary

Selected terms and concepts employed in the present volume for a discussion of behavioral flexibility.

**Adaptation:** Evolutionary response ( $\rightarrow$ fitness) to environmental conditions. Environments may be simple or complex (multifactorial, including interactive), and adaptation may be local or global.

**Age polyethism:** See “temporal polyethism.”

**Behavioral flexibility:** Reversible, within-individual alternative behavioral phenotypes.

**Categorization:** The process of differentiating events in the world into groups using the rule “similar to or different from” (McGarty and Turner, 1992).

**Coefficient of competition:** A measure of ecological overlap (resource utilization) of members of a community (Schoener, 1974).

**Cognition:** Higher-order neural processes, not necessarily conscious and aware.

**Communication:** The provision of information by a sender to a receiver, and the subsequent use of that information by the receiver in deciding how to respond (Bradbury and Vehrencamp, 1998).

**Compromise models of reproductive skew:** These models assume that neither dominant nor subordinate controls reproduction (see Hager, 2003). “Tug-of-war models” assume that both dominant and subordinate allocate a fraction of group productivity to themselves to increase their share of reproduction.

**Condition:** The proportion of total available resources acquired by an individual.

**Condition-dependent:** Relative to or dependent upon individual state, including potential monopolization of limiting resources.

**Cue:** A stimulus whose perception by other organisms is not beneficial to the emitter (Bradbury and Vehrencamp, 1998).

**Decision:** An endogenously or exogenously induced rule leading to a response. A response may be a decision not to respond.

**Division of labor:** The apportionment of reproductive labor within a group or society. In the extreme case, some individuals may forego all or some proportion of their selfish reproduction to assist other members of the group or society to raise offspring, and may demonstrate irreversible morphological and behavioral characteristics. Any set of individuals in a given group or society that exhibits both morphological and behavioral specializations (Wilson, 1971, Chapter 11). The presence or absence of division of labor is often employed as a diagnostic criterion for higher grades of sociality (Chapter 8).

**Environmental grain:** The effective size of a “patch” relative to the size and motility of an organism (Emlen, 1973).

**Environmental heterogeneity:** Spatial and temporal variation in stimulus or stimulus array endogenous or exogenous to the organism and representing selection pressures possibly resulting in the maintenance of genetic polymorphism.

**Epigenetic effects:** Within-individual heritable causal interactions between genes and their products during development. Also discussed as contributions by genes in certain cells to genetic effects in other cells.

**Facultative response:** Response capable of expression under varying environmental conditions. Reversible phenotypic alternative. Facultative responses (e.g., timing of births) are ubiquitous in primates. Nothing is implied about the role of genes in determining the phenotype although the “switch” mechanism is assumed by most authors to be genetically induced (see “polyphenism” below). “Facultative” response is sometimes used interchangeably with “condition-dependent” response.

**Female emancipation:** Condition operating when females are relatively unencumbered by direct monopolization by males in time and space. Female emancipation is thought to result from high unpredictability and/or heterogeneity of limiting resources required by females (Emlen and Oring, 1977) and may facilitate intersexual selection (“female choice”). Probable examples of “female emancipation” in primates occur in *Alouatta palliata* (Jones and Cortés-Ortiz, 1998), *Brachyteles arachnoides* (Strier, 2000), and *Pan paniscus* (Vervaecke *et al.*, 2003).

**Functional magnetic resonance imaging (fMRI):** The recording of firing nerve cells, which metabolize oxygen from surrounding blood. This imaging process produces a scan of neural processes not measurable by observing that component of the phenotype exposed to the environment. Interpretation of fMRI scans is controversial.

**Generalist:** Species or individuals adopting a broad range of solutions (e.g., social parasitism, increased niche breadth) to environmental challenges.

**Generation time (T):** The average age at which a female reproduces.

**Genetic correlation:** Association between alleles and traits.

**Genomic imprinting:** An epigenetic process whereby alleles from both parents are present but only one is expressed due to some mechanism of inactivation (e.g., gametogenic suppression).

**“Green beard” effect:** An “outlaw” gene inducing the phenotype to employ a trait “as a convenient *label* for the presence or absence of itself” (Dawkins, 1999, p. 143, emphasis in original).

**Individuality:** The capacity to express one’s own selfish interests (directly or indirectly) relative to abiotic and biotic, including social, constraints. A component of “individuality” is those traits characteristic of the individual that are relatively stable over time and space (“personality”).

**Intergenomic conflict:** Conflicts among genes between organisms.

**Interlocus contest evolution:** An evolutionary “chase” resulting from genomic conflict.

**Intersexual antagonistic coevolution (“sexual conflict”):** “[T]he evolution of traits that increase the reproductive success of members of one sex at a cost to members of the opposite sex” (Holland and Rice, 1999). Intersexual antagonistic coevolution is a form of intergenomic conflict.

**Intersexual ontogenetic conflict:** A type of conflict “manifest during development when expression of the same allele, on average, moves one sex toward, and the other sex away from, its phenotypic optimum” (Rice and Chippendale, 2001, p. 685).

**Intragenomic conflict:** Conflicts among genes within organisms.

**Intraspecific social parasitism:** The coexistence of conspecifics in which one or more exploits the time and energy of others for fitness benefits to the parasite(s) at a fitness cost to the host(s).

**Learning:** A relatively permanent change in behavior resulting from experience.

**Lifetime reproductive success:** Number of offspring an individual produces over a lifetime.

**Maternal effects:** A component to environmental variation representing covariances between the maternal environment (from cytoplasm to maternal care) and a mother’s condition.

