

Environmental Toxicology

RESOURCE ALLOCATION-BASED LIFE HISTORIES: A CONCEPTUAL BASIS FOR STUDIES OF ECOLOGICAL TOXICOLOGY

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Abstract—Whereas ecological assessments of contaminants are concerned with populations and higher levels of organization, most mechanistic work in toxicology is directed at effects on individuals and their parts. We propose that studies based on individuals can be useful in ecological analysis of polluted systems when based on the concepts of resource allocation-based life history analysis. At the heart of the resource allocation approach is the concept of operative environments of individuals (i.e., environmental factors influencing birth, death, or migration). Contaminants can have strong influences on operative environments, modifying resource allocation strategies that reflect changes in energy assimilation and demands. By examining contaminant-induced responses of individuals from the perspective of changing operative environments, individual-based changes and population dynamics can be addressed in an ecologically rigorous manner.

Keywords—Resource allocation Life history Energy budget Metabolism

INTRODUCTION

The utility of ecotoxicological studies is tied to the goal of being able to predict population responses to contaminant exposure. However, much toxicological research has focused on the individual as the unit of observation, with the tacit assumption that a biomarker endpoint is indicative of the individual's health (the assessment endpoint). The search for bioindicators that can be quickly and inexpensively measured, combined with recent technological advances in the ability to detect toxicant effects at the cellular and molecular level, has focused research efforts at those levels of organization. As a result, a disparity exists between common toxicological approaches and the need to determine ecotoxicological effects at the individual and population levels. At present, endpoints for ecological risk assessments are still being developed and their usefulness debated, primarily because of conceptual, logistical, and empirical difficulties posed by the need to integrate molecular and cellular effects to a higher level of complexity, such as individuals, populations, and communities [1–5]. Clearly, conceptual and theoretical frameworks, rather than just technological ability, should be primary drivers for research questions and approaches. Such frameworks influence definitions of problems, determine research protocols, and drive development of new technologies needed for ecotoxicological studies at higher levels of biological organization; all three are required for subsequent enhancement of risk assessment results.

The field of ecological toxicology, by definition, requires understanding of population-level effects. We believe the gap between individual effects and population-level phenomena

can be best bridged using the concept of resource allocation-based life histories [6–8]. The fundamental difference between approaches that concentrate on population dynamics and the resource allocation-based life history approach is that the latter focuses on how variation in resource allocation among individuals causes population changes. Resource-based life histories are the heritable set of rules that specify allocations of available time and assimilated resources to competing energy budget compartments (i.e., functions) of maintenance, growth, storage, and reproduction [sensu 6] and the apportionment of total resources allocated to reproduction (reproductive investment) among individual offspring (parental investment [7–14]). Because the resource-based life history approach focuses on individuals (the units of natural selection) rather than on mean cohort demographic traits (classical life history traits), it provides a conceptual and mechanistic framework necessary for determining population responses to contaminants and for the study of life history evolution as well.

The goal of this article is to combine ideas developed from studies of life histories, ecological energy budgets, and resource-based life histories to begin development of a conceptual foundation for ecotoxicological research. To accomplish that goal, we will review classical life history concepts, develop the concept of resource allocation-based life history traits as the nexus between individual traits and population dynamics, discuss how the concepts relate to ecotoxicological research, and identify areas of technology development that will improve our ability to study resource allocation and toxicology of organisms.

CLASSICAL LIFE HISTORY CONCEPTS AND THEORY

Natural historians have been interested in all aspects of organismal biology, including variation in the body size, morphology, physiology, life history, and ecology of organisms.

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Table 1. Examples of classical and resource-based life history traits

Classical life history traits	Resource-based life history traits
Age-specific survivorship	Egg and propagule size
Age-specific fecundity	Growth rates
Age at maturity	Size at maturity
Lifespan	Age at maturity

