Chapter 12

Resource Acquisition and Allocation among Animals

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12.1 INTRODUCTORY CONSIDERATIONS

12.1.1 RESOURCE BUDGETS

Previous chapters have considered various aspects of the energetics of foraging as well as the budgeting of time, matter, and/or energy in digestive processes, predator avoidance, tissue maintenance and repair, storage, growth, and (last, but far from least) reproduction. These activities cannot be dealt with adequately in isolation since they usually make conflicting demands on an animal's finite resources and hence require trade-offs and compromises. Time spent foraging to gather materials and energy results in greater exposure to predators and thus requires increased expenditure of energy on predator escape behaviour. Similarly, energy and matter devoted to tissue repairs or growth are rendered unavailable for reproduction. Ultimately, of course, successful offspring are the only currency of natural selection so that any expenditures on non-reproductive (somatic) tissues and/or activities will enhance the animal's fitness only to the extent that they can in fact be translated into progeny at some future time. For example, investing in growth should be viewed in the context of how the resulting increase in size influences fecundity, perhaps indirectly by altering competitive ability and/or survivorship as well as directly by increasing the volume of the body cavity in which eggs and progeny develop. Constraints and interactions among the vital activities listed above are numerous and can sometimes be exceedingly subtle.

12.1.2 UNITS OF MEASUREMENT

Ideally, analyses of resource budgets would be couched in terms of relative lifetime reproductive success; however, fitness has proven to be exceedingly difficult or even impossible to measure (even if one were able to count progeny

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produced, each must be weighted by its own fitness!). Not all offspring are equivalent—those born late in the season may usually have more remote prospects of reaching adulthood than those produced earlier, even if they have similar genotypes. Comparable considerations apply to progeny of different sizes (for literature on this subject, see Brockelman, 1975; Pianka, 1976; Smith & Fretwell, 1974).

As pointed out in Chapter 1, energy is often used as a 'lowest common denominator' as a currency for such studies, almost by default. In vertebrates as disparate as red squirrels (Smith, 1968), cotton rats (Randolph (McClure) *et al.*, 1977), and stickleback fish (Wootton, 1977), females have been shown to be energy stressed during reproduction. Recognizing the failings and limitations of such an energetic approach, I nevertheless ultimately finish up overemphasizing energy myself. Only a few highlights in the extensive literature on animal bioenergetics can be considered here.

I shall proceed by outlining a series of specific studies, each of which illustrates a given trade-off that may not be particularly evident or discernable in the others. Since all animals face many of the same or at least very similar dilemmas, this disparate collection of seemingly unrelated cases may help in attaining an overview by providing some building blocks for the construction of a more general and complete unified framework. As you read through these various synopses, bear in mind that the individual animal must function smoothly as an integrated entity so that the entire phenotype is the true unit of natural selection.

12.2   CASE HISTORIES

Far from being static, energy budgets change both with immediate environmental conditions and with age. Indeed, altering the energy budget may often be the most effective way of coping with a dynamic environment, including unpredictable ones. During a mild winter on the British sea-coast, foraging rock pipits (*Anthus spinoletta*) spent about $6\frac{1}{2}$ h of the 9-h day feeding, but during a harsher winter, birds of the same species spent a full $8\frac{1}{4}$ h foraging (Gibb, 1956). In another study, Gibb (1960) estimated that English tits must find an insect on the average once every $2\frac{1}{2}$ s during daylight hours in order to balance their energy budgets during wintertime.

12.2.1   PEA APHIDS: AGE-SPECIFIC ENERGY BUDGETS

Even in a relatively constant environment, time and energy budgets change during ontogeny. Young (pre-reproductive) animals frequently allocate a