**Motivation:** Mechanisms that initiate, maintain, and direct response(s).

**Negative phenogroup assortment:** Disfavoring members of one's phenogroup.

**Negative reinforcement:** Removal of an aversive stimulus leading to an increased likelihood of the operative behavior's expression.

**Norm of reaction:** The function of the correspondence between different environments and their resulting phenotypes.

**Obnoxious phenotype:** A phenotype having a disruptive and/or damaging effect on one or more conspecifics' phenotypes by employing offensive or objectionable behavior to obtain selfish benefits.

**Operational sex ratio (OSR):** The ratio of reproductively active males to fertilizable females.

**Persistence:** Maintaining one or more states or conditions over time as a tactic to obtain mating or other opportunities potentially benefiting fitness.

**Persuasion:** Employing one or more behavioral tactics to influence a conspecific's behavior in a manner beneficial to one's own interests.

**Phenogroup:** A set of individuals exhibiting similar traits for resource exploitation.

**Phenotype matching:** Employment of one or more of an individual's traits to direct responses to other conspecifics sharing those phenotypic characteristics.

**Phenotypic flexibility:** The reversible within-individual component of phenotypic plasticity. The focus of these studies in primatology often involves studies of behavior (e.g., behavioral flexibility) or physiology (e.g., acclimation or acclimatization).

**Phenotypic plasticity:** Phenotypic variation expressed by reproductive individuals throughout their lifetime. Following models of population genetics (after Piersma and Drent, 2003, p. 231), phenotypic plasticity is understood to include the total phenotypic variance of a population divisible into a genotypic (G) component, an environmental (E) component, and interaction between these ( $G \times E$ ). Also included in total phenotypic variance is an error term,  $\epsilon$ . G is divisible into three effects (additive, dominance, and epistatic), and measures of phenotypic plasticity can vary over time within individuals. Within-individual variation = G + reversible and irreversible fractions of phenotypic variance. As applied to quantitative (continuously distributed) characters, research (especially in behavioral genetics) has often focused upon estimates of heritability (the heritable fraction of total phenotypic plasticity). Recent treatments have advised subdividing E into two measures: a reversible fraction

(flexibility) and an irreversible fraction (ontogenetic or developmental stage) of total phenotypic variance. While most authors argue or imply that the phenotype is a function of developmental stage (see Piersma and Drent, 2003, p. 231), West-Eberhard (2003) discusses the phenotype as a “bridge” between the environment and the genotype.

**Pleiotropy:** Multiple effects of a gene.

**Polymorphism:** Genotypically regulated alternative responses implying a locus with two or more alleles. For example, cooperatively breeding marmosets and tamarins may be polymorphic for helping behavior, possibly in response to population density (interaction rates) and/or the availability of breeding sites.

**Polyphenism:** Environmentally switched alternatives. Most discussions assume that the “switch” is “hard-wired.”

**Polyspecialist:** Species or individuals exhibiting a limited number of distinctive alternative characteristics in behavior, morphology, physiology, cognition, etc.

**Positive phenogroup assortment:** Favoring members of one’s phenogroup.

**Quantitative character:** Genes contributing to continuous (quantitative) variation in a phenotype for which the average phenotypic difference between genotypes are small compared with the variation between individuals within genotypes.

**Queuing:** Waiting for things, events, states, or conditions.

**Reproductive skew:** The apportionment of reproduction among same-sex members of a group. At one extreme, one individual monopolizes all breeding (e.g., some marmosets and tamarins), at the other extreme, reproductive output is distributed more or less equally among all individuals of a sex (female *Brachyteles*). All other things being equal, reproductive skew will be higher in males than in females (Trivers, 1972).

**Reproductive value ( $v_x$ ):** The relative number of offspring that will be produced by each female surviving to age “x.”

**Resource dispersion:** Distribution and abundance of limiting resources in time and space. It is often necessary, in addition, to discuss *resource quality*.

**Resource holding potential (RHP):** Ability of an individual to monopolize a limiting resource (e.g., food, mates).

**Resource quality:** The characteristics of a resource, usually a limiting resource, beneficial to the consumer.

**Response accuracy:** Percent adaptive or beneficial responses.

**Signal:** The vehicle providing the information in communication (Bradbury and Vehrencamp, 1998).

**Signature:** As employed in this book, a trait, schema, or behavioral program characteristic of primates and presumed to be expressed for the optimization of fitness in response to environmental heterogeneity.

**Social cognition:** The ways in which organisms understand conspecifics as “intentional and mental agents” (Call and Tomasello, 2003; Bering and Povinelli, 2003; Essock-Vitale and Seyfarth, 1987).

**Social learning:** Learning by observation, particularly observation or imitation of conspecifics.

**Specialist:** Species or individuals exhibiting a narrow range of traits especially suited to a particular regime (e.g., food supply or social conditions).

**Temporal polyethism:** The regular changing of labor roles by members of a group or society as they age.

**Theory of mind:** A state in which one individual is capable of assuming the perspective of a conspecific and assesses the other’s differential (condition-dependent) costs and benefits.

**Totipotent:** The ability of an individual to perform most or all of a society’s roles.

**Transactional models of reproductive skew:** The primary assumption of these models of reproductive skew is that a dominant individual controls group membership and benefits from the presence of subordinates (see Hager, 2003). Transactional models are classified as either “concession models” or “restraint models”. In the former, treatments analyze relations between subordinates and dominants in a variety of conditions (e.g., when subordinates are evicted). In the latter, subordinates are assumed to be limited only by the dominant’s ability to evict the subordinate from the group.

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