individuals should punish other individuals[9]. An extension could assess and incorporate the optimal degree of punishment to inflict given the costs and benefits of punishment. A further extension might address how the benefits and costs of space use and contests should affect the optimal degree of alteration in site attractiveness following a visit to a site (with or without an aggressive interaction). A marriage of game theory and Stamps and Krishnan's process-based proximate modeling approach should move us towards to a deeper, more integrative understanding of animal space use and territoriality.

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Meeting Report

The physiology of life histories

Martin Wikelski and Robert E. Ricklefs

The Physiological Basis of Life-History Traits and Tradeoffs Symposium of the Comparative section of the American Physiological Society, was held at the Experimental Biology Conference, Orlando, FL, USA, from 31 March to 4 April 2001.

Life-history studies traditionally address behavior and demography, focussing on measures such as foraging success, reproductive success and survival, which all express the outcome of the interaction between the organism and its environment. Physiological aspects of organism function, including metabolism, immunocompetence and endocrine controls, are seen primarily as supporting, rather than controlling, life-history responses to the environment. A recent symposium at the FASEB meeting, organized by Tony Williams (Simon Fraser University, Vancouver, Canada) and Barry Sinervo (University of California, Santa Cruz, CA, USA) has emphasized that physiology also can have a constraining role in life-history tradeoffs.

A recurring theme of the symposium was that organisms can trade off different physiological functions, such as immune and endocrine responses to environmental challenges. Such physiological functions are often reflected in energy expenditure, which can thus serve as a common currency to gauge the outcome of life-history tradeoffs. It is also evident that constraints might occur because of competing demands for body tissues (e.g. flight versus refueling during long-distance migration) or for control mechanisms (e.g. parental investment versus intraspecific aggression), as well as for time, energy and nutrients.

The participants agreed that experimental manipulation is a powerful tool for understanding the pathways of how physiological constraints occur. Long-term selection and hormone manipulations are particularly good candidates for studying variation in life-history traits[1]. Phenotypic engineering of life-history strategies[2] allows researchers to isolate experimentally individual phenotypic correlations between life-history traits and to study their physiological and fitness consequences. Williams reported that tamoxifen, an antiestrogen, decreases egg size in zebra finches *Taeniopygia guttata*, whilst simultaneously affecting other life-history characteristics, for example, increasing clutch size. Hormonal manipulation might also break the pervasive correlation between egg size and the nutritional state of a female[3]. Such manipulations might help us to understand why egg size and clutch size are genetically correlated in lizards, but not in birds (Sinervo and Williams).

Neil Metcalfe (University of Glasgow, UK) showed that energy allocation underlies the extreme variation in age at maturity of anadromous salmon *Salmo salar*, which can occur between nine months and nine years of age. Standard metabolic rate, which measures the rate of transformation of energy, determines early growth rate, which is correlated with the age at which individuals migrate to sea (and later mature). Interestingly, growth rate is related to metabolic rate relative to other individuals in the same social group rather than to absolute metabolic rate. Thus, energy metabolism and growth rate appear to be affected by social relationships, including aggression and dominance, which in turn influence physiological and life-history traits[4]. An interesting twist on the theme of energy allocation during growth is that individuals that invest in accelerated growth to recover from unfavorable circumstances often pay a cost in terms of reduced fecundity or reduced survival later in life[5].

Energy allocations also appear to underlie seasonal differences in immune function, reported Randy Nelson (Ohio State University, Columbus, OH, USA). Winter conditions might be challenging immunologically, and many animals, including humans, boost their immune system in anticipation of particularly