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greater fraction of the energy available to growth than do older animals, which typically show greatly slowed growth rates or even cease growing entirely in order to devote more to reproduction. One of the most detailed studies of such age-specific changes in energy budgeting is that of Randolph (McClure), Randolph & Barlow (1975) on pea aphids (*Acyrthosiphon pisum*) in the laboratory. These workers monitored daily energy flow to growth, reproduction, moulted exoskeletons, oxygen consumption (respiration) and honeydew production (Fig. 12.1) in a parthenogenetic strain of aphids. Total energy budgets of individual aphids varied with age by more than an order of
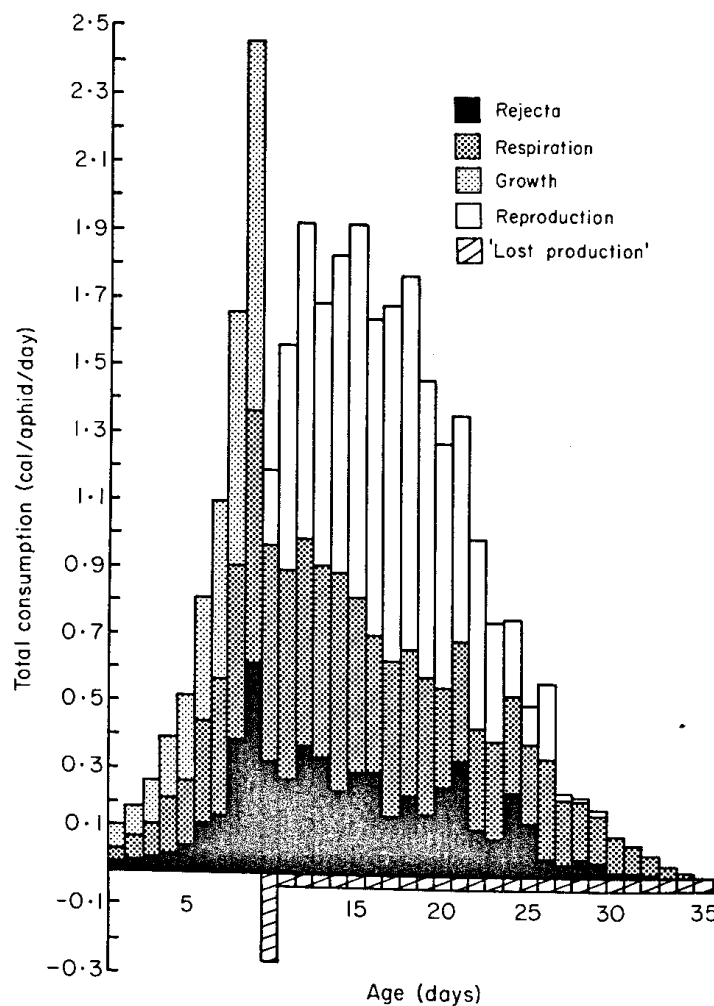
Fig. 12.1 Energy budgets of pea aphids at different ages. Total consumption is shown by the height of each bar, which is partitioned into five fractions: rejecta, respiration, growth, reproduction and 'lost production'. Note that all growth occurs prior to day 10, when reproduction starts (from Randoph (McClure) *et al.*, 1975).

magnitude: total consumption of energy increased approximately exponentially during the first 9 days of growth and then levelled off during the reproductive period and declined in old age (Fig. 12.1). The fraction of energy devoted to various activities changed greatly during the aphid's 35–39 day lifespan. All growth occurred prior to day 10, when reproduction began. Absolute amounts of energy expended on reproduction, growth, maintenance and rejecta all varied markedly with age, as did the efficiency of respiration, although efficiencies of assimilation and production did not.

As elegant as this study is, it unfortunately sheds little light on one of the central problems in the evolutionary approach to physiological ecology: *why* are resources (in this case, energy) partitioned exactly as they are?

12.2.2 ROTIFERS: COSTS OF REPRODUCTION

In a similar laboratory study, age-specific survivorship and fecundity of the rotifer *Asplanchna brightwelli* were monitored by Snell & King (1977). These rotifers proved to be variable in lifespans and rates of reproduction: those that had a high fecundity tended not to live as long as those that reproduced at a lower rate (Fig. 12.2). Reproduction at any given age markedly decreased survival to subsequent age classes (Fig. 12.3). In these rotifers, reproduction is clearly deleterious to survival (and hence, future reproductive success).
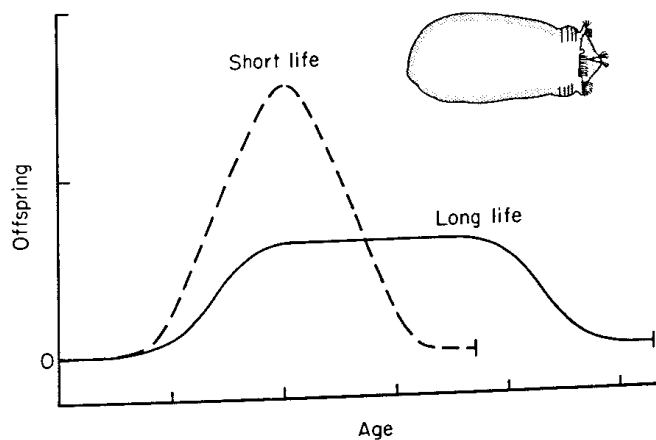

