# ADAPTIVE INTRINSIC GROWTH RATES: AN INTEGRATION ACROSS TAXA

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ABSTRACT

*The evolution of intrinsic growth rate has received less attention than other life history traits, and has been studied differently in plants, homoiotherms, and poikilotherms. The benefits of rapid growth are obvious, so the problems is to explain the costs and tradeoffs that cause organisms to grow below their physiological maximum. Four prevailing themes emerge from the literature: (1) slow growth is adaptive for dealing with nutrient stress, (2) the tradeoff between growth rate and development limits growth in species that require mature function early in life, (3) rapid growth evolves when a minimum size must be reached quickly, such as for sexual maturation or overwintering, and (4) rapid growth may evolve to compensate for slowed growth owing to environmental conditions. Evidence for each of these themes is detailed for plants, homoiotherms, and poikilotherms. In addition, empirical evidence is reviewed for costs of rapid growth, including increased fluctuating asymmetry, reduced immune capacity, and reduced ability to respond to environmental stress.*

## INTRODUCTION

LIFEHISTORY evolution has received much attention over the past few decades, with current ideas being summarized in three recent publications (Roff 1992; Stearns 1992; Charnov 1993). Case (1978) noted, despite the wealth of papers on life history, that theory has focused primarily on the evolution of reproductive traits, neglecting growth and development in general. With only a few exceptions, the evolution of intrinsic growth rate and its impact on life history has continued to be neglected over the intervening years since Case's review of growth rates in terrestrial vertebrates.

Is intrinsic growth rate important for life history? The optimal life history strategy for a species has been defined as the one that maximizes lifetime reproduction, which is determined by maximizing age-specific survival and fecundity (Roff 1992; Stearns 1992). For most organisms, however, it is size rather than age that determines both survival probabilities (Gross 1981; McGraw and Wulff 1983; Werner 1988) and fecundity (McGraw and Wulff 1983; Aarssen and Clauss 1992; animals reviewed in Shine 1988). Growth rate defines the relationship between size and age, and therefore it is clearly an important factor to consider in life history theory (e.g., Gotthard et al. 1994). Why, then, has it been neglected? Usually a fixed amount of resources is assumed to be divided among fixed maintenance cost, growth, and reproduction (Gadgil and Bossert 1970; Stearns 1992). This suggests that an organism's growth rate should be at its physiological maximum whenever it is not reproducing, especially since there does not appear to be any

advantage for increasing size at a slow rate. We might therefore predict naively that organisms will always grow as fast as possible to achieve the benefits of large size, at least until the age of first reproduction (e.g., Ricklefs 1969).

Theoretical predictions that assume maximal growth rates do not fit empirical data (Ricklefs 1969; Case 1978). There is abundant evidence that most organisms are capable of growth rates far in excess of what is typical in nature (reviewed in Calow 1982; Atchley 1984), suggesting the existence of tradeoffs between growth rate and other life history traits. Moreover, growth rates are heritable (Garnett 1981; Gjerde 1986; Dijkstra and Lambers 1989; Heath et al. 1993;) and often vary greatly among populations (Macdonald and Thompson 1988; Elliott 1989; Aronson et al. 1992). Thus, there is plenty of genetic material on which natural selection can operate to optimize growth rates within the physiological constraints of a species. Given the importance of growth rate in determining fitness in general, and the large heritable variation that exists in growth rates, two questions need to be answered: (1) Why are most growth rates not maximized (i.e., what are the likely tradeoffs), and given these tradeoffs, (2) What selective forces determine the optimal growth rate for any organism?

A number of concepts are associated with growth rate, including optimal size, development, and growth potential. Here I attempt to distinguish selection for growth rate — the rate at which an organism increases its size per unit time — from these other concepts. For example, although size and growth rate are often correlated both within and between species (Charnov 1993; Niklas 1994), selection for increased size does not necessarily mean that growth rate will increase (see, e.g., Lynch and Arnold 1988). Overall size can be increased through many mechanisms, especially by increasing initial size (e.g., Reznick 1982; Elliott 1989), or the length of time during which growth occurs (Korner and Menendez-Riedl 1989; Neat et al. 1995). Moreover, conditions that select for large size may actually select for slow growth rates. For example, Millar and Hickling (1990) argue that large size improves fasting endurance in mammals. In contrast,

Langham (1983) argues that slow growth in terns may allow them to endure periods without food  (see also Gotthard et al. 1994 and Conover and Schulz 1997). If we assume that selection for large size also means selection for rapid growth, it is hard to see how juveniles of any species could survive the rapid growth necessary for them to reach a large size when periodic food shortages are common. Slow growth and large size are either alternative strategies for dealing with fasting, or else large size is achieved in these individuals only after a long period of slow growth. Issues of size aside, selection for growth potential includes shifts in growth reaction norms across environmental gradients and scheduling of growth. For example, many marine invertebrates from arctic populations have growth rates that peak at lower temperatures than those from temperate populations (Levinton 1983; Lonsdale and Levinton 1985). Thus the two populations may have similar maximal growth rates, but these peaks may occur at different environmental temperatures. Experiments conducted over a narrow range of temperatures may conclude that each population has evolved a different growth rate. Growth schedules also lead to confusion when an inappropriate time scale is used. If growth rate is defined as a change in size over a single season, then differences in timing of reproduction may give the appearance of differences in growth rate. For example, an annual plant that ceases growth and begins reproduction early in fall will be smaller than one that stops growing later in fall, although both may have had the same growth rate. Use of inappropriate environmental conditions or inappropriate time scale are problems that plague many experiments looking for tradeoffs.

This review updates and extends Case's (1978) paper beyond the terrestrial vertebrates to include plants, aquatic vertebrates and some invertebrates. The special problems of clonal growth will not be considered here. Ideas about the evolution of growth rates have developed in isolation across disciplines, and have emphasized different factors. This can be partially justified by differences among the taxa, but it also reflects a lack of communication and a difference in research interests.

The first three sections of this review de-

scribe the key hypotheses about the evolution of growth rates for plants, homoiotherms, and poikilotherms, respectively. The fourth section integrates these hypotheses, including the importance of competition and mortality factors in selecting for rapid growth, and nutrient conditions selecting for slow growth. Countergradient variation indicates, however, that the effects of nutrient conditions are not entirely straightforward. The tradeoff between growth rate and cellular differentiation is also discussed. The final section suggests some costs of rapid growth that can lead to optimization rather than maximization of growth.

## PLANTS

### EVOLUTION OF GROWTH RATE IN RESPONSE TO STRESS AND DISTURBANCE

One of the first attempts to relate intrinsic growth rates to local conditions was developed by Grime and Hunt (1975). Relative growth rates of 132 flowering species were measured in greenhouse conditions. Because growth rates were measured prior to flowering, they should be considered equivalent to juvenile growth rates in animals. Grime and Hunt (1975) correlated these growth rates with the ecological conditions under which each species was found in nature. Species were arranged along two independent gradients that Grime (1977) called *stress* (any factor limiting growth such as moisture, temperature, or nutrient levels) and *disturbance* (rates of damage or mortality). These two forces, considered orthogonally, produce four extreme conditions with four corresponding life history strategies: "competitors" are found under low stress and low disturbance, "ruderals" are found under low stress but high disturbance, and "stress-tolerators" are found under high stress but low disturbance; no life history strategy is described for the fourth condition, high stress and high disturbance, because Grime (1977) believed that this combination would preclude plant life (Figure 1). However, a life history strategy has been described for animals under this condition (Sibly and Calow 1985; Taylor et al. 1990), although only reproductive traits were described. These are only the extreme strategies, and the majority of organisms will naturally exhibit intermediate life history strategies.

The "competitor" and "ruderal" strategies both show rapid growth, but for different reasons. "Competitors" are described as having fast growth in order to outsize other plants; competitive pressure has sometimes been considered a third gradient along with stress and disturbance (Southwood 1988). "Ruderals" are found in ephemeral habitats (high disturbance) and show rapid growth not for dealing with competitors but in order to reach reproductive size before mortality occurs. "Competitors" and "ruderals" also differ in their reproductive strategies: the former mature late and produce a few large offspring, while the latter switch their resources in order to reproduce early, and produce many small offspring. "Competitors" and "ruderals" also correspond roughly to the concepts of r- and K-selected species of MacArthur and Wilson (1967), although these terms have fallen into disfavor with many working on life history evolution (Stearns 1983).

In contrast to the previous strategies, "stress-tolerators" show slow intrinsic growth rates that are relatively unresponsive to an improvement in conditions (Grime 1979; Chapin 1980). Although the physiological effects are well known for many types of stress (e.g., Osmond et al. 1987) and appear to have similar effects on growth rate (Chapin 1991), nutrient stress has been tested most extensively with respect to intrinsic growth rates (Chapin 1980) and will be considered here. Odum and Pinkerton (1955) suggest that when resources are limiting, organisms should maximize the efficiency of resource use at the expense of the power (rate) of resource use. Because of an assumed inherent tradeoff between rate and efficiency (Odum and Pinkerton 1955; Smith 1976), a slow growth rate may allow stress-tolerators to make the most efficient use of what few nutrients are available. This does not mean that stress-tolerators are especially efficient at capturing resources, but rather that they are efficient at retaining and using resources (Grime 1977; Chapin 1980; Chapin et al. 1982). For example, Shaver and Melillo (1984) compared N and P use in three species of marsh plants: *Carex lacustris*, *Calamagrostis canadensis*, and *Typha latifolia*. They found that
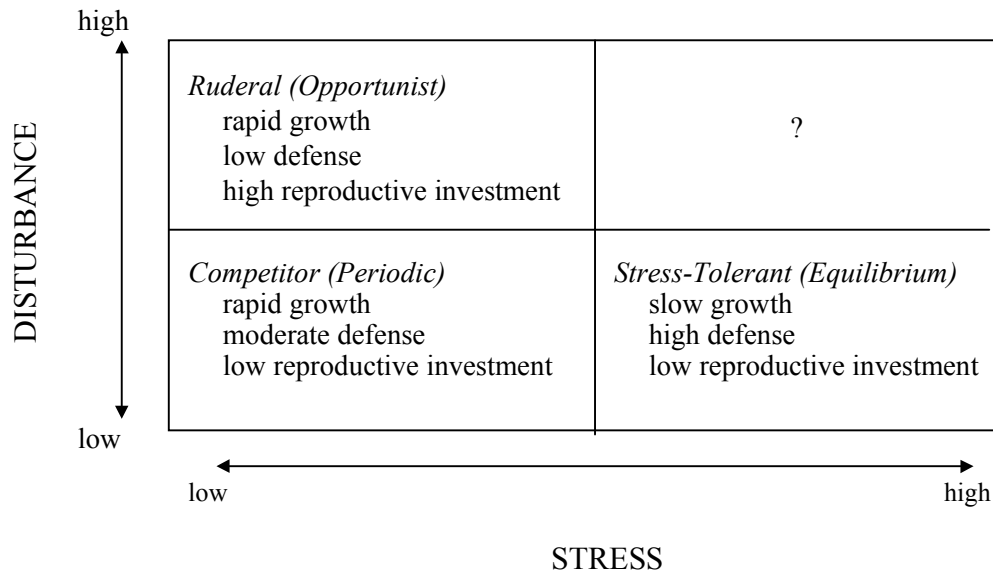
| | | |
|---|---|---|
| high | | |

DISTURBANCE

| *Ruderal (Opportunist)*<br>rapid growth<br>low defense<br>high reproductive investment | ? |
|---|---|
| *Competitor (Periodic)*<br>rapid growth<br>moderate defense<br>low reproductive investment | *Stress-Tolerant (Equilibrium)*<br>slow growth<br>high defense<br>low reproductive investment |

low

low                                      high

STRESS

FIGURE 1. HABITAT-TEMPLET FOR STRESS AND DISTURBANCE GRADIENTS

Plant strategies (after Grime and Hunt 1975) are labeled in bold, equivlanet fish strategies (after Winemiller and Rose 1992) are in parentheses. The life history strategy found under high stress and    high disturbance is not represented, as growth rates have not been described.

the slowest-growing species, *C. canadensis*, was intermediate in efficiency of nutrient uptake, but most efficient at recovering nutrients from senescent leaves and converting nutrients into biomass.