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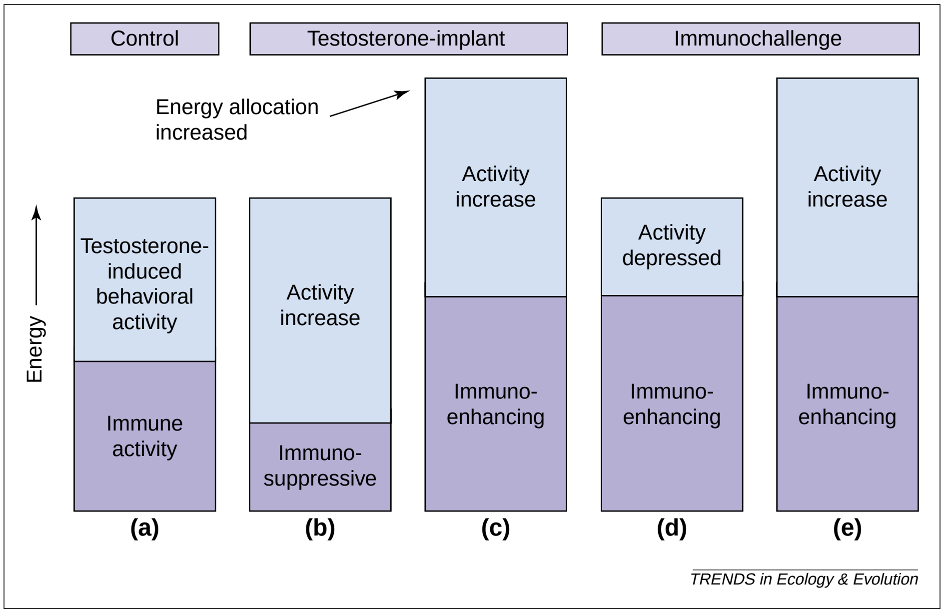

Fig. 1. Tradeoffs between testosterone (T)-induced functions (activity) and immune responses of organisms during experimental challenges (e.g. T implantation[16] or immunochallenges with inactivated viruses). The energy allocated to each of these physiological systems provides a common currency: (a) the total amount of energy allocated to immune function and T-induced activity could be quantified in control (unchallenged) situations. Energy allocation differences might explain seemingly contradictory results: (b) T implantation could increase activity and decrease immune response if total energy allocated to these functions remains the same. (c) The same T-implantation might boost both activity and immune system if energy allocation increases. Similar arguments can be made for immune challenges, which can either enhance immune response and decrease activity (d), or enhance both activity and immune response (e). Thus, a comprehensive understanding of physiological tradeoffs underlying life-history traits can be gained by challenging one system and measuring the response of several others, including that of energy metabolism.

stressful conditions during the short winter days. Melatonin, a hormone secreted during the night, apparently increases immune function in some species in autumn whilst decreasing locomotor activity (and often curtailing somatic growth). Such short-day lethargy helps to compensate metabolically for an increased allocation of resources into a costly immune defense[6]. At the same time, melatonin might have direct interactions with the immune system[7]. Understanding physiological tradeoffs in the immune response[8], whether they are based on resource allocation[9] or on control mechanisms, might help to solve a long-standing mystery: why do mammals periodically arouse during hibernation? Challenging the immune system of hibernating individuals stimulates no fever response. However, fever is elicited during arousals. Thus, arousal might have an important function in immune defense during winter hibernation.

Variation in the allocation of resources between reproduction and survival has a genetic basis, as shown by Michael Rose (University of California, Irvine, CA, USA) in fruit flies *Drosophila* spp. Laboratory selection can increase average longevity[10] twofold within ~70 generations and generally produces a correlated response in the form of increased starvation resistance[11]. However, longevity also increases with selection on starvation resistance[12]. Surprisingly, the connection between longevity and starvation resistance was the result of the total energy content of flies rather than the metabolic rate: fatter flies resisted starvation better (no surprise) but also lived longer than did thinner flies. Longevity of flies in the laboratory is a demographic trait with a clear physiological basis, illustrating the key connection between physiology and life history[13].