Fig. 12.2 Diagrammatic representation of the relationship between reproductive pattern and lifespan in laboratory populations of the rotifer *Asplanchna* (from Snell & King, 1977).
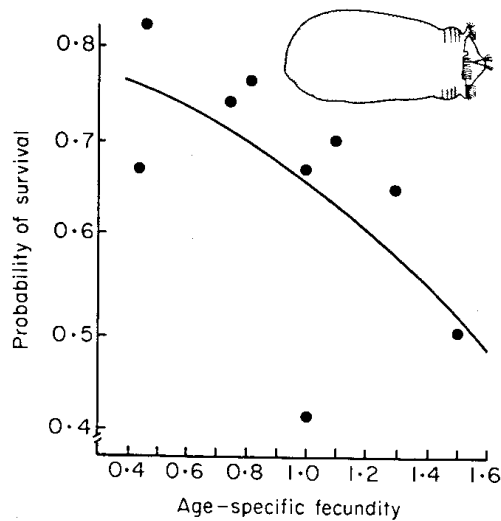
Fig. 12.3 Plot of probability of survival to the next age class versus fecundity at a given age (each data point represents ten rotifers) (from Snell & King, 1977).

12.2.3　ISOPODS: GROWTH VERSUS REPRODUCTION

Trade-offs between growth and reproduction in terrestrial isopods have been examined by Lawlor (1976). In these animals (*Armadillidium vulgare*), female fecundity increases with body size as it does in the majority of invertebrates and many other animals including most fish, amphibians and reptiles (perhaps birds and mammals are aberrant due to their determinant growth and/or parental care).

Female isopods that reproduce in the Spring do not grow as much as those that forgo this opportunity for reproduction. Further, the effect of such reduced growth on *future* reproductive success is considerably greater for small females than it is for larger ones. For example, a small 20-mg female not producing a Spring brood grows about 15 mg, hence increasing her body mass and resultant Summer fecundity by a full 75 %, whereas an equivalent growth increment of 15 mg (in lieu of Spring reproduction) would increase Summer fecundity of a large 100-mg female by only about 15 %. Hence small females have much more to gain from growth than do larger ones: such diminishing returns dictate that growth rates must decrease with size and age. Of course, growth and reproduction will usually vary inversely since costs in one constitute benefits in the other. In these isopods, reproductive females devote from 8 to 26% more energy to growth plus reproduction than non-reproductive females expend on growth alone.

To maximize total number of progeny produced during their lifetimes, Lawlor (1976) argues that isopod females below a threshold spring weight (about 45–50 mg) should elect for spring growth rather than reproduction. Essentially, allocation of resources to growth during the springtime increases a small female's expectation of future offspring (her 'reproductive value') more than would the immediate expenditure of those same resources on a spring brood (current reproduction). By means of spring growth, these small females can bear more offspring in their single large summer brood than they could if they opted instead for reduced growth and both a spring and a summer brood (the sum of two such smaller broods is less than that of the single larger brood). However, above the size threshold, pay-offs for single-broodedness versus double-broodedness are reversed, with the low-growth two-brooded tactic producing more total offspring (Fig. 12.4). Hence, small females are single-brooded whereas larger (older) ones reproduce twice each year.
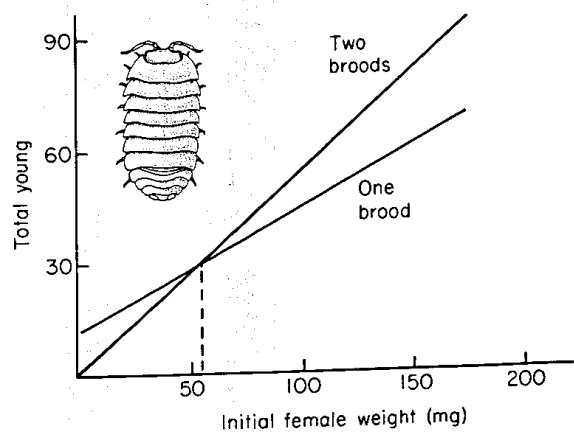
Fig. 12.4 Size–fecundity relationships for female isopods producing one and two broods. Below the threshold initial weight of about 50 mg, females leave more progeny by opting for growth and a single brood. Above this size threshold, females are double-brooded (from Lawlor, 1976).