Efficient nutrient use is further increased in stress-tolerators through slow turnover rates of leaf and root tissue (Chapin 1980). The tradeoff between growth rate and efficient nutrient use means that, although faster-growing species often maintain their growth advantage even when nutrients are low, they tend to exhaust local resources. Elberse and Berendse (1993) found that under low nutrient conditions, fast growing grass species quickly exhausted the nutrients available and growth ceased (see also references in Chapin et al. 1982). Given a minimum size for flowering (van der Meijden and van der WaalsKooi 1979; Gross 1981; Young 1985; Grulke and Bliss 1988), fast-growing species may use up the available nutrients prior to reproduction and will be unable to invade nutrient-poor habitats despite their size advantage (see e.g., Aarssen and Taylor 1992). McGraw and

Chapin (1989) found just such a situation for two *Eriphorum* species; one fast-growing and found on nutrient rich soils (competitor), the other slow-growing and found on nutrient-poor soils (stress-tolerant). In reciprocal transplants, the fast-growing species produced many more flowers than the slow-growing species at a nutrient-rich site, but failed to flower at all at a nutrient-poor site. The slow-growing species had a similar rate of flowering at both sites.

Poorter (1989; see also Poorter and Remkes 1990; Lambers and Poorter 1992) suggests that slow growth is not itself adaptive (in terms of increased efficiency) but is merely the consequence of morphological traits that improve nutrient retention and incidentally limit growth rate. Having found a positive correlation between leaf surface area and relative growth rate, Poorter suggests that the need to retain nutrients in stress-tolerators has selected for small, long-lived leaves, and this in turn imposes a slow growth rate. Small leaves prevent leaching of nutrients and investment in mechanical and chemical anti-herbivory de-

vices to protect long-lived leaves may also limit growth rates (other characters are described in Poorter and Lambers 1992). Poorter (1989; Lambers and Poorter 1992) rejects selection for species that do not exhaust their rhizosphere in nutrient-poor habitats, claiming this would not be an evolutionarily stable strategy since rapidly growing species will still outcompete slower-growing species. However, if rapid growth limits or even prevents reproduction as described above, then slow-growing species should still be evolutionarily stable in the long run. A similar argument has been made recently by Clauss and Aarssen (1994) with respect to reproductive output. Although morphological adaptations definitely limit growth rate, we cannot reject an adaptive function to slow growth. In the end, it would probably be better to look at adaptive suites of traits (e.g., Chapin et al. 1993)

Although Grime and Hunt (1975) originally used stress and disturbance gradients to categorize differences in growth rates, the three strategies described above were also correlated with reproductive traits and became the focus of Grime (1977). Most ensuing plant studies have also emphasized reproductive traits. As far as empirical studies on growth rate are concerned, it is only the slow growth of stress-tolerators that has received much attention (Mowatt and Myerscough 1983; Atkinson and Farrar 1983; Poorter and Remkes 1990; Elberse and Berendse 1993). Finally, the stress/disturbance gradients for classifying life history traits has become quite popular and many such "habitat-templets" (*sensu* Southwood 1988) exist for reproductive traits of other organisms, including poikilotherms (reviewed by Southwood 1988; see also Winemiller and Rose 1992), but not for growth rates.

## GROWTH-DIFFERENTIATION BALANCE IN PLANTS

An alternative viewpoint to the ecological templet described above is a physiological perspective, focusing on the tradeoff between growth rate and differentiation rate. This has been called the growth-differentiation balance hypothesis (Loomis 1932). In multicellular organisms, different cell lines are specialized for certain tasks. As cells differentiate to perform their specialized tasks, they usually lose the ability to divide and thereby contribute to growth (Cameron and Jeter 1971; Lyndon 1990). This suggests that the rate of growth for a given tissue, organ, and ultimately the entire organism should be proportional to the number of undifferentiated dividing cells present (Ricklefs and Webb 1985). That differentiation rates may set the pace for the growth rate of individual units, such as leaf growth, has been considered for plants (Herms and Mattson 1992), but how this relates to the evolution of growth rates for the entire plant has not been developed as it has for some animals (see below). Rather, plant ecologists interested in the growth-differentiation balance hypothesis have focused on the products of differentiation, namely the production of secondary metabolites and their function in herbivore defense (Herms and Mattson 1992; Tuomi 1992; Lerdau et al. 1994). Because the focus of this paper is the evolution of growth rate, I will to some extent be reversing the usual description of the growth-differentiation tradeoff in plants.

The growth-differentiation balance hypothesis as developed by Herms and Mattson (1992) is an extension of the optimal herbivore defense theory and the carbon-nutrient balance hypothesis (Tuomi 1992). The optimal defense theory suggests that allocation of resources towards defense (at the expense of growth and other functions) is optimized for the level of herbivory a species typically experiences. The carbon-nutrient balance suggests that carbon-based secondary metabolites tend to accumulate when growth is limited by low levels of mineral nutrients, regardless of levels of herbivory. The growth-differentiation balance hypothesis explicitly addresses the developmental constraints on secondary metabolism as well as external factors, and thus attempts to unite optimal defense and the carbon-nutrient balance (Herms and Mattson 1992; Tuomi 1992). The growth-differentiation balance hypothesis predicts that any environmental factor that slows growth more than it slows photosynthesis will increase the resource pool available for secondary metabolism and promote differentiation processes (Herms and Mattson 1992). Note that this falls under the definition of *stress* given by Grime and Hunt (1975). As such, a growth-differentiation bal-

ance predicts increased allocation towards secondary metabolites under many stressful conditions such as moderate drought and low temperature, not just nutrient stress as predicted by the carbon-nutrient balance. In addition, the level of herbivory is also important in determining differentiation, as herbivory can induce secondary metabolism in ecological time and select for greater chemical defense over evolutionary time. Herms and Mattson (1992) rank plant life history tactics along a growth-differentiation continuum. Growth-dominated plants invest in processes and structures that further enhance growth, while differentiation-dominated plants invest in nongrowth processes and structures required to retain and make efficient use of resources. Herms and Mattson (1992) note that growth-dominated plants correspond to Grime and Hunt's (1975) competitor and ruderal strategies described earlier, while differentiation-dominated plants correspond to the stress-tolerant strategy. Because production of secondary metabolites as a defense against herbivores is the nongrowth product emphasized by Herms and Mattson (1992), the relevant selective forces in determining a plant's position along the growth-differentiation continuum are competition (which selects for rapid growth) and herbivory (which selects for enhanced differentiation). This may often correspond to a gradient of nutrient stress because as resource levels increase competition becomes more important relative to herbivory. Conversely, as resource levels decline herbivory becomes more important than competition. Herms and Mattson (1992) assume, however, that the importance of herbivory may also vary independently of resource levels (e.g., Grubb 1992).

Many plant ecologists view increased differentiation in stress-tolerant species as an adaptation for resource conservation. Decreased growth, then, is considered a by-product of adaptations that enhance resource conservation rather than an adaptation per se to stressful environments (Coley et al. 1985; Chapin et al. 1993; Lambers and Poorter 1992; Herms and Mattson 1992). The production of chemical defenses by slow-growing species is explained by the need to protect long-lived leaves in order to conserve nutrients. Rapid growth and chemical defenses then become

alternative, mutually exclusive strategies for dealing with herbivory (van der Meijden et al. 1988). Which strategy evolves depends upon whether or not nutrient levels are sufficient to sustain growth that is fast enough to outpace herbivores. High concentrations of chemical defense are common in slow-growing species and rare in fast-growing species because (1) the relative cost (in terms of slowed growth) of producing secondary metabolites is less for slow-growing species and (2) the relative impact of herbivores on slow-growing species is greater than on fast-growing species; thus the need for protection is greater (Coley 1987; de Jong 1992). Selection for increased differentiation at the expense of rapid growth may in part drive the evolution of growth rates in plants for several reasons. Secondary metabolites may serve functions other than herbivore defense, such as enhanced tolerance to drought and nutrient stress, and maintenance of high rates of photosynthesis when accumulation of photosynthates would otherwise cause feedback inhibition (reviewed by Herms and Mattson 1992), all of which are beneficial under growth limiting (i.e., high stress) conditions. These other functions of secondary metabolites increase the benefits of rapid differentiation under stressful conditions. Given this, the tradeoff between growth and differentiation is also expected to occur between factors other than herbivore defense which require cellular specialization. The need for extensive support structures should also lead to slow growth, and woody plants do in fact show slower growth than herbaceous species (Grime and Hunt 1975). Any time cells can differentiate (either chemically or mechanically) to alleviate stress, growth is likely to be compromised. Although herbivore defense is the primary focus of Herms and Mattson (1992), Loomis (1932) originally applied the growth-differentiation balance hypothesis more generally to explain variation in the growth rates of plants.

In conclusion, two frameworks have emerged for describing the evolution of growth rates in the plant literature. The first framework emphasizes the ecological conditions of disturbance and stress under which different growth rates are adaptive. The primary tradeoff considered here is between power output (such as growth rate) and efficiency of resource use

(Odum and Pinkerton 1955). That is, as growth rate increases, the efficiency with which energy and materials are used decreases. The second framework focuses on physiological processes and constraints underlying growth strategies. The primary tradeoff here is between growth rate and development rate. These frameworks are not mutually exclusive, in fact they may often complement each other, as suggested by Herms and Mattson (1992). In either case, rapid growth rate evolves in plants under low stress conditions either to improve competitive ability or to allow rapid completion of the life cycle.

### HOMOIOTHERMS

Investigators working with homoiotherms typically use field measures to estimate growth rate. Unfortunately, this confounds environmental effects on growth rate with the intrinsic growth rate characteristic for a species. Field measures of growth rate are easy to obtain and serve as important estimates of ecological conditions. The problem arises when ecological data are used to test evolutionary questions about intrinsic growth rates. Indeed, Wroot et al. (1987) and Ferron and Ouellet (1991) both warn that variation in growth rates within a species may be greater than that among closely related species; it is often not known what variation is due to environmental effects and what is due to intrinsic differences among populations. This often makes it difficult to interpret growth rates for homoiotherms.