The theory of evolution by natural selection followed by the modern synthesis of evolutionary biology provided conceptual and theoretical frameworks for organismal biology that had been lacking in early natural history studies. Investigators such as Lack, Cole, and Williams [15–20] focused attention on suites of traits that are closely related to Darwinian fitness (number and size of offspring, age- and size-specific reproduction and survival, life span, and age and size at maturity), which became known as life history traits (Table 1). Life historians subsequently focused on patterns of covariation among life history traits within and among related groups of organisms. It was the recognition that suites of life history traits coevolved, that constraints on the types of life history traits could co-occur (i.e., some life history trait values are not possible in a given situation), and that tradeoffs occurred among existing traits within a population (i.e., more offspring often results in smaller offspring) that led to formulations of life history theory and concepts [18–20]. Two major categories of evolutionary life history theories were developed. These are R- versus K-selection theory, which identified per capita resource availability [21–23], and demographic theory, which identified the demographic environment [19,20,24–27] as the major selective factors in life history evolution. The suite of life history traits (Table 1, column a) will hereafter be referred to as classical life history traits [see 26–29 for review of life history concepts].

Although studies of life histories have contributed greatly to our understanding of population structure and dynamics, we have to ask the question “Why hasn’t classical life history theory provided a functional bridge between variation in individual traits (that arise naturally or in response to contamination) and population dynamics?” We argue that, in combination, the following problems prevent the classical life history approach from providing mechanistic linkages between individuals and populations. Classical life history traits are primarily emergent characteristics of populations (e.g., age-specific survivorship or fecundity of a cohort or population). Cohort traits are assumed to represent individual traits, an assumption that has resulted in flawed predictions (e.g., reproductive effort, the proportion of the total resource budget allocated to reproduction, should increase with age), and mechanisms that connect variation in individual traits (the level acted upon by natural selection) to population-level phenomena are often not explicitly stated. Classical life history theories are often stated in a mix of both resource (individual) and demographic (cohort or population) terms, and in some theories, the demographic environment seems to become both the source and target of selection. If life histories are the bridge between individual and population levels of organization, we need to develop a new paradigm that focuses on causes of variation among individuals.

RESOURCE ALLOCATION-BASED LIFE HISTORIES

Selection for a suite of allocation-based life history traits, just as for any other kind of trait, occurs in a specific envi-

Table 2. Categories of operative environments

Operative environments	Examples
Resource	Time, food, space
Biophysical	Substrate, temperature, light
Social/demographic	Dominance, territory, mating structure
Exploitative	Predation, disease, etc.
Contaminants	Organics, inorganics, heat

ronment. If variation in any category of environment alters birth, mortality, or migration rates of a population, then that category constitutes an operative environment (Table 2) and it must be included in any attempt to understand the dynamic behavior of the population. Since contaminants have been shown to directly alter many traits of organisms, they should also be viewed as a category of operative environment.

A life history is the set of interactions whereby variation in operative environments (Tables 1 and 2) is transduced into age- or size-specific birth rates and probabilities of mortality and migration (Fig. 1). As such, a life history may be viewed as a heritable set of rules that specifies three fundamental sets of allocation decisions made by individuals. These are allocation of available time to activities such as mate and resource acquisition, which may be a prime determinant of social status and net resources available for future allocation; allocation of assimilated resources (water, energy, amino acids, nutrients, etc.) into the competing functions of growth, maintenance, activity, storage, and reproduction [6]; packaging of reproductive allocation into individual offspring, which determines, in part, offspring size, the number of offspring, the frequency with which offspring are produced, and the provisioning of individual offspring (Figs. 1 and 3 of Dunham [8]).

All allocation categories are specified given the physiological state of the organism, the trade-offs and constraints imposed by its physiology (including stoichiometries of scale and the requirement that heat and mass budgets be balanced), and the constraints imposed by the biophysical, demographic, social, predation environments, and resource limitation. The range of phenotypic outcomes from allocation of resources within a population results in a set of life history traits (e.g., age-specific fecundity, growth rate, body size, allocation to and use of stored energy, offspring size, age at maturity, and age at death [that time when all allocation processes made by the individual cease]). When the life history traits are integrated over a set of individuals comprising a population and over a biologically meaningful time period, the demographic characteristics of that population result. As with any complex system, one major goal of ecotoxicology or life history studies is to determine which system-specific operative environments have the most influence on population dynamics. Success in identifying important operative environments will be greatly enhanced by detailed knowledge of the basic ecology of the organisms in uncontaminated environments.