12.2.4 WEASELS: COSTS AND PROFITS OF BEING LONG AND THIN

Next consider a somewhat more physiological example of resource allocation, involving thermal and energetic consequences of body shape in weasels (Brown & Lasiewski, 1972). Due to their long thin bodies and short fur, cold-stressed weasels must metabolize nearly twice as much energy to maintain body temperature than do more compactly shaped mammals of the same size and weight. Energetic costs of the weasel body form are therefore substantial

and must, of course, be balanced by concomitant benefits. The major ecological advantage of the weasel body plan is that it allows these tiny predators to enter burrows of small mammals (their major prey), hence increasing access to food, facilitating foraging success and making an increased energy requirement possible. Factors involved in the evolution of the elongate body shape of weasels are summarized in Fig. 12.5. Still another ramification of the weasel body shape is sexual dimorphism in body size, enabling males and females to exploit prey of different sizes (other members of the family Mustelidae are not nearly so dimorphic in size).

12.2.5   HUMMINGBIRDS AND BUMBLEBEES: TIME BUDGETS AND FORAGING ENERGETICS

Nectivorous animals are particularly well suited for certain observations on resource budgeting because time spent feeding can be readily converted directly into energetic gains. Pearson (1954) pioneered work on hummingbirds, keeping time budgets of individuals for a complete diurnal cycle of activity (Fig. 12.6). Subsequent studies have examined various aspects of the costs and profits of territoriality and foraging energetics (Wolf & Hainsworth, 1971; Wolf, Hainsworth & Stiles, 1972; Feinsinger, 1978). Analogous observations on the energetics of foraging in bumblebees (Heinrich, 1975, 1979) have underscored the intricate energetic interplay between plants and their pollinators.

12.2.6   MAMMALS: METABOLIC RATES AND REPRODUCTIVE TACTICS

In a recent review of mammalian energetics, McNab (1980) demonstrated that differences between species in basal metabolic rates varied in a systematic fashion with trophic habits: for a given body weight, insectivores have lower metabolic rates than frugivores or herbivores. Further, instrinsic rate of increase is correlated with rate of metabolism among mammal species. Finally, fluctuations in population size increase in amplitude with increasing rate of metabolism. McNab suggests that mammal species with larger energy budgets must have high metabolic rates. He implicates food type as the major causal factor limiting energy budgets and metabolic rates: in turn, these constrain reproductive tactics and thus determine maximal rates of increase, which dictate potential for population fluctuation. Under McNab's interpretation, interspecific variation in fecundity among mammals does not arise from
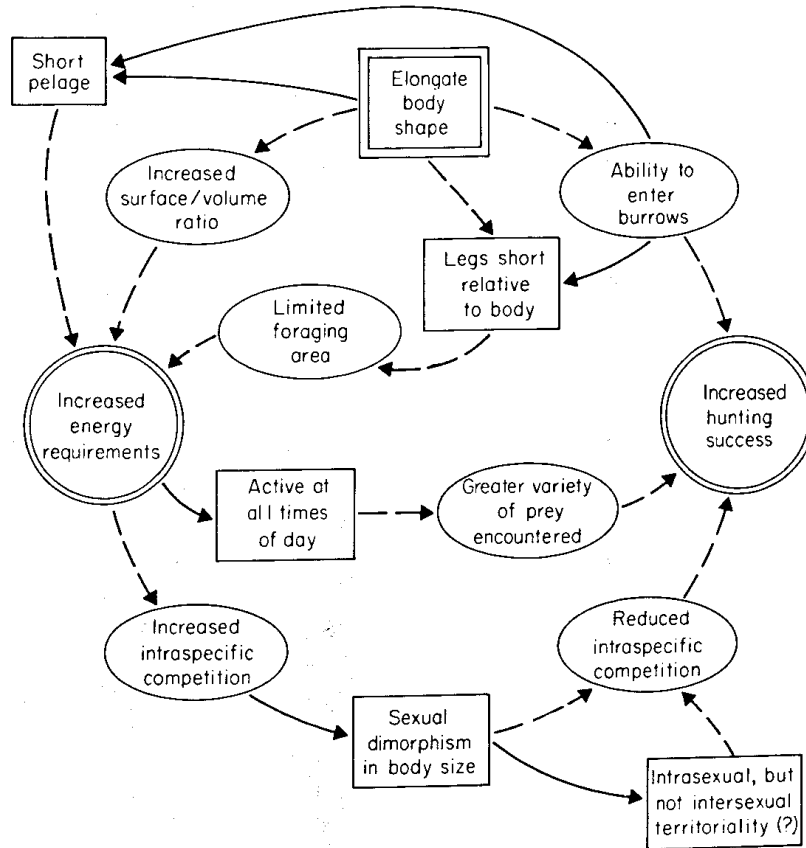
Fig. 12.5 Schematic representation of the factors involved in the evolution of elongate body shape in weasels. Primary consequences of evolving a long, thin body configuration are shown with circles; ellipses depict secondary consequences and rectangles show phenotypic characteristics affected by the evolution of the weasel body shape. Selective pressures portrayed by unbroken lines and causal sequences by dashed lines. As long as natural selection favours a more elongate shape, changes proceed as indicated by the arrows (from Brown & Lasiewski, 1972).