Outside of the laboratory, the physiological bases for many life-history traits remain elusive. In a classic example of life-history variation, tropical passerine birds worldwide lay two–three eggs per clutch, whereas their temperate counterparts lay between five and 12 eggs per clutch. Most explanations for this latitudinal gradient are based on ecological factors, such as food availability and nest predation, or varying parental investment that are associated with gradients in adult survival. However, these variations in life-history traits are also associated with variation in hormone profiles related to the relatively aseasonal tropical environment[14] and perhaps also to differences in immune system function related to greater pathogen burden in the tropics. Higher adult survival in the tropics might also select for higher investment in self-maintenance (including stronger stress responses and prolonging potential life span) at the expense of parental investment in offspring. Tradeoffs between physiological systems could then channel these selection pressures into a common response: an energetically slow pace of life. Tropical birds do have low androgen hormone levels[15], which could result in low activity rates and low metabolic rates compared with temperate-zone birds. Immune system parameters have not been compared between different latitudes, but high demands on the immune systems of tropical birds might constrain other functions. It is currently unclear how the presumed high demands on the immune system of tropical birds might compare with the demands on the immune system of temperate animals during the winter months (as discussed earlier).

The future

Building upon insights generated by this symposium, researchers might begin to understand life histories as the outcome of interactions and tradeoffs among three physiological systems (energy metabolism, endocrine control mechanisms and the immune system) in response to different environmental challenges (Fig. 1). Understanding tradeoffs in this way could also reconcile different outcomes of manipulations on life-history patterns. With respect to the influence of hormones on the immune system, for example, testosterone-treated individuals might energetically overcompensate[16] in response to immune challenges under good conditions but suffer immune system suppression under poor conditions[17]. Thus, understanding energetic or other constraints on immune function would explain how testosterone could exhibit both an enhancing and a suppressing effect on the immune system.

Studying the physiological bases of life histories might have implications reaching far beyond working out the details of tradeoffs: physiological systems also provide a link between the environment and the genome. Testosterone, for example, is induced by social interactions[18], but in turn regulates gene transcription. To the extent that genetic variation in life histories – the strategic decisions of organisms during their lifetime – reflect gene-by-environment interactions, further knowledge about the translation of genetic information into physiology and subsequent life history is urgently needed.

Acknowledgements
We thank Michaela Hau, L.B. Marty Martin, Alex Scheuerlein, Tony Williams, Michael Rose, Neil Metcalfe and Randy Nelson for constructive comments on this article.

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The challenges of studying dispersal

Ran Nathan

The 2001 Annual Symposium of the British Ecological Society on Dispersal was held at the University of Reading, UK, from 3–5 April 2001.

Dispersal – the movement of organisms away from their parent source – is a fundamental biological process that operates at multiple temporal and spatial scales. The process therefore has overwhelmingly important implications at multiple scales of organization: for the survival, growth and reproduction of individuals; for the composition, structure and dynamics of populations and communities; and for the persistence, evolution and geographical distribution of species[1]. Although the importance of dispersal was emphasized by Charles Darwin, Alfred Russel Wallace, Philip Darlington, Robert MacArthur, among others, dispersal has been condemned as immeasurable and unimportant (see Ref. 2 for review).

However, those days are over, now that the study of dispersal has evolved to be a major theme in biology, unifying and incorporating fields of research as diverse as ecology, evolutionary biology, microbiology, molecular biology, mathematics, physics, epidemiology, agricultural and atmospheric sciences, engineering and geography. The current bloom in dispersal research was illustrated by this recent British Ecological Society Dispersal symposium, which included discussions of multiple facets of dispersal for a wide range of organisms in diverse ecosystems across multiple spatial scales.

Describing dispersal patterns

The most fundamental task in studying the process of dispersal is describing the patterns that it generates. The immense difficulty of measuring dispersal, especially long-distance dispersal (LDD), was mentioned by nearly all speakers. Fortunately, many of them also suggested and exemplified potential solutions, reflecting major technological advances that enable one to measure dispersal systems that were previously impossible to measure. Three major methodological groups were emphasized: (1) movement–redistribution methods and direct tracking of individuals in particular; (2) genetic analyses; and (3) mathematical models.

Using movement–redistribution methods

The direct measurement of movements of an individual depends on appropriate methods being used relative to the body size of the organism being studied, especially for species dispersing over large distances. Tracking larger organisms is easier and can be more comprehensive than tracking small organisms (tracking is simply impracticable for the smallest organisms), but technology is advancing rapidly.

  PII: S0169-5347(01)02272-8