RESOURCE ALLOCATION PHENOTYPES

Assimilated energy is allocated to major energy budget categories (maintenance and production) that are differentiated based on whether or not they directly result in tissue formation. Allocations to maintenance include standard maintenance (the cost of being), activity maintenance (the cost of doing, see [30]), and specific dynamic effect or action (the cost of assimilating energy). In a time-ordered sequence, energy demands

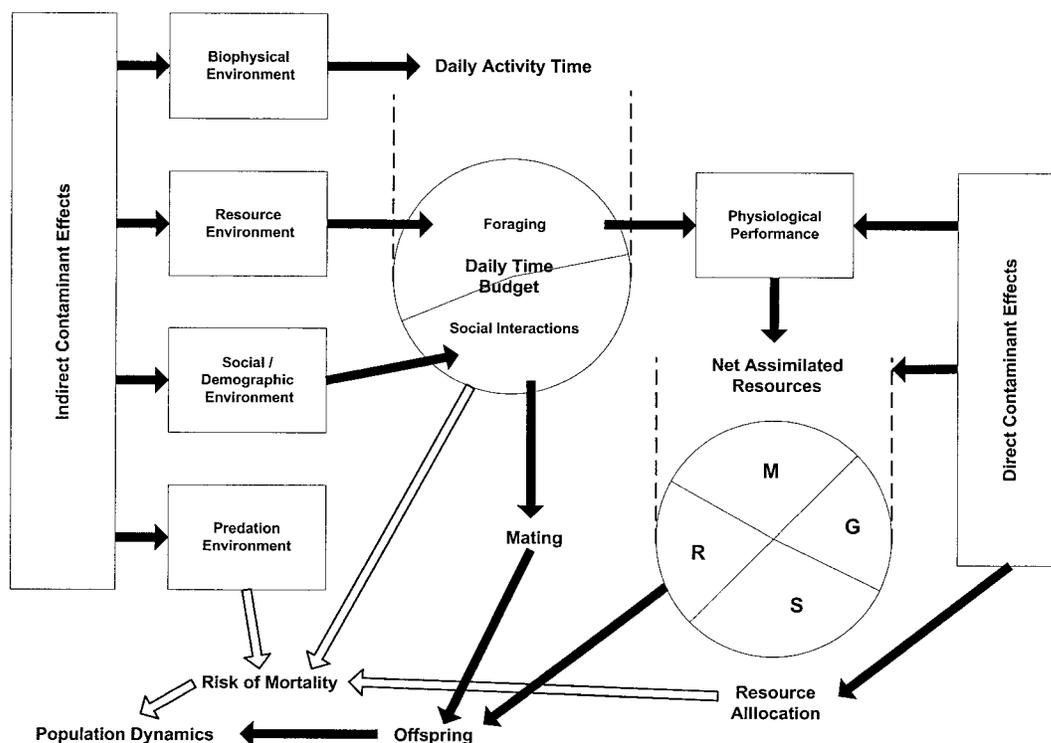


Fig. 1. Summary of the factors affecting the daily activity and resource budgets of individual organisms. Illustrated are the operative environmental types that potentially influence the time available for allocation to the competing functions of social interaction (mate and territory acquisition and defense, etc.) and foraging. The allocation of available time results in the daily time-activity budget, and each different allocation potentially incurs a different risk of mortality. Foraging success and assimilation rates determine the amount of net assimilated resource (energy, water, nutrients, etc.) available for allocation to the competing functions of growth (G), storage (S), maintenance and activity metabolism (M), and reproduction (R). This allocation determines the mass-energy budget, and each different allocation potentially incurs a different risk of mortality as well as determining the age-specific growth and reproductive rates. Indirect contaminant effects are those that alter operative environments. Direct contaminant effects are those that alter the physiological performance of individual organisms and thereby affect resource allocation phenotypes. Both types of contaminant effects have the potential to alter the reproductive rates and/or the mortality rates of populations and may consequently determine population densities and survival.

necessary to sustain and continue life (standard maintenance and specific dynamic action) must be met before allocations to the remaining energy compartments are made (i.e., activity maintenance, growth, storage, and reproduction). In contrast with the directional and relatively permanent nature of allocations to other categories of the production budget, the primary function of the storage compartment is temporary housing and subsequent retrieval of energy reserves. The use of lipids for fueling maintenance costs of overwintering, aestivation, and reproductive activities and for direct allocation to reproduction (e.g., eggs, milk production) combine to make the storage compartment critical for understanding bioenergetics of animals. Because the maintenance category of an energy budget represents 80% or more of an organism's total energy budget [6], small increases in allocation to maintenance (e.g., those caused by contaminants) can result in proportionally larger reductions to production (growth, storage, and reproduction) that can result in variation in life history phenotypes such as offspring size or number, growth rates, size and age at maturity, and reproductive output.