differences in energy allocation to reproduction but rather stems primarily from differences in diets, overall energy budgets and metabolic rates.

12.2.7 DESERT LIZARDS: CONSEQUENCES OF FORAGING MODE

Like many predatory animals, desert lizards separate into two natural groups:
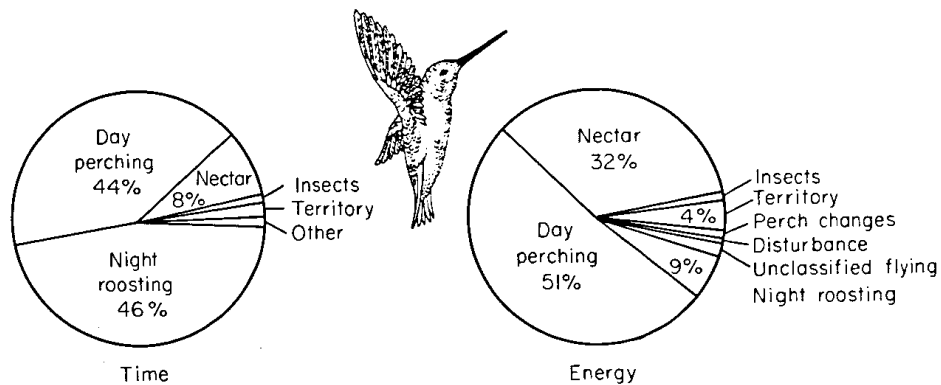
Fig. 12.6 Daily budgets of time (left) and energy (right) of a male hummingbird (from Pearson, 1954).

1 those that 'sit-and-wait' for their prey, capturing it by ambush;

2 those that hunt actively and 'forage widely' for their food (Pianka, 1966).

This dichotomy is fairly clean and few intermediates exist. In most lizard families, all members belong to either one category or the other; thus agamids and iguanids are invariably 'sit-and-wait' foragers, whereas skinks and teids tend to forage widely. However, lizards in the family Lacertidae exploit both foraging modes, even within the lacertid genus *Eremias*.