In his review of growth rates in terrestrial vertebrates, Case (1978) suggested that the evolution of homoiothermy allowed mammals and birds to achieve potential growth rates an order of magnitude greater than in other vertebrates. The association of homoiotherms with high metabolic rate is undeniable, but simply the ability of homoiotherms to maintain a constant body temperature is not sufficient to explain their greater growth rates. It has been suggested that altricial birds have the fastest growth rates among homoiotherms precisely because they delay the development of homoiothermy in ontogeny (details and references below). It is possible that the mechanisms which allow homoiothermy, such as higher metabolism (see Klassen and Drent 1991), may also indirectly accelerate growth rates.

Case (1978) then turned his attention to growth rates solely among homoiotherms, and concluded that the most important factors that determine growth rate in homoiotherms are juvenile mortality, mainly from predators, and the ability of parents to provision their offspring. High juvenile mortality should select for rapid growth that would enable the young to escape the vulnerable nestling stage as quickly as possible (similar to rapid growth in the ruderal strategy of plants). In contrast, if the risk of juvenile mortality is low, slow growth would allow adults to raise a larger brood with the same rate of food delivery. That is, clutch size and growth rate should be inversely related (Lack 1968).

### PREDATION PRESSURE SELECTS FOR RAPID GROWTH

Lack (1968) and Case (1978) suggest that rapid growth may allow juvenile birds to grow through the nestling stage as quickly as possible, thus reducing the amount of time they are vulnerable to nest predators; growth rate is predicted to increase as predation rates increase. Although predation pressure has been very important conceptually for explaining differences in growth rates among homoiotherms, surprisingly few studies have tested directly the impact of predation rates on growth rates. Ricklefs (1969) found no correlation between growth rate and predation among temperate passerine birds. Case (1978) argued that Ricklefs failed to find a correlation because growth rate and mortality were often estimated from different populations. Case then provided some evidence that mammalian growth rates increased with increasing predation rate, but added no data for birds, suggesting only that birds grow faster than mammals overall because their nests are more exposed to predators than are the dens and burrows mammals tend to use.

Ricklefs (1976) found that growth rates in neotropical passerines from Trinidad and Panama were 23% lower on average than that of temperate passerines (see also Bryant and Hails 1983). Ricklefs suggested that, because predation rates in the tropics are as high or higher than in temperate regions, something

other than predation must be determining growth rates in birds. In support of the suggestion that predation is unimportant, Trevelyan and Read (1989) found no difference in growth rates when comparing 14 bird species found in both Australia (where predation is high) and New Zealand (where predators have only recently been introduced by man). However, Oniki and Ricklefs (1981) found that growth rates of passerines measured in Brazil were intermediate to the Central American and temperate species, but not significantly different from the temperate species. This confuses the issue greatly, and makes it unclear whether predation effects should be dismissed entirely.

What evidence, then, is there that predation pressure influences growth rate among birds? Case (1978) pointed out that, in general, cavity-nesting passerines have lower mortality rates and slower growth rates than do species that nest in the open. Robertson (1988) found a similar trend among species of British pigeons and doves. Martin and Li (1992) compared open-nesting species with cavity-nesters, further dividing the cavity-nesters into species that excavate their own cavities and those that do not. Nest holes used by nonexcavators are usually older and more accessible to predators than are those of excavators, and the predation rates reported by Martin and Li reflect this. Length of nestling period was longest in excavators and shortest for open nesters as predicted from mortality rates. In addition, among open nesting species, ground-nesting birds are often assumed to suffer higher predation than offground-nesting birds (Martin 1993). Although this relationship holds for shrub/grassland habitats, Martin (1993) found that ground-nesting birds actually have lower predation rates than offground-nesters in forest habitats. As long as current predation rate reflects evolutionary predation pressure, this reversal in relative predation would make a comparison of grassland and forest habitats a strong test for the effects of predation on growth rate in birds.

Overall, the evidence seems about evenly divided for and against predation pressure as being important in determining growth rates. In birds, this is probably because nest predation is not size-specific. Fledging in birds must depend on developmental state, not on size, and therefore does not necessarily depend upon growth rate. This means that predation pressure is selecting not to increase size as rapidly as possible, but to complete the nestling stage as rapidly as possible. For example, precocial birds have done away with the nestling stage entirely, presumably to avoid nest predation, at the expense of rapid growth (for this reason, all of the examples cited below deal with altricial birds). There often appears to be lack of distinction between growth and development for homoiotherms; indeed, Lack (1968) used fledging time as his measure of growth rate, thus confounding growth and development. Although Martin and Li (1992) only describe length of nestling period, their introduction and discussion imply that this reflects growth rate. Investigators may have more success in correlating some aspect of developmental rate rather than growth rate with juvenile predation in birds.

## FOOD LIMITATION AND QUALITY SELECT FOR SLOW GROWTH

In homoiotherms, the rate at which parents are able to provide food is an important factor determining growth rates (Case 1978). Slow growth is predicted to evolve both in response to low resource availability (which I call the "food-limitation hypothesis") and poor quality food (or food that is unbalanced in terms of nutrients). Unfortunately, studies of homoiotherms are plagued by a failure to control for rates of food delivery across broods. Thus the extent to which growth rates reflect adaptive intrinsic differences, as opposed to differences in rate or amount of food delivery, is rarely clear. Birds especially are thought to be food limited (Martin 1987), and food limitation is often invoked to explain reproductive life history differences (Martin 1995). Working with Yellow-eyed Penguins (*Megadyptes antipodes*), Van Heezik and Davis (1990) found that the fastest growing chicks had the highest mortality rates in a year with poor feeding conditions. This suggests that growth rates should be adjusted to local food levels.

The effects of nutrient stress in immature homoiotherms is further complicated because most food is delivered by parents who may not provide food to offspring as fast as they are able to collect it. For example, Nur

(1984a) manipulated clutch size to see what effect brood size had on feeding rates in blue tits (*Parus caeruleus*). He found that delivery rate increased with clutch size, and that feeding rate per chick decreased when clutches were small. However, the feeding rate per chick became constant for the mean population clutch size and larger (see Tarburton 1987 for similar results in white-rumped swiftlets). In addition, weight loss by the mother, but not the father, increased as delivery rate increased regardless of feeding rate per chick. Nur concluded that the rate at which parents feed their offspring is not limited by their ability to capture food. Rather, parents trade off feeding rate, which determines juvenile survival, with their own weight loss, which determines their survival and future chances to breed (Nur 1984b). Although Nur was interested in how feeding rate influenced optimal clutch sizes, it seems clear that the feeding rate should also affect growth rates. As another example, Chaurand and Weimerskirch (1994) showed that the blue petrel (*Halobaena caurulea*), a pelagic seabird, alternated long feeding trips with short feeding trips. Although the short, near shore feeding trips increased the rate at which chicks were fed, adults lost weight. In contrast, adults gained weight during the long trips while chicks had to wait four times longer between feedings. Because parents are often capable of delivering food at a faster rate than they actually do, chick growth rate is not dependent upon the productivity of the local environment but rather on their parent's propensity to deliver food. However, if the energetic cost to the parent of provisioning young is a reflection of local productivity, little modification of the food-limitation hypothesis need be made. Unfortunately, feeding rates are sometimes determined by factors unrelated to food availability. In Atlantic Puffins (*Fratercula arctica*), chicks experience low mortality rates in the nest, but parents are vulnerable to gull predation as they arrive at and leave the nest (Ydenberg 1989). Adults nesting at vulnerable sites make fewer food deliveries than do those nesting at safer sites. Thus, although environmental productivity may set an upper limit to growth rate, it is the actual rate at which parents deliver food that determines the optimal growth rate. Unfortunately,

these studies again confound phenotypic components (amount of food delivered) and genotypic components of growth rate.

Some studies do clearly show that slow growth evolves in birds as a response to poor food quality. Several groups of seabirds that raise single offspring broods show extraordinarily slow growth. Both small clutches and slow growth have usually been interpreted as a response to severe energy limitation, because parents must travel great distances to feeding areas (Case 1978; but see Ricklefs 1973). However, the fish and squid these birds feed their young has an extremely high lipid content, and slow growth has also been suggested as a mechanism for bringing the lipid intake into balance with protein and carbohydrate levels (Ricklefs 1979a; 1992). This would also explain why these chicks build up large fat reserves prior to fledging. Fruit-eating birds are another group with a low-quality diet. Their slow growth may be explained by the low protein content of their fruit-based diet (Ricklefs 1979a). Finally, Case (1978) noted that in birds and mammals, species in which both parents feed the young grow faster than those in which only the mother provides nourishment. It is not clear, however, whether this is intrinsic growth rate or merely a phenotypic response to increased food delivery.

## GROWTH AND DEVELOPMENTAL TRADEOFFS IN HOMOIOTHERMS

Just as cellular differentiation may limit growth rates in plants, several investigators have emphasized differentiation as a constraint on growth rates in homoiotherms (Ricklefs et al. 1994). Within the homoiotherm literature, comparisons of differentiation rates have primarily been between altricial and precocial species. In birds, altricial species have rapid growth rates, but thermoregulation and muscle coordination develop slowly during the growth phase. In contrast, precocial species thermoregulate and are quite mobile upon hatching, but have much slower growth rates. Ricklefs (1979a) suggested that these differences are owing to a tradeoff between cellular proliferation and mature function in muscles. It is likely that the tissue which must mature the earliest (leg muscle in precocial species and breast muscle in

altricial species) is the tissue with the slowest growth rate and thus they constrain the growth rate of the entire organism (Ricklefs 1979a). Muscle tissue is a good candidate for the limiting tissue in birds, because muscles function in thermoregulation as well as movement. However, the tradeoff between growth rate and maturation has also been demonstrated for skeletal development in gulls (Carrier and Leon 1990) and flight feathers (Redfern 1994). Not only is the limiting tissue likely to vary widely among species (Ricklefs et al. 1994), but its location will also vary depending upon the primary form of juvenile locomotion (leg versus wing). For example, the California Gull (*Larus californicus*) is a semiprecocial bird, capable of running and swimming only a few days after hatching, but the ability to fly develops slowly. Accordingly, their leg bones are relatively large and more fully developed at hatching than are their wing bones (Carrier and Leon 1990). However, the wing bones grow faster than the leg bones. Ricklefs (1979b) found similar differences in muscle development. The precocial common tern (*Sterna hirundo*) and Japanese quail (*Coturnix coturnix japonica*) move about at hatching and have mature leg muscles, while the altricial starling (*Sturnus vulgaris*) does not. In addition, quail chicks begin to fly while only half grown, and their pectoral muscles must mature at this time. This means quail have early maturing leg and wing muscles, terns have early maturing leg muscles but late maturing wing muscles, and both legs and wings mature late for starlings; correspondingly, the starling grows faster than the tern, and the tern grows faster than the quail.