INDIRECT VERSUS DIRECT ALTERATION OF LIFE HISTORY PHENOTYPES

Contaminants alter life history phenotypes indirectly by altering operative environments (e.g., resource availability, cover, thermal characteristics, availability of mates, risk of predation). For example, contaminants such as heat and her-

bicides can reduce plant cover and food availability while altering levels of risk associated with exposure to predators or changes in predator densities. Alternatively, pesticides such as insect growth regulators can reduce fish populations indirectly by reducing their crustacean prey populations (Table 3).

Contaminants also alter life history phenotypes directly by altering the development or physiology of the organism itself (in this case, contaminants, by definition, become a category

Table 3. Indirect effects of contaminants caused by alteration of potential operative environments

Categories	Alteration
Physical	Temperature Light Cover pH Dissolved O ₂
Resource	Prey species diversity Prey abundance Prey habitat Prey quality
Risk	Exposure to predators Number of predators
Competitive	Number of competitors Type of competitors
Social	Number of agonistic encounters Number of potential mates

of operative environment; Fig. 1, Tables 2 and 3). Contaminant uptake by individuals has been shown to alter activity levels, or performance physiology [31–33], ability or desire to harvest resources [34–37], energy assimilation [38], and standard metabolic rates [35,39–44]. All of the above responses, alone or in combination, can substantially reduce the portion of total assimilated energy that is available for allocation to production.

Clearly, environmental stressors can cause substantial among-individual variation in resources available for storage, growth, or reproduction. Identification of bioenergetic mechanisms that have substantial impact on the total amount of assimilated energy and are sensitive to contaminants is one important goal of ecotoxicology [45,46]. We suggest that specific dynamic effect, the energy required to assimilate food resources, may be one such mechanism that should be examined. Ectotherm organisms expend up to 37% of the energy in an ingested meal during digestion [47]. Contaminants may affect the amount of energy available by increasing the specific dynamic effect cost or by reducing the amount of energy that is assimilated.

A DEMOGRAPHIC EXAMPLE

How important is variation in allocation to the production compartments of an energy budget in demographic terms? We present one example from a long-term study of painted turtle (*Chrysemys picta*) life history in southeastern Michigan [48]. Primiparous (first lifetime reproduction) females ranged from 6 to 13 years of age and from 114 to 138 mm in carapace length. Growth rates of small- and large-bodied adults are similar at less than 1 mm per year; as a result, relative body size within the population is fixed at maturation and remains throughout life. Both clutch size and egg size increase with body size among females [11,49]. Since the growth rates of adults of different sizes are similar, average clutches of the female maturing at 114 mm carapace length would remain two eggs smaller than the female maturing at 138 mm carapace length. For this example, we allow both females to live to 30 years of age (the oldest known-age females in the population are over 50 years of age) and assume an average of one clutch per year (clutch frequency in this population averages approximately 1.2 clutches per year). As a result, the small female will produce 60 fewer eggs over her lifetime, a number that approximates eight average clutches for the population. The difference in energy allocation to each clutch is 58 kJ or, over 30 years, 1,740 kJ. Because painted turtles postpone maturity for more than six years, contaminants that reduce growth rates are capable of causing such differences in body size and reproductive output of females. The differences between females in the above example are conservative in that the frequency of second clutches is higher for large-bodied females than for small-bodied females (J. Congdon, unpublished data).

A PLEA FOR THE DEVELOPMENT OF TOOLS

Field studies of resource allocation require that individuals be identified and followed through time and be reliably recaptured at reasonable intervals to monitor survival, growth, reproduction, and other physiological state variables. Field studies of bioenergetics are severely hampered by the need for two major categories of tools.