In the Kalahari semidesert of southern Africa (Pianka, Huey & Lawlor, 1979; Huey & Pianka, 1981), two species of lacertids, *Eremias lineo-ocellata* and *Meroles suborbitalis*, sit and wait for prey; several other syntopic species, including two other species of *Eremias*, forage widely for their food. Time budgets of these lacertids reflect their modes of foraging (Fig. 12.7). Foraging widely is energetically expensive and those species that engage in this mode of foraging appear to capture more food per unit time than 'sit-and-wait' species, judging from their stomach volumes. Indeed, Huey & Pianka (1980) estimate that overall energy budgets of widely-foraging species are from 1.3 to 2.1 times those of 'sit-and-wait' species. As might be expected, sedentary foragers tend to encounter and eat relatively mobile prey whereas more active widely-foraging predators consume less active prey. Compared with 'sit-and-wait' species, widely-foraging lacertid species eat more termites (sedentary, spatially and temporally unpredictable but clumped prey). One widely-foraging species, *Nucras tessellata*, specializes on scorpions (by day, these are non-mobile and exceedingly patchily distributed prey items).
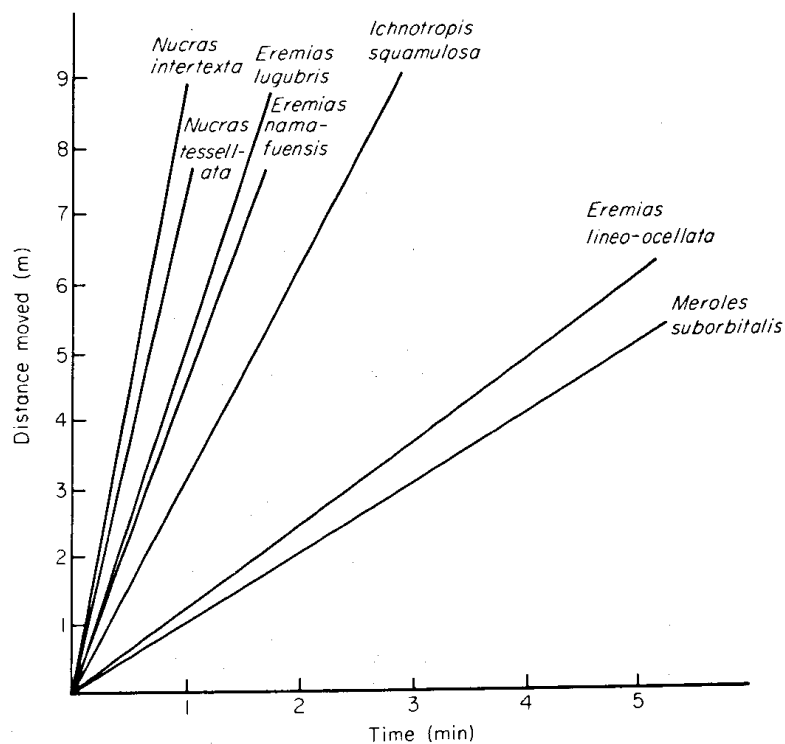
Fig. 12.7 Time budgets showing the average rates of movement of seven species of lacertid lizards in the Kalahari desert of southern Africa.

Another ramification of foraging mode in these lizards concerns exposure to their own predators. Widely-foraging species tend to be more visible and seem to suffer higher predation rates (frequencies of broken regenerated tails are high). However, widely-foraging species fall prey to lizard predator species that 'sit-and-wait', whereas 'sit-and-wait' lizard species tend to be eaten by predators that forage widely, so that 'crossovers' in foraging mode occur between trophic levels. Widely-foraging species tend to be more streamlined and to have longer tails than 'sit-and-wait' species.

Yet another spin-off of mode of foraging involves reproductive tactics. Clutch sizes of widely-foraging species tend to be smaller than those of sit-and-wait species, probably because the former simply cannot afford to weight themselves down with eggs as much as can the latter. Hence, foraging style (energy aquisition or input phenomena) constrains reproductive prospects (energy expenditure or output phenomena) in an important way. Some of the ecological correlates of foraging mode are summarized in Table 12.1. Similar patterns have been described in insectivorous birds (Eckhardt, 1979).

Table 12.1 Some general correlates of foraging mode (from Huey and Pianka, 1981).

	Sit-and-wait	Widely-foraging
Prey type	Eat active prey	Eat sedentary and unpredictable (but clumped or large) prey
Volume prey captured/day	Low	Generally high but low in certain species
Daily metabolic expense	Low	High
Types of predators	Vulnerable primarily to widely-foraging predators	Vulnerable to both sit-and-wait and to widely-foraging predators
Rate of encounters with predators	Probably low	Probably high
Morphology	Stocky (short tails)	Streamlined (generally long tails)
Probable physiological correlates	Limited endurance (anaerobic)	High endurance capacity (aerobic)
Relative clutch mass	High	Low
Sensory mode	Visual primarily	Visual or olfactory
Learning ability	Limited	Enhanced learning and memory, larger brains

12.2.8 HORNED LIZARDS: ADAPTIVE SUITES

In discussing the intricate physiological and ecological factors involved in water balance in desert-adapted kangaroo rats (genus *Dipodomys*), Bartholomew (1972) coined the term 'adaptive suite' to describe a constellation of integrated co-adapted phenotypic traits (several examples of such adaptive suites have already been considered above, e.g. see sections 12.2.4 and 12.2.7).