The difference between altricial and precocial growth rates in mammals is less clear. In a survey of African rodents, Neal (1990) found that precocial species did have slower growth rates than altricial species. Case (1978) found no trend across a large number of mammalian taxa. Webb and McClure (1989) also found no difference in growth rates for the precocial cotton rat (*Sigmodon hispidus*) and altricial wood rat (*Neotoma floridana*), a curious reversal from earlier work by McClure (McClure and Randolph 1980) on the same two species. However, this was probably an inappropriate comparison as thermoregulation in wood rats

is metabolic while cotton rats rely more on insulation. Indeed, Hill (1992) questioned the validity of a thermoregulatory definition for precociality and altriciality in mammals, as was used in the above studies. It may be better to examine other developmental characteristics as limiting growth rate. For example, neural development appears to be a major constraint on placental growth rates in mammals (Sacher and Staffeldt 1974; Grand 1992), although it does not appear to correlate with neonatal growth (Case 1978). Rather, neonatal growth rates correlate with birth weight (Case 1978; Burnett and Kunz 1982; Bassett 1984). Birth weight is probably constrained by the size of the birth canal, and rapid postnatal growth rate may have evolved in mammals as a way of compensating for a small birth size.

In conclusion, high juvenile mortality, mainly due to predation, seems to select for rapid growth in homoiotherms while, nutrient stress selects for slow growth. Rapid growth allows juveniles to escape a vulnerable developmental stage. This means, however, that high mortality should select for rapid development rather than rapid growth. It is likely that the use of field data to determine growth rates accounts for the many examples of seemingly contradictory data. The tradeoff between growth and development rates is well recognized for homoiotherms, focusing primarily on the altricial/precocial distinction. Analysis of a growth-differentiation tradeoff in mammals is hampered by a failure to make the meaningful comparisons. Development must follow the same pattern across species if rates of growth and differentiation are to be compared.

## POIKILOTHERMS

### EVOLUTION OF GROWTH RATE IN RESPONSE TO STRESS AND DISTURBANCE

Two key hypotheses to emerge from the previous sections are that high mortality (owing to either predation pressure or disturbance) selects for rapid growth, while nutrient stress selects for slow growth. The same appears to be true for fishes. In a multivariate analysis of life history traits across fish species, Winemiller and Rose (1992) found evidence for three life history strategies arranged along gradients of resource availability and mortality

rates, which they likened to Grime's (1977) habitat-templet for plants (Figure 1). According to Winemiller and Rose (1992), rapid growth in fish is correlated with (1) the "periodic" strategy, found under conditions of high periodic mortality or mortality, which tends to affect only small size classes, and (2) the "opportunistic" strategy, found under high disturbance. A slow intrinsic growth rate is correlated with (3) the "equilibrium" strategy, found under resource-limited conditions. The "opportunistic" strategy is analogous to that of "ruderal" plants, but the other two strategies differ from those described for plants. Winemiller and Rose attribute the nutrient stress experienced by the "equilibrium" strategy to competition, but traits associated with this strategy, including a slow growth rate, correspond more closely to the "stress-tolerant" strategy rather than to the "competitor" strategy of plants. The latter is better approximated in fish by the "periodic" strategy, except that for fish rapid growth has evolved to avoid size specific mortality rather than competition. However, if competition in plants results in size-dependent mortality, then these strategies are very similar.

A number of studies in poikilotherms confirm Winemiller and Rose's (1992) finding that slow growth is associated with low resource levels. Niewiarowski and Roosenburg (1993) found that fence lizards (*Sceloporus undulatus*) from a low food site not only had a slower growth rate than those from a high food site, but were also unable to increase their growth rate when excess nutrients were provided. Such insensitivity to nutrient levels has already been noted for stress-tolerant plants (Grime 1977; Iwasa 1991). Sinervo and Adolph (1994), also working with fence lizards, found that populations that experience short daily activity periods oeing to ambient temperatures, and thus can feed only for a short period of time each day, have slower intrinsic growth rates than those from populations with long daily activity periods. Riha and Berven (1991) suggested the slower intrinsic growth of two eastern populations of wood frogs in comparison with a Michigan population is due to nutrient stress in the eastern populations. Intrinsic growth rate in the land snail *Arianta arbustorum* showed a negative correla-

tion with altitude, which Baur and Raboud (1988) also interpreted as a stress-tolerant strategy. Gotthard et al. (1994) demonstrated thatlarvae of the speckled wood butterfly (*Pararge aegeria*) with slow growing genotypes showed a better fasting endurance than did fast-growing genotypes. Clarke (1983) attributed the generally slow growth rates of polar marine ectotherms, both vertebrate and invertebrate, to low resource levels that prevail throughout most of the year. Unfortunately, it is not clear whether the growth rates referred to by Clarke are maximal growth rates or annual growth rates. Because productivity in polar regions is usually confined to a short summer season, growth is also largely confined to this time. Such a situation may actually select for very rapid growth rates when food is available (e.g., Conover and Present 1990). Nonetheless, it is clear that a slow intrinsic growth rate is found across many taxa under conditions of nutrient stress.

## COUNTERGRADIENT VARIATION

A slow intrinsic growth rate will not inevitably evolve under nutrient stress. Ferguson and Talent (1993) compared two populations of fence lizard, one from Utah having slow growth in the field and one from Oklahoma having a faster growth rate in the field. Under laboratory conditions the growth rates reversed, however, with the Utah lizards growing faster than the Oklahoma lizards. It is not clear whether the Utah population showed faster growth rate in the laboratory because of the relatively long photoperiod, or constant availability to food. In either case, this example provides a sharp contrast to Niewiarowski and Roosenburg (1993) and Sinervo and Adolph (1994), who found a reduced intrinsic growth rate in response to low food levels and short photoperiods respectively. This suggests that the same conditions may select for slow growth (Niewiarowski and Roosenburg 1993; Sinervo and Adolph 1994) and at other times select for rapid growth (Ferguson and Talent 1993), even within the same species. Examples where fast growth has evolved when we would normally expect slow growth are relatively common for poikilotherms and may be common for other taxa as well (see below).

The idea of countergradient variation is a
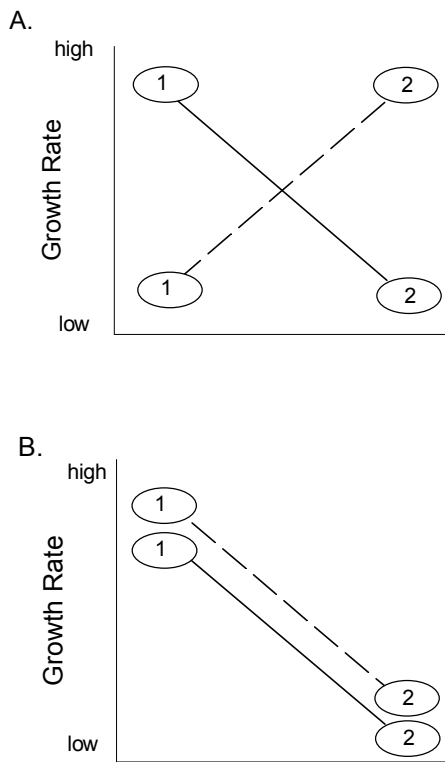
A.



B.



FIGURE 2.          (A) COUNTERGRADIENT VARIATION
AND (B) COGRADIENT VARIATION

Solid lines depict relative growth rates of two genotypes (1 and 2) measured in their native habitats. Dashed lines depict relative growth rates found when the two genotypes are raised under common conditions.

key concept to emerge from poikilotherm studies (Conover and Schultz 1995). Countergradient selection (called antagonistic selection by Falconer 1990) is said to occur when the genetic response to an environmental gradient opposes the phenotypic response (Levins 1969) (Figure 2). For example, *Drosophila* raised under cool conditions are larger as adults than those raised under warm conditions (Partridge et al. 1994). Levins (1969) found that flies taken from cool sites in Puerto Rico were larger than those taken from warm sites, but when these same flies were raised in the laboratory, those from the warm site produced larger adults, the opposite of the field

measures. Adult size had evolved to compensate for the effects of environmental conditions on size. Rapid growth may evolve to compensate in part (Levinton 1983; Berven and Gill 1983) or even in full (see MacDonald and Thompson 1988 for a possible example) for environmental effects. Because environmental conditions have a strong effect on growth rate in poikilotherms, comparisons from different environments provide little information about variation in intrinsic growth rates within a species. Common garden and reciprocal transplant experiments are needed to reveal population differences in intrinsic growth rates, including countergradient effects. One reason why countergradient selection was first recognized by ecologists working with poikilotherms is the emphasis on proximal advantages of growth rate. Rather than large interspecific comparisons as have been described above for plants and homoiotherms, poikilothermic research has focused on the specific factors that select for either slow or rapid growth, and has tested these ideas primarily with intraspecific comparisons. The following sections highlight some of these factors.

## MIGRATION SELECTS FOR RAPID GROWTH

We can predict that rapid growth is advantageous to species that migrate in the first year of life, because large size reduces energetic costs for movement; relative metabolic needs and relative energetic demands for movement decrease with size (Peters 1983; Priede 1985). In addition, endurance (Videler 1993) and cruising speed (Hunter 1981) increase with size for fish. In fact, the relative and absolute costs of swimming, walking, and flying should decrease with size for all organisms (Thompson 1942). Migratory species should therefore be larger than non-migratory species. Roff (1988; 1991) argued that migratory fish should also have faster growth rates, but only because migratory fish are able to find nutrient rich locations (i.e., they do not necessarily have a faster *intrinsic* growth rate). Although Roff (1988) did find that migratory species of fish grow faster than nonmigratory species, he did not offer evidence that this was anything other than a phenotypic response to resource availability. A genetic component for rapid growth is likely to exist when migration occurs with

a time constraint. Snyder (1991) compared a nonmigratory population of threespine stickleback (*Gasterosteus aculeatus* L.) with two populations that migrate seasonally between breeding and overwintering sites. Because young from the migratory populations would have to reach a large size prior to the fall migration, they should have a faster growth rate than the nonmigratory population. The migratory fish did grow faster than the nonmigratory fish throughout the first summer of life. The same is true when comparing migratory (sockeye) and nonmigratory (kokanee) forms of *Oncorhynchus nerka* (Wood and Foote 1990), as well as for migratory (riverine) and nonmigratory (lacustrine) populations of Southern smelt (*Retropinna retropinna*) in New Zealand (Meyer-Rochow and Ingram 1993). However, it is unclear whether there is a time constraint on migration in either of these species. The same argument for rapid growth and migration should hold for flying organisms as well as aquatic organisms (Thompson 1942; Roff 1991). Chaplin and Chaplin (1981) showed that a migratory milkweed bug (*Oncopeltus fasciatus*) had a faster growth rate than a nonmigratory relative (*Lygaeus kalmii*) when raised under identical conditions. However, insects usually migrate to escape ephemeral habitats (Roff 1991), a condition that should also select for rapid growth (e.g., as in the "ruderal/ opportunistic" strategy). Thus it is difficult to determine whether migratory pressures alone can select for rapid growth in insects or fishes.

## LENGTH OF GROWING SEASON

Overwintering survival in animals often depends upon body size. Because the length of the growing season usually declines with increasing latitude, many species should show an increase in growth rate at higher latitude. Case (1978) did not find this to be true for mammals. Although temperate birds seem to grow faster than tropical birds, length of growing season predicts that arctic species should grow faster still — yet arctic birds grow at the same rate as temperate birds (Ricklefs 1976). However, intraspecific comparisons among several groups of poikilotherms have shown that short growing seasons do select for rapid growth rates. Conover and Present (1990) found a latitudinal gradient for growth rate

in Atlantic silverside (*Menidia menidia*). Since temperature patterns create a shorter growing season at higher latitudes, northern populations must reach the minimum overwintering size in a shorter period of time. Accordingly, growth was more rapid for a northern population than for a southern population when the two were compared under identical conditions (other examples for fish can be found in Conover and Schultz 1997). Ayres and Scriber (1994) found a similar situation in the Canadian tiger swallowtail (*Papilio canadensis*). Alaskan populations of this butterfly experience a growing season only 60% as long as those from Michigan, so we would expect Alaskan butterflies to have faster intrinsic growth rates. The results Ayres and Scriber present tend to support this, but the pattern changed slightly between years: In 1988 the Alaskan butterflies grew faster only at the lower temperatures tested (12 and 18°C), while the Michigan butterflies grew faster at 24 and 30°C — temperatures never experienced by the Alaskan populations and only rarely by the Michigan populations. When the same experiment was repeated in 1989, the Alaskan butterflies grew faster even at the warmer temperatures.

Length of growing season also shortens with altitude. Berven (1982) showed differences in growth rate for wood frogs (*Rana sylvatica*), which must reach a minimum size before metamorphosis (Berven and Gill 1983). A high altitude population (that experiences cooler daily temperatures) showed a faster intrinsic growth rate than a lowland population. Another altitudinal gradient in growth rates is found in *Chrysomela* beetles (Smiley and Rank 1986). Reciprocal transplants revealed that beetles from a high altitude population (shorter growing season) grew faster at both high and low altitudes, but were more vulnerable to predation, which only occurred at the lower elevation. The reasons for the growth rate-predation risk tradeoff were unknown, but may be related to either production of chemical defenses or grouping behavior.

### COMPETITIVE REFUGES SELECT FOR RAPID GROWTH

Large body size often increases an organism's competitive ability and rapid growth ensures a size advantage throughout ontogeny.

Winemiller and Rose (1992) suggested that competition, by causing nutrient stress, selected for slow growth of the "equilibrium" strategy in fishes. This may be true in scramble competition, where a large body size may even have an energetic disadvantage, but not for interference competition. Moreover, if ontogenetic niche shifts are size mediated, then rapid growth may allow an organism to escape even scramble competition. For example, predation pressure confines juvenile pumpkinseed sunfish (*Lepomis gibbosus*) and bluegill sunfish (*L. macrochirus*) to the shallow, vegetated regions of lakes where they compete for food (Mittelbach 1984). However, once bluegill sunfish reach 70 mm standard length they are beyond the gape limit of most predators, and are then free to enter the open water, where they become planktivorous. At this same size, pumpkinseed sunfish become large enough to crush the shells of snails, their dominant adult food source (Mittelbach 1984). As a result, these species compete only when they are less than 70 mm in length (Osenberg et al. 1988). Size specific competition should select for rapid growth in both species, minimizing the amount of time they compete. My research has shown that pumpkinseed sunfish derived from populations sympatric with bluegill have a significantly faster intrinsic growth rate than pumpkinseed from populations where bluegill were absent. Ontogenetic niche shifts are often determined by size (Werner 1988; Law 1991; Ebenman 1992), and rapid juvenile growth may evolve whenever competition can be escaped through growth. Size-dependent niche shifts appear to be common among freshwater fishes (e.g. perch and roach, Persson and Greenberg 1990; or bloater and alewife, Crowder and Crawford 1984), and have been documented for scorpions (Polis 1984) and plants (Parrish and Bazzaz 1985), although growth rate responses are unknown for these cases.

## PREDATION REFUGES SELECT FOR RAPID GROWTH

Predators are often gape limited, and large size can thus provide a refuge from predation (e.g., Hambright 1991; Schael et al. 1991; Reimchen 1991). *Chaoborus*, an invertebrate predator, selectively preys on small cladocer-

ans, and the presence of *Chaoborus* selects for rapid growth rates and larger body size in *Daphnia* (Spitze 1991). Similarly, killifish (*Rivulus hartii*) prey selectively on juvenile guppies, and guppies from populations where killifish are present grow more rapidly than do those from where they are absent (Reznick 1983). These studies demonstrate genetic changes in growth rate, but some animals are capable of a facultative growth response to predation threat. Bluegill sunfish (*L. macrochirus*) raised with predators have faster growth rates and deeper bodies than fish from the same population raised without predation (Belk and Hales 1993). In addition, Crowl and Covich (1990) and DeWitt (1995) found accelerated growth for physid snails raised in the presence of crayfish, which is advantageous because crayfish prey selectively on smaller snails (DeWitt 1995).

## GROWTH AND DIFFERENTIATION IN POIKILOTHERMS

The tradeoff between growth and differentiation rates, which has been actively studied in plants and birds, is rarely considered in poikilotherms. Wieser (1991) suggests that, as in altricial birds, development in larval fish is generally slow because of the need for rapid growth. There is some evidence that the intrinsic growth rates of fishes are determined by proliferation of muscle cells (Weatherley and Gill 1987; Weatherley et al. 1988). Fast-growing species of teleosts sustain recruitment of new muscle fibers until they reach a large size, whereas for slow-growing species, recruitment of new fibers ends quickly, and muscle growth thus depends primarily on increasing the diameter of fibers already present. This means that a higher percentage of muscle fibers are of small diameter in faster-growing species (Weatherley et al. 1988). Muscles with a high percentage of small fibers are likely to be less efficient than muscles with large fibers. Manipulations of growth rate with bovine growth hormone provides evidence that rate of muscle recruitment determines somatic growth rate. Grass pickerel (*Esox americanus vermiculatus*) continue muscle recruitment to a large size, and treatment with growth hormone increases growth rates from two to three times. In contrast, bluntnose minnow (*Pimephales no-*

*tatus*) and longnose dace (*Rhinichthys cataractae*) are slow growing and muscle recruitment ceases early. Administration of growth hormone to bluntnose minnow and longnose dace resulted in no increase in growth rate (Weatherley and Gill 1987). Looking at the same trait within a species, Meyer-Rochow and Ingram (1993) have recently found that a migratory riverine population of Southern smelt (*Retropinna retropinna*) grow faster and maintain recruitment of muscle fibers longer than does a nonmigratory lacustrine population. This means that the migratory fish have more muscle fibers (and larger fibers) when they migrate. However, it is not known whether rapid fiber recruitment translates into decreased agility or swimming ability for fish early in life. One clue that poikilotherms may trade off growth rate and development comes from research with *Drosophila*. Body size of *Drosophila melanogaster* increases as the temperature at which individuals are raised decreases; Partridge et al. (1994) found that this was owing in part to increased cell size and in part to cell number. Low temperature slows both growth and development rates in flies, but the increased cell number suggests that it may slow development more than it slows growth.

One difference between many poikilotherms and homoiotherms is that growth and differentiation may be partially decoupled in poikilotherms. This occurs in some tadpoles (Berven 1982) and many insect species. For insects with complete metamorphosis (e.g., Lepidoptera and Coleoptera), growth is largely confined to the larval stage, while most development occurs in the pupal stage. Such complexity may explain why a growth-differentiation tradeoff has received little attention in poikilotherms. The problem of decoupling may be resolved by determining appropriate developmental markers to use for comparison (recall the difficulties present in mammals). Some investigators have considered the length of the larval period as one measure of developmental rate (e.g., Janz et al. 1994). This seems appropriate as much cellular differentiation does occur within a stage. For example, larval lepidopterans must develop new cuticle with each molt, and there may be a tradeoff between rate of cuticular differentiation and growth rate. The ecological effects of the growth-differentiation balance remain an unexplored area for poikilotherms.

In conclusion, poikilotherms show that rapid growth is advantageous when survival rate increases with size, while slow growth may be adaptive under stress. However, the existence of countergradient variation shows that habitat-templets (e.g., Winemiller and Rose 1992) are only appropriate for large-scale comparisons. Poikilotherms provide specific examples of circumstances which may call for either accelerated or retarded growth rates. These more proximate determinates of intrinsic growth rate should be incorporated into plant and homoiotherm studies. Recognition of the ecological importance of the growth-differentiation tradeoff is generally lacking in poikilotherm research.

## COMPARISONS ACROSS TAXA

One of the greatest strengths of life history theory is that its predictions can be applied across a broad range of taxa (e.g., Gadgil and Bossert 1970). What has emerged from the empirical examples described above are several frameworks for examining the evolution of growth rate, which in general apply to all organisms, although they have not all been considered within each taxa. These factors (Table 1) are not mutually exclusive; for example competition may select for rapid growth because it results in size-dependent mortality.

## COMPETITION

Large size is often advantageous in competitive interactions, and rapid growth allows an individual to achieve and maintain a size advantage. Evolution of rapid growth in response to competition is a successful strategy for plants (i.e., the "competitor" strategy of Grime and Hunt 1975). In plants, and probably sessile animals such as most bivalves (Petraitis 1995), rapid growth can provide an advantage in both scramble competition (e.g., for space) and interference competition (e.g., shading). However, for most animals rapid growth is probably only advantageous for interference competition (e.g., Hill et al. 1993), although a size-dependent niche shift may allow an animal to escape competition (Mittelbach 1984). Competition does not appear to

TABLE 1
*Summary of selection pressures on growth rate for plants, homoiotherms, and poikilotherms*

| Selection Pressure | Plants | Homoiotherms | Poikilotherms |
|---|---|---|---|
| **Competition** | | | |
| Fast growth | *Competitor* strategy | Nest parasites? | Sessile species, size-dependent niche shifts |
| **Disturbance-mortality** | | | |
| Fast growth | | | |
| Age-specific | *Ruderal* strategy | Nest predation, migration? | *Opportunist* strategy |
| | (minimum size to reproduce) | | migration, overwintering, stage-dependent niche shifts |
| Size-specific | Competition? | ? | *Periodic* strategy predation refugia, size-dependent niche shifts |
| **Nutrient stress** | | | |
| Slow growth | | | |
| Amount available | *Stress-tolerant* strategy | Frugivorous birds | *Equilibrium* strategy |
| Frequency of availability | ? | Pelagic sea birds | Fasting endurance |
| Other stresses | *Stress-tolerant* strategy | ? | ? |
| Fast growth | | | |
| Countergradient variation | ? | Length of growing season? | Length of growing season, competition |
| **Growth-differentiation** | Secondary metabolites | Altricial versus precocial | Muscle development in fish? |

Note: Question marks suggest categories that have only limited or circumstantial evidence. Categories with only question marks have not been considered for the group.

be important in the evolution of growth rates for homoiotherms. This is probably because both birds and mammals provide extensive care to their offspring while they are growing; the only direct competition they experience is with siblings. One instance in which interspecific competition may mimic sibling competition is in nest parasitism. Several species, including cuckoos, cowbirds, and widow-birds lay their eggs in the nests of other species who then often raise the young as their own (Welty and Baptista 1988). Widow-birds ar least are reported to grow faster than their adopted nest-mates (Welty and Baptista 1988).

### MORTALITY

The "ruderal" or "oportunistic" strategy associated with highly disturbed habitats is well documented among all groups of plants and animals. These organisms must complete their life cycle or get through vulnerable stages, such as the nestling stage of birds, as quickly as possible. What is really needed in these species is a rapid developmental rate. Rapid growth and a low degree of differentiation will only occur in this situation if they hap-

pen to be correlated with rapid development. Highly disturbed habitats may select for rapid growth directly in two situations: (1) if organisms must reach a minimum size in order to reproduce, and (2) if the mortality or damage caused by disturbance decreases with size. These situations are considered in more detail in the next two sections.

### TIME CONSTRAINTS: RAPID GROWTH AND ESCAPE FROM STAGE- OR AGE-SPECIFIC MORTALITY

Intraspecific comparisons, especially those for poikilotherms, suggest that rapid growth evolves when there is a need to reach a minimum size within a limited time. This situation is probably common in temperate zones where many organisms must reach a minimum size in order to overwinter successfully (Conover and Present 1990). Rapid growth also appears to be important for migratory animals, especially if migration is seasonal. Although there is strong evidence for this among fishes (Snyder 1991), little has been done with homoiotherms. Martin (1995) found that reproductive traits can be corre-

lated with migration in birds suggesting that growth rate may also be correlated. In support of this, Bjornhag (1979) found a weak correlation for faster growth rates among migratory species of birds. Whether nest predation is important in determining growth rates of birds (Case 1978) depends upon whether size has an effect on age at fledging.

### SIZE CONSTRAINTS: RAPID GROWTH AND ESCAPE FROM SIZE-SPECIFIC MORTALITY

When a minimum size must be reached before organisms can reproduce, then organisms found in habitats subject to high disturbance also must deal with time and size constraints. This may explain why "ruderal" organisms have evolved rapid growth (Grime 1979), even though rapid reproductive development is what should be selected for when death is imminent. In many circumstances there may not be a clear time constraint, as in seasonal activities. However, rapid growth should also evolve to minimize the amount of time an organism spends in a vulnerable size class. Thus rapid growth can be important for reaching size-determined competition refuges (Mittelbach 1984) and predation refuges (Reznick 1983; Spitze 1991). Whenever there is a time constraint on growth, intrinsic growth rates are likely to be rapid. This prediction should be easy to test experimentally with a wide variety of organisms.

### NUTRIENT AVAILABILITY

Nutrient stress seems to affect growth rate primarily through the tradeoff between rate of growth and efficiency of growth (Odum and Pinkerton 1955). This is not simply conversion efficiency (gram of organism made/gram of nutrient used), as the mass of organism created depends upon body composition. Slow growth allows organisms that experience nutrient stress to use what nutrients are available most efficiently (Chapin 1980; Winemiller and Rose 1992), and to survive longer periods between feeding (Gotthard et al. 1994). This tradeoff is implied in the growth rate/clutch size balance in birds (Lack 1968), and has been invoked to explain the slow growth of frugivorous and pelagic birds. Examples of stress-tolerant species also exist for lizards (Niewia-

rowski and Roosenburg 1993), frogs (Riha and Berven 1991), and snails (Baur and Raboud 1988). Poorter (1989; Poorter and Remkes 1990; Lambers and Poorter 1992) suggests that slow growth in plants may not in itself be adaptive, but merely a result of morphological traits (such as low leaf area or production of secondary metabolites) that *are* adaptations to nutrient stress. The morphological adaptations detailed in Lambers and Poorter (1992) are an important contribution to understanding growth rates in plants, but it is hard to see how the same argument would hold for animals that have similar growth strategies without morphological changes. Although morphological traits undoubtedly constrain growth rates, slow growth is probably advantageous in its own right because of physiological advantages such as increased efficiency of nutrient recycling (e.g., Hawkins et al. 1986).

### COUNTERGRADIENT VARIATION

Rapid growth may evolve to compensate for the phenotypic effects of environmental stress. This is called countergradient selection (Levins 1969) because the evolved response on growth counteracts environmental influences on phenotypic variation across a gradient, resulting in a reduction of environmental sensitivity, i.e., the reaction norm (Falconer 1990) (Figure 2). This has been documented in plants as well as poikilotherms (reviewed by Conover and Schultz 1995). Countergradient variation can only be detected in either common garden or reciprocal transplant experiments (Conover and Schultz 1995), which might make it difficult to demonstrate for homoiotherms, although there is no theoretical reason why it should not have occurred. Indeed, a likely example of countergradient variation in homoiotherms may have been found by Rhymer (1992) with respect to development rate in ducks. In a transplant experiment, she showed that, within a genotype, hatchlings raised in Canada fledged at a younger age than those raised in California. However, hatchlings derived from California fledged at a younger age than did those from Canada at both locations. Thus the phenotypic effect (slower development at the California site) is countered by the genetic differences (faster development in California strains).

Conover and Schultz (1995) describe countergradient variation as a negative covariance between the genotype and the environment. This contrasts with cogradient variation where the two have a positive covariance. In terms of growth rate evolution, the slow growth of stress-tolerant strategies is a good example of cogradient variation. However, a given ecological factor will not necessarily result in either cogradient or countergradient selection. There is at least one example in which both cogradient (Niewiarowski and Roosenburg 1993 and Sinervo and Adolph 1994) and countergradient variation (Ferguson and Talent 1993) seem to have occurred in response to nutrient stress in the same species, in this case, fence lizards. Which strategy evolves may simply depend upon the severity of the stress, with mild stress resulting in countergradient variation and severe stress resulting in cogradient variation. It may also depend upon phylogenetic constraints, or correlations with other environmental factors or other life history traits. If slow growth is an adaptation for dealing with stress, then other forces must be acting to maintain a faster growth rate despite the effects of stress when countergradient selection occurs. One likely hypothesis is that countergradient selection only occurs when there is a time constraint on growth such as a short growing season (e.g., Conover and Present 1990; Berven and Gill 1983).

## Growth-Differentiation Balance

The tradeoff between growth and differentiation appears to be universal for multicellular organisms. Cell division and enlargement contribute to an organism's growth rate, while cellular differentiation contributes to the development of mature function. Cellular differentiation can affect growth in two ways: by the level of differentiation an organism undergoes and by the rate at which differentiation occurs. In plants, most of the variation in differentiation seems to stem from levels (amount of secondary metabolites produced, number of thorns produced) rather than the rate at which this occurs (e.g., Herms and Mattson 1992). Because a fully differentiated state exists for animals, it may be more natural to think of rates rather than levels of differentiation (although Ricklefs usually discusses differentiation in birds in terms of degree of mature function). It is as yet unclear to what degree the level and rate of differentiation are independent in either plants or animals, and whether a distinction between the two will ultimately prove to be useful.

As an alternative to the growth-differentiation balance, Olson (1992; see also Hill 1992) suggests that growth patterns may relate to energy allocation rather than cellular differentiation. For example, in birds thermoregulation is an energy-demanding process. Because thermoregulation develops relatively late in altricial birds, they have more energy available for growth. The growth-differentiation hypothesis and the energy allocation hypothesis are not mutually exclusive (Ricklefs 1979a), but I know of no experiments that have attempted to determine the relative importance of each for growth rates.

Although the growth-differentiation tradeoff has received increasing attention (Herms and Mattson 1992; Ricklefs et al. 1994), current evidence remains largely correlative. It is hoped that explicit tests for the ecological importance of this tradeoff will be conducted. In order to test the balance between growth and differentiation, one must determine local selection pressures on both growth rate and differentiation. Unfortunately, it is rare for both factors to be considered in a single study. A good example of how to approach such a study is illustrated by Berven and Gill (1983), who examined developmental rate and size at metamorphosis in wood frogs (*Rana sylvatica*). In a low latitude population, size at metamorphosis was positively correlated with survival, but there was no correlation between length of larval period and survival. In a tundra population, there was no correlation between size at metamorphosis and survival, but length of larval period was negatively correlated with survival. Therefore, we might expect the low latitude population to grow rapidly at the expense of development and the tundra population to develop rapidly at the expense of growth. Under laboratory conditions, the tundra population had the faster development rate and metamorphosed at a smaller size, but it is difficult to tell from the data whether it had the slower growth rate predicted. Nonetheless, such intraspecific comparisons that

include fitness measures are necessary to determine the validity of an adaptive balance between growth and development.

The above hypotheses suggest that slow growth is adaptive for dealing with chronic stress, but that otherwise growth rate should always be maximized. However, the ability of most organisms to show compensatory growth after perturbation, as well as endocrine control of growth rates and feeding levels in animals, suggest that even under ideal conditions growth rates are rarely, if ever, at their physiological maximum (Calow 1982; Atchley 1984). Theoretical work has shown that predictions for optimal growth rate are accurate only if there is some survival cost for rapid growth (Ricklefs 1969; Case 1978; Sibly et al. 1985; Sibly and Calow 1986). The growth rate versus growth efficiency and cellular proliferation versus differentiation tradeoffs do not appear to be adequate for explaining all of the variation in growth rates seen across organisms. In addition, the existence of countergradient selection suggests that there are situations (e.g., annual migration) in which growth should be accelerated beyond what local stress conditions dictate, even if it comes at the expense of other functions. Thus there must be other tradeoffs with growth rate that have not been considered. The following section suggests some functions that may be sacrificed in situations where rapid growth is needed.

## TRADEOFFS WITH RAPID GROWTH

Energy and nutrients must be budgeted among numerous functions in an organism. Given a limited amount of resources, an increase in allocation for one function will decrease allocation for another. I have broadly categorized these functions as: growth, development, maintenance, repair, defense, reproduction, and behavior. Because energy and nutrients allocated to growth cannot be used for other functions, a tradeoff exists between allocation for rapid growth and for maintenance or defense. Following are a number of examples of such tradeoffs. Most of these studies were not designed specifically to address costs of rapid growth directly, however, so some caution must be taken in interpreting them.

## DEVELOPMENT

Aside from the tradeoff between growth rate and differentiation discussed above, development may also be compromised to increase growth by decreasing the "quality control" of a developmental program, thus increasing developmental error (Sibly and Calow 1986). Fluctuating asymmetry, random differences between the right and left half of bilaterally symmetrical traits, is often used as an inverse measure of developmental stability (Van Valen 1962; Leamy 1984). This is because a perfectly symmetrical organism is assumed to be the ideal for which a developmental program is striving (Polak and Trivers 1994). If rapid growth compromises the mechanisms controlling development, asymmetry should increase with intrinsic growth rate. Leamy and Atchley (1985) found that fluctuating asymmetry was significantly greater in a line of rats selected for rapid growth than in a control line. However, selection increases homozygosity, a factor that is also expected to increase fluctuating asymmetry (e.g., Leamy 1984; Leary et al. 1985; Polak and Trivers 1994). Leamy and Atchley also included a line of rats selected for slow growth in their study. This line should have had a similar degree of homozygosity as the rapid growth line, but actually showed a decrease in fluctuating asymmetry relative to the control line. Therefore, it appears that rapid growth, and not homozygosity, has increased developmental error in this case.

Occasionally developmental error can be seen on a gross scale. Serafin (1982) found that up to 25% of Greater Sandhill Cranes (*Grus canadensis tabida*) fed diets that allowed very rapid growth formed skeletal deformities in the wings and legs. It is difficult to determine the influence of diet in this study, but because the deformities did not follow patterns typical of either nutritional deficiency or imbalance, Serafin felt that the deformities were due to rapid growth. Moreover it was the fastest growing chicks in each treatment that developed disorders regardless of diet. Developmental errors due to disproportionate skeletal growth appear to be common in domestic animals selected for rapid growth (e.g., Riddell 1981; Yamasaki and Itakura 1988). The Sandhill Crane example is especially interesting because this is a wild population that shows

rapid growth at the expense of developmental stability.

Changes in body proportions owing to different growth rates among tissues may not always be pathological as in the previous example. Ricklefs and Marks (1985) reported that a line of Japanese quail selected for rapid growth had different body proportions than a control line, specifically shorter legs and wings (see also Riddell 1981). Kemp and Bertness (1984) found that the marine snail *Littorina littorea* was more globular when abundant resources allow rapid growth. In contrast, Boulding and Hay (1993) showed that a congeneric snail became more elongate with rapid growth, and that this effect had a heritable component. Although fitness effects correlated with changes in proportion have not been demonstrated in these systems, they are likely to exist for snails. Very round shells also have a large aperture, making them vulnerable to predators that reach into the shell. Snails with elongate shells are vulnerable to predators that crush the shell because this shape does not distribute crushing pressures as effectively as globular shells (DeWitt 1995).

The growth rates of some tissues are physiologically limited and total body growth may occur at the expense of these tissues. For example, the rate of calcium deposition during shell formation is limited in snails (Palmer 1981). However, body size obviously cannot exceed shell size. In order to maintain rapid shell formation, the shell must be thin in rapidly growing individuals, making these individuals vulnerable to predators (Boulding and Hay 1993). Not only do *Littorina littorea* become globular with rapid growth rates as described above, but they also have thinner shells (Kemp and Bertness 1984). Boulding and Hay (1993) showed that the *Littorina* sp. they studied also had thin shells with fast growth even though the change in shell shape was different from *Littorina littorea*. Vertebrates may be limited in rates of calcium deposition in skeletal elements. Leterrier and Nys (1991) compared tibial development in fast- and slow-growing strains of chickens. Ash per volume of bone was lower in fast-growing chicks, thus their bones were less dense than those of slow growing chicks. Hedhammar (1973) provides a phenotypic example of the same phenomenon. He compared growth rates of Great Dane litter mates fed either *ad libitum* or a restricted diet (two-thirds of *ad lib*.). The dogs fed *ad lib*. grew significantly faster than those on the restricted diet. In addition to developmental errors similar to those already described above for Sandhill Cranes, the *ad lib*. dogs had bones with a lower mineral content (i.e. density) than their siblings on the restricted diet.

## MAINTENANCE AND REPAIR

Maintenance costs are often assumed to be met before energy can be allocated to either growth or reproduction (e.g., Pandian 1987; Griffiths and Griffiths 1987; De Roos et al. 1992). However, processes associated with maintenance appear to be relatively plastic (e.g., Wieser 1991), and may be compromised when additional energy or materials are needed. Indeed, it is well known that maintenance may be compromised in favor of reproduction in many species of fish (Roff 1984; Calow 1985). The same may occur when rapid growth is needed. For example, rates of protein turnover decrease as growth rate increases (Hawkins 1991), probably because protein used for building new structures cannot be used to replace old protein. Reduced turnover causes the accumulation of proteins with errors, and compromises an organism's ability to adjust to environmental changes (Hawkins 1991). In addition, rapid growth requires increased reading of DNA which increases damage to DNA; accumulation of error in DNA has been implicated in the senescence of animals (Hart and Setlow 1974). Strains of rodents selected for rapid growth have shorter lifespans and greater tumor production than control strains, lending support to these ideas (Eklund and Bradford 1977; Kajiura and Rollo 1994). Bradford and Famula (1984) noted that the same strains have an unusual susceptibility to external parasites suggesting that they also have poorly developed immune systems (see below). In addition, Saunders et al. (1992) noted an increase in coronary lesions with rapid growth rate in Atlantic Salmon (*Salmo salar*). Age, diet, and maturation were rejected as factors leading to these arterial lesions, but no direct physiological connection between growth rate and development of coronary lesions was sug-

gested. These correlations suggest that rapid growth may compromise maintenance, but a clear relationship has not yet been determined.

One form of maintenance that has been examined extensively is heavy metal tolerance. Although it is well known that heavy metals reduce growth rates in both plants (reviewed in Macnair 1987) and animals (e.g., Posthuma 1990), the costs of tolerance to heavy metals have not been well explored. Wilson (1988) compared several genotypes of the plant *Agrostis capillaris* under common conditions. He found that those genotypes with the greatest heavy metal tolerance had the slowest growth rates when raised without metals present. In contrast, Shaw (1988) found that the most copper-tolerant genotypes of a moss (*Funaria hygrometrica*) also had the fastest growth rates regardless of metal concentration. Likewise, Posthuma et al. (1993) found a positive genetic correlation between cadmium tolerance and growth rate in a terrestrial invertebrate, the springtail (*Orchesella cincta*). Could this be a case of countergradient variation? Dey et al. (1993), working with Atlantic tomcod (*Microgadus tomcod*) from the Hudson River, provides an example of a vertebrate relating detoxification with growth rate. These fish showed an increase in the occurrence and severity of liver damage with growth rate.

### DEFENSE

Allocation towards defense has already been discussed with respect to antiherbivore secondary metabolites in plants. Many animals also produce chemical defenses, although they have received comparatively little attention (Berenbaum 1995). Smiley and Rank (1986) compared two populations of chrysomelid beetle that had different growth rates. In a reciprocal transplant, the fast-growing beetles suffered higher mortality than slow-growing beetles, largely from a higher susceptibility to predators. However, it is unclear whether the tradeoff between growth rate and protection from predation was due to differences in production of the antipredator compound salicylaldehyde, or due to differences in grouping behavior (another antipredator response) between the populations. While secondary metabolite production provides pro-

tection from predators, the immune system is responsible for defense against pathogens. An inverse relationship between growth rate and immunity is well known in aquaculture (Kirpichnikov et al. 1993), although this appears to be largely anecdotal. Smoker (1986) found that faster growing wild strains of chum salmon tended to be more susceptible to bacterial infection than slower growing strains, but his sample size was too small to provide statistically significant results. In plants, Bergelson (1994) showed significant fecundity costs of resistance to both aphids and downy mildew in two cultivars of lettuce. This fecundity cost appeared to be mediated by a reduced growth rate.

### REPRODUCTION

The tradeoff between growth and reproduction has been studied extensively (see Roff 1992; Stearns 1992). This has mainly been concerned with switching between growth and reproduction (e.g., Berglund 1991; Iwasa 1991; Kozlowski 1992; Reekie and Bazzaz 1992), in which case the tradeoff is time allocated towards growth versus reproduction, or demonstrating decreased growth following reproduction (e.g., Snow and Wigham 1989; Primack and Hall 1990), in which case the tradeoff is between size and reproduction. Rarely has a tradeoff between *growth rate*, especially juvenile growth rate, and reproduction been considered. If an increase in growth rate requires additional energy and materials, less energy would be available for reproduction. Juvenile growth rate could impact reproduction if organisms are not perfectly flexible in their ability to reallocate energy to reproduction (e.g., Reznick 1983). Reznick (1982) has shown that guppies from populations with fast growth tend to mature later and have a lower reproductive output than do those from populations with slower growth. However, the reproductive traits have also been interpreted as adaptive, and it is unclear if this is a tradeoff (see e.g., Reznick 1983), or if traits are simply correlated. Aarssen and Clauss (1992) showed that, although fecundity increases with size for all genotypes of the plant *Arabidopsis thaliana*, the rate of this increase varied among genotypes. Moreover, fecundity was negatively correlated with maximum plant size. If maximum

size depends upon growth rate, then there is a clear tradeoff between growth rate and fecundity. Unfortunately, their procedure does not allow growth rate to be estimated for each genotype, so the negative correlation may be an artifact of differences in switching time. Nonetheless, the differences in slope in the size / fecundity relationship suggests that there is at least potential for tradeoffs with growth rate. Finally, among domestic animals, selection for rapid growth in turkey (Anthony et al. 1991) and quail (Peebles and Marks 1991) has resulted in decreased lifetime fecundity. Reduced fecundity is also common among transgenic animals that have had genes inserted that increase growth rate (Lachmansingh and Rollo 1994).

## BEHAVIOR

Movement has a high energetic cost, and animals that are growing rapidly may reduce levels of activity (e.g., Wieser et al. 1988). However, increased movement may result in increased access to resources resulting in positive correlations between activity and growth rate. One way to get around this confound is with transgenic organisms. "Supermice" contain multiple copies of rat growth hormone genes and grow twice as fast as untransformed mice. But because this increased growth rate is achieved with a slightly lower mass-specific feeding rate (Kajiura and Rollo 1994), tradeoffs should be apparent. Supermice make up for the energetic cost of rapid growth by spending significantly more time asleep and are less active when awake than wildtype siblings (Lachmansingh and Rollo 1994).

Clearly, there are many functions that may be compromised when intrinsic growth rates are accelerated to meet evolutionary challenges. Conversely, if selection is acting to improve any of these functions, intrinsic growth rates may be retarded. Many of the costs of rapid growth have been poorly explored with respect to their adaptive ramifications. Indeed, most of the studies cited earlier were not specifically concerned with intrinsic growth rates, but simply reported them as correlated effects. Attention to the tradeoffs discussed earlier may help explain much of the variation in growth rate that exists among organisms beyond what can be attributed to stress and disturbance gradients, and may help explain how high disturbance strategies achieve rapid development and rapid growth at the same time.

## CONCLUSIONS

This review has endeavored to examine a diffuse literature where communication has been lacking. Several general factors have emerged. First, rapid growth seems to be favored under conditions of low environmental stress, especially if mortality and/or competition are size-dependent. Rapid growth is also favored when there are time constraints for reaching a minimum size. As environmental stress increases, growth rates decrease in order to increase the efficiency of resource use, either directly or indirectly (Lambers and Poorter 1992). Second, differentiation appears to be in conflict with rapid growth. Ecological conditions may favor one over the other. In plants, as herbivory becomes relatively more important, rapid differentiation is favored. In animals, rapid growth may be favored when predation is size dependent, but differentiation may be favored when mobility decreases predation pressure (i.e., precocial versus altricial birds). Countergradient variation is at odds with stress tolerance, suggesting that rapid growth may evolve in spite of stress.

Although tradeoffs with respect to growth rate are often assumed (Case 1978; Sibly et al. 1985), there are few clear examples of the costs of rapid growth (Gotthard et al. 1994). I have detailed several likely examples, but rarely were costs to growth rate (or the reverse) the subject of the study. It is often difficult to show tradeoffs among traits in general (see Stearns 1992 for an overview), but it is vital to do so, as such tradeoffs form the basis of all life history theory. The nature of these tradeoffs, what they are and under what ecological circumstances they occur, is necessary for understanding and testing life history theory in general, and the ecological importance of the growth-differentiation balance in particular.

I suggest moving away from the use of habitat-templets. Although this has proven useful for identifying life history tactics in higher taxa, they do not appear to be useful for understanding evolution at an intraspecific level (Stearns 1980). This is made especially obvi-

ous when we recognize countergradient variation. Moreover, habitat-templets are not useful in determining what causes certain growth rates to evolve (Stearns 1976). Rather, we should look at the specific selective forces that give rise to a given growth rate. Since growth rate is simply the increase in size per unit time, the two most important parameters should be size and time. To understand why specific growth rates evolve we must understand what functions tradeoff with growth rate, and how they interact under a given selective regime, that is, with respect to size and time constraints.

## REFERENCES

Aarssen L W, Taylor D R. 1992. Fecundity allocation in herbaceous plants. *Oikos* 65:225-232.

Aarssen L W, Clauss M J. 1992. Genotypic variation in fecundity allocation in *Arabidopsis thaliana*. *Journal of Ecology* 80:109-114.

Anthony N B, Emmerson D A, Nestor K E. 1991. Genetics of growth and reproduction in the turkey. 12. Results of long-term selection for increased 180-day egg production. *Poultry Science* 70:1314-1322.

Aronson J, Kigel J, Shmida A, Klein J. 1992. Adaptive phenology of desert and mediterranean populations of annual plants grown with and without water stress. *Oecologia* 89:17-26.

Atchley W R. 1984. Ontogeny, timing of development, and genetic variance-covariance structure. *The American Naturalist* 123:519-540.

Atkinson C J, Farrar J F. 1983. Allocation of photosynthetically-fixed carbon in *Festuca ovina* L. and *Nardus stricta* L. *New Phytologist* 95:519-531.

Ayres M P, Scriber J M. 1994. Local adaptation to regional climates in Papilio canadensis (Lepidoptera: Papilionidae). *Ecological Monographs* 64: 465-482.

Bassett J E. 1984. Litter size and postnatal growth rates in the Pallid bat, *Antrozous pallidus*. *Journal of Mammalogy* 65:317-319.

Baur B, Raboud C. 1988. LIfe history of the land snail *Arianta arbustorum* along an altitudinal gradient. *Journal of Animal Ecology* 57:71-87.

Belk M C, Hales, L S, Jr. 1993. Predation-induced differences in growth and reproduction of bluegills (*Lepomis macrochirus*). *Copeia* 4:1034-1044.

Berenbaum M R. 1995. The chemistry of defense: Theory and practice. *Proceedings of the National Academy of Sciences* 92:2-8.

Bergelson J. 1994. The effects of genotype and the environment on costs of resistance in lettuce. *The American Naturalist* 143:349-359.

Berglund A. 1991. Egg competition in a sex-role reversed pipefish: subdominant females trade reproduction for growth. *Evolution* 45:770-774.

Berven K A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica* II. an experimental analysis of larval development. *Oecologia* 52:360-369.

Berven K A, Gill D E. 1983. Interpreting geographic variations in life-history traits. *American Zoologist* 23:85-97.

Bjornhag G. 1979. Growth in newly hatched birds. *Swedish Journal of Agricultural Research* 9:121-125.

Boulding E G, Hay T K. 1993. Quantitative genetics of shell form of an intertidal snail: constraints on short-term response to selection. *Evolution* 47:576-592.

Bradford G E, Famula T R. 1984. Evidence for a major gene for rapid postweaning growth in mice. *Genetical Research* 44:293-308.

Bryant D M, Hails C J. 1983. Energetics and growth patterns of three tropical bird species. *The Auk* 100: 425-439.

Burnett C D, Kunz T H. 1982. Growth rates and age estimation in *Eptesicus fuscus* and comparison with *Myotis lucifugus*. *Journal of Mammalogy* 63: 33-41.

Calow P. 1982. Homeostasis and fitness. *American Naturalist* 120:416-419.

Calow P. 1985. Adaptive aspects of energy allocation. In P Tytler, P. Calow, editors. *Fish Energetics: new perspectives*. Baltimore: The Johns Hopkins University Press. pp 13-31.

Cameron I L, Jeter J R. 1971. Relationship between cell proliferation and cytodifferentiation in embryonic chick tissues. In I L Cameron et al., editors. *Developmental Aspects of the Cell Cycle*. New York: Academic Press. pp 191-222.

Carrier D, Leon L R. 1990. Skeletal growth and function in the California gull (*Larus californicus*). *Journal of Zoology* 222:375-389.

Case T J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology* 53:243-282.

Chapin F S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233-260.

Chapin F S. 1991. Integrated responses of plants to stress. *BioScience* 41:29-36.

Chapin F S, Follett J M, O'Connor K F. 1982. Growth, phosphate absorption, and phosphorus fractions in two *Chionochloa* species. *Journal of Ecology* 70:305-321.

Chapin F S, Autumn K, Pugnaire F. 1993. Evolution of suites of traits in response to environmental stress. *American Naturalist* 142:S78-S92.

Chaplin S B, Chaplin S J. 1981. Comparative growth energetics of a migratory and nonmigratory insect: the milkweed bugs. *Journal of Animal Ecology* 50:407-420.

Charnov E L. 1993. *Life History Invariants*. Oxford: Oxford University Press.

Chaurand T, Weimerskirch H. 1994. The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *Journal of Animal Ecology* 63:275-282.

Clarke A. 1983. Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanography and Marine Biology, an Annual Review* 21:341-453.

Clauss M J, Aarssen L W. 1994. Phenotypic plasticity of size-fecundity relationships in *Arabidopsis thaliana*. *Journal of Ecology* 82:447-455.

Coley P D, Bryant J P, Chapin F S. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895-899.

Coley P D. 1987. Interspecific variation in plant antiherbivore properties: the role of habitat quality and rate of disturbance. *New Phytologist* 106:251-263.

Conover D A, Present T M C. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* 83:316-324.

Conover D O, Schultz E T. 1995. Phenotypic similarity and the evolutionary significance of countergradient selection. *TREE* 10:248-252.

Conover D O, Schultz E T. 1997. Natural selection and the evolution of growth rate in the early life history: what are the trade-offs? In R C Chambers, E A Trippel, editors. *Early Life History and Recruitment in Fish Populations*. New York: Chapman Hall. In press.

Crowder L B, Crawford H L. 1984. Ecological shifts in resource use by bloaters in Lake Michigan. *Transactions of the American Fisheries Society* 113:694-700.

Crowl T A, Covich A P. 1990. Predator induced life-history shifts in a freshwater snail. *Science* 247:949-951.

De Roos A M, Diekmann O, Metz J A J. 1992. Studying the dynamics of structured population models: a versatile technique and its application to Daphnia. *American Naturalist* 139:123-147.

Dewitt T J. 1995. Functional tradeoffs and phenotypic plasticity in the freshwater snail physa. [PhD thesis]. State University of New York, Binghamton,

Dey W P, Peck T H, Smith C E, Kreamer G-L. 1993. Epizoology of hepatic neoplasia in Atlantic Tomcod (*Microgadus tomcod*) from the Hudson River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1897-1907.

Dijkstra P, Lambers H. 1989. A physiological analysis of genetic variation in relative growth rate within *Plantago major* L. *Functional Ecology* 3:577-587.

Ebenman B. 1992. Evolution in organisms that change their niches during the life cycle. *American Naturalist* 139:990-1021.

Eklund J, Bradford G E. 1977. Longevity and lifetime body weight in mice selected for rapid growth. *Nature* 265:48-49.

Elberse W T, Berendse F. 1993. A comparative study of the growth and morphology of eight grass species from habitats with different nutrient availabilities. *Functional Ecology* 7:223-229.

Elliott J M. 1989. Growth and size variation in contrasting populations of trout *Salmo trutta*: an experimental study on the role of natural selection. *Journal of Animal Ecology* 58:45-58.

Falconer D S. 1990. Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance. *Genetical Research* 56:57-70.

Ferguson G W, Talent L G. 1993. Life-history traits of the lizard *Sceloporus undulatus* from two populations raised in a common laboratory environment. *Oecologia* 93:88-94.

Ferron J, Ouellet J P. 1991. Physical and behavioral postnatal development of woodchucks (*Marmota monax*). *Canadian Journal of Zoology* 69:1040-1047.

Gadgil M, Bossert W H. 1970. Life historical consequences of natural selection. *American Naturalist* 104:1-24.

Garnett M C. 1981. Body size, its heritability and influence on juvenile survival among great tits, *Parus major. International Journal of the British Ornithologist's Union 1*23:31-41.

Gjerde B. 1986. Growth and reproduction in fish and shellfish. *Aquaculture* 57:37-55.

Gotthard K, Nylin S, Wiklund C. 1994. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia* 99:281-289.

Grand T I. 1992. Altricial and precocial mammals: a model of neural and muscular development. *Zoo Biology* 11:3-15.

Griffiths C L, Griffiths R J. 1987. Bivalvia. In T Pandian, et al., editors. *Animal Energetics: Bivalvia through Reptilia*. New York: Academic Press, pp 2-89.

Grime J P, Hunt R. 1975. Relative growth rate: its range and adaptive significance in a local flora. *Journal of Ecology* 63:393-422.

Grime J P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169-1194.

Grime J P. 1979. *Plant Strategies and Vegetation Processes*. New York: John Wiley & Sons.

Gross K L. 1981. Predictions of fate from rosette size in four "biennial" plant species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. *Oecologia* 48:209-213.

Grubb P J. 1992. A positive distrust in simplicity—lessons from plant defences and from competition among plants and among animals. *Journal of Ecology* 80:585-610.

Grulke N E, Bliss L C. 1988. Comparative life history characteristics of two high arctic grasses, Northwest territories. *Ecology* 69:484-496.

Hambright K D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120:500-508.

Hart R W, Setlow R B. 1974. Correlation between deoxyribonucleic acid excision-repair and lifespan in a number of mammalian species. *Proceedings of the National Academy of Science, USA* 71:2169-2173.

Hawkins A J, Bayne B L, Day A J. 1986. Protein turnover, physiological energetics and heterozygosity in the blue mussel, *Mytilus edulis*: the basis of variable age-specific growth. *Proceedings of the Royal Society of London B* 229:161-176.

Hawkins A J S. 1991. Protein turnover: a functional appraisal. *Functional Ecology* 5:222-233.

Heath D D, Bernier N J, Heath J W, Iwama