Tracking devices for small animals

Although powerful transmitters are readily available for large animals, smaller and longer-lived transmitters (or some

other technology) are necessary to locate and capture small-bodied individuals. Even in species where adults are large enough to carry transmitters, neonates are often too small to carry them. Ideally, transmitters would also record data on physiological state variables (e.g., body temperature, heart rate, or other indicators of behavior or activity levels). Harmonic radar systems using a passive tag that can be attached to individuals as small as beetles are a promising development [50]. At present, the portable transmitter-receivers are expensive and the detection range of the system limits application to organisms that do not move rapidly or over long distances.

Nondestructive whole body lipid assay

A relatively simple and nondestructive way to determine whole body nonpolar lipid reserves would allow investigators to monitor lipid dynamics of individuals. Historically, whole body nonpolar lipids have been extracted from systematic destructive samples of individuals captured over different periods of a year or activity season. Major problems with the technique are that analyses are destructive and thus individuals cannot be followed through time; temporal variation in lipid stores due to past resource histories are not known, although large samples can improve statistical power; the amount of time and labor involved in sample processing also increases; and large samples may not be available in contaminated areas or destructive samples may not be legal for protected species or from protected areas.

At present, two methods are currently available for determining whole body lipids nondestructively; however, each has serious limitations. Total body electrical conductivity (TOBEC) estimates total lean body (lean soma + water) mass [51,52], and lipids are calculated by subtracting estimated lean body mass from total body mass. The technique is quick and is limited only by the size of the organism that can fit inside of the induction coils (however, many animals are smaller than the smallest induction coils). The major problems with the TOBEC method are that the technique relies on calibration curves comprised from TOBEC readings and lipid levels determined by extraction derived from the same individuals, the technique is sensitive to variation in body water content, and since the lean compartment of an organism usually represents the majority of an organism's total body wet mass (80–90%), errors estimating lean mass are compounded in the estimate of lipid mass [53–56].

The cyclopropane absorption method of measuring whole body lipids also can determine whole body lipids. Cyclopropane gas is about 24 times more soluble in fat than in lean tissues. Therefore, for two animals of the same body mass, more cyclopropane would dissolve into an individual with more fat reserves than in a thin animal [57,58]. Problems with the technique include that the chambers must be made to fit the animal being measured, the technique is labor intensive and requires about 2 to 3 h per measurement, a single measurement requires controlling or recording gas volumes and pressures and temperatures within the chambers, and the possible short- or long-term effects on the study animals are not known [58].

Although present lipid extraction techniques do not provide the level of precision and accuracy required for following single organisms through time, new technological developments may lead to ways that improve either existing lipid extraction methods or to totally new approaches. In our opinion, for resource-based studies of toxicology, bioenergetics, and life

histories, it is almost impossible to overstate the importance of a nondestructive way to monitor the temporal dynamics of whole body lipids of individuals. We hope that by pointing out how critical the problem is we will help stimulate interest in developing new technologies that will create a solution.

CONCLUSIONS

Because most early life history theories are demographically based, the goals of bioenergetic and life history studies have remained conceptually independent. Recent convergence of goals is based on recognition that variation in many life history trait values are determined by differences in resource allocation among energy (resource) budget compartments. As a result, resource-based variation in life history trait values now provides a conceptual basis for studying resource allocation. Stresses caused by contamination provide an unfortunate, but excellent, opportunity to study allocation-based life history variation and sublethal effects of contamination. Sublethal contaminant exposures can cause relatively rapid changes in resource allocation patterns of individuals compared with natural processes. In addition, the way changes are caused may be contaminant specific and thus provide an opportunity to study mechanism-specific responses of individuals and populations. For example, smaller size at maturity caused by exposure to anthropogenic stressors can be the result of reduced allocation to growth by juveniles, decreased age at maturity, or both. Results from resource-based life history studies at contaminated sites have the potential to provide valuable insights into the dynamics of contaminant-based sublethal effects and life history evolution.

Development of small and reliable devices to track individuals and monitor physiological state variables, combined with development of a quick and user friendly nondestructive or noninvasive method for making repeated measures of whole body lipids of individuals over time, will revolutionize the field of bioenergetics and resource-based life history studies of contaminant effects.

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