To illustrate, consider another, rather different, example. Desert horned lizards, *Phrynosoma platyrhinos*, are ant specialists, eating little else. Various features of the anatomy, behaviour, diet, temporal pattern of activity, thermoregulation and reproductive tactics can be profitably interrelated and interpreted to provide an integrated view of the ecology of this interesting animal (Pianka & Parker, 1975b; Fig. 12.8). Ants are small and contain much undigestible chitin, so that large numbers must be consumed. Hence an ant specialist must possess a large stomach for its body size (this horned lizard's stomach averages about 13% of the animal's overall mass, a substantially larger fraction than stomachs of other lizard species). This large gut requires a tank-like body form, reducing speed and decreasing the lizard's ability to escape from predators by movement. As a result, natural selection has favored a spiny body form and cryptic behaviour rather than a sleek body and rapid
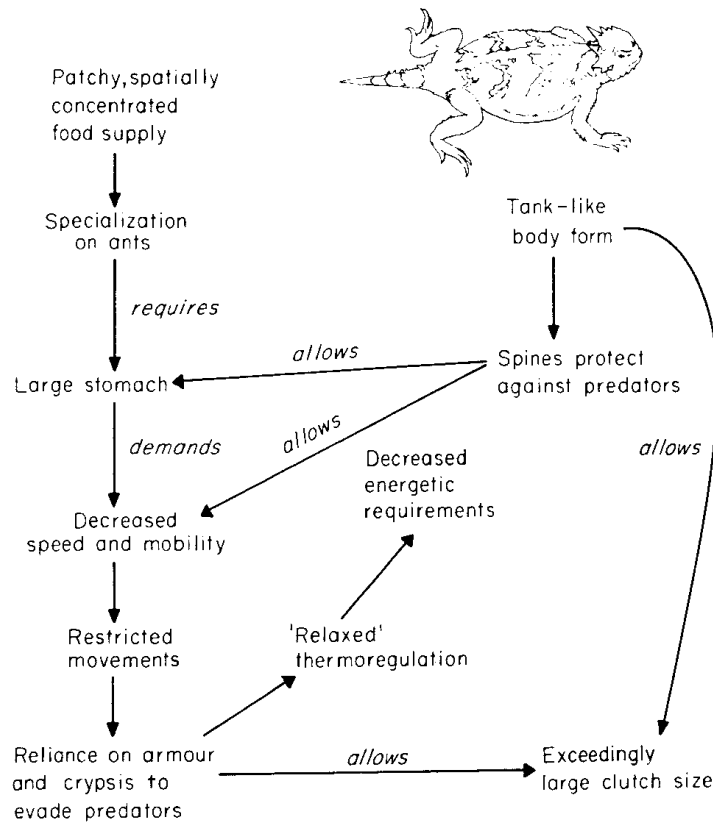
Fig. 12.8 Summary of the major factors influencing the ecology of the desert horned lizard, *Phrynosoma platyrhinos*. The complete constellation of co-adapted phenotypic traits represents this lizard's 'adaptive suite'.

movement to cover as in the majority of lizards. Long periods of exposure while foraging in the open presumably increase risks of predation. A reluctance to move, even when actually threatened by a potential predator, could well be advantageous: movement might attract the predator's attention and negate the advantage of concealing coloration and contour. Such decreased movement doubtless contributes to the observed high variability in body temperature of *Phrynosoma* (significantly greater than that of all other species of sympatric lizards). Wide fluctuations in horned lizard body temperatures under natural conditions presumably reflect both their long activity period and perhaps their reduced movements into or out of the sun and shade (most horned lizards are in the open sun when first encountered). A consequence is that more time is made available for activities such as feeding

(foraging ant eaters must spend considerable time feeding). Food specialization on ants is economically feasible only because those insects usually occur in a clumped spatial distribution and hence constitute a concentrated food supply. To make use of this patchy and spatially concentrated, but at the same time not overly nutritious, food supply, *P. platyrhinos* has evolved a unique constellation of adaptations that include its large stomach, spiny body form, an expanded period of activity and 'relaxed' thermoregulation (eurythermy) (Fig. 12.8). The high reproductive investment of adult horned lizards is doubtlessly also a simple and direct consequence of their robust body form. Lizards that must be able to move rapidly to escape predators would hardly be expected to weigh themselves down with eggs to the same extent as animals like horned lizards that rely almost entirely upon spines and camouflage to avoid their enemies. The *Phrynosoma* adaptive suite is depicted in Fig. 12.8.

12.3   CONCLUSION AND PROSPECT

Understanding an animal's tactics of resource acquisition and allocation is clearly a massive challenge. Numerous dimensions demand simultaneous consideration. Input–output phenomena (foraging versus reproduction) are complexly intertwined and may severely constrain one another. Foods eaten and foraging mode may place fundamental limitations on metabolic rates as well as on overall resource budgets. This complexity is further confounded by temporal variation (including ontogenetic changes) in survivorship probabilities and conditions for acquiring resources (which are by no means independent themselves!). All the above factors interact in important, sometimes subtle, ways, both among themselves and with reproductive tactics. The latter in turn affect growth, foraging success, survivorship and prospects for future reproduction. Clearly it is premature to attempt to make generalizations about resource budgeting among animals. However, in lieu of such a synthesis, some useful directions for future research can perhaps be anticipated.

A fitting way to conclude this chapter would have been to compare the budgeting of energy (and/or other resource dimensions) among a variety of different animal species. Elements for such a summary are outlined in Table 12.2. Note that even two different studies on the same animal, the flour beetle *Tribolium castaneum*, gave markedly different estimates. Unfortunately, entries in this preliminary table are not strictly comparable for a number of reasons:

Table 12.2 Estimates of the fractions of total assimilated energy budgets allocated to three major activities for various animal species, with source references.

Animal species	Maintenance	Growth	Reproduction	Source
Pond snail (*Lymnaea stagnalis*)	64–67	22	11–14	Scheerboom (1978)
Pea aphid (*Acyrthosiphon pisum*)	42.0	23.7	34.3	Randolph (McClure) et al. (1975)
Rice weevil (*Sitophilus oryzae*)	73.9	11.8	14.3	Singh et al. (1976)
Granary weevil (*Sitophilus granarius*)	63.0	13.9	23.1	Campbell et al. (1976)
Flour beetle (*Tribolium castaneum*)	55.8	4.2	40.1	Klekowski et al. (1967)
Flour beetle (*Tribolium castaneum*)	88.3	11.7		Prus & Prus (1977)
Dobson fly (*Cordydalus cornutus*)	29.9	53.1	17.0	Brown & Fitzpatrick (1978)
Gila topminnow (*Poeciliopsis occidentalis*)	93.8 (89.9–95.4)	4.3 (3.9–7.0)	1.9 (0.7–4.6)	Constantz (1979)
Mountain salamander (*Desmognathus ochrophaeus*)	43.1	8.6	48.3	Fitzpatrick (1973)
Sagebrush swift (*Sceloporus graciosus*)	75.4	1.2	23.4	Tinkle and Hadley (1975)
Yarrow's spiny lizard (*Sceloporus jarrovi*)	76.8	11.3	11.9	Tinkle and Hadley (1975)
Side-blotched lizard (*Uta stansburiana*)	78.5	2.2	19.3	Tinkle and Hadley (1975)
Cotton rat (*Sigmodon hispidus*)	70.6–84.0	5.4–6.5	9.5–24.0	Randolph (McClure) et al. (pers. comm., 1977, 1980)

1 some studies were performed under laboratory conditions, with food supplied more or less *ad libitum*, whereas others were done in more natural food-limited situations;

2 some energy budgets are individual, others populational;

3 time-scales of different studies cannot be easily standardized either, since some are expressed as lifetime budgets whereas others are seasonal or annual.

Among these dozen or more studies, the fraction of energy allocated to reproduction varies by more than an order of magnitude (from about 2 to 48%), as does that expended on growth (from 1.2 to 53%). Expenditure on maintenance (respiration) is less variable, ranging only from about 30 to 94%.

More informative comparisons could presumably be made if standardized techniques for studies of resource budgeting were adopted.

In addition to such comparative descriptive efforts, further work is needed on precisely why resources are allocated as they are. For example, studies like those on pea aphids and rotifers (sections 12.2.1 and 12.2.2) could lend themselves to fruitful experimental analyses. In a relatively constant laboratory environment, animals could be experimentally induced to devote *more* (and *less* in a companion experimental group) than the supposed 'optimal' amount (this would constitute the 'control') to various activities such as growth, maintenance and reproduction. (Some ingenuity and luck might be required to 'trick' many animals into adopting such suboptimal tactics!) Of course, experimental groups would be expected to suffer reduced reproductive success (fitness) compared to the control group. Yet another provocative line of investigation would be to monitor the performance of such experimentally treated animals under varying environmental conditions, as with altered levels of resource availability and/or intensity of predation, etc. These sorts of manipulations would certainly begin to elucidate ultimate factors underlying the causality of resource budgeting among animals. Indeed, such studies could easily become minor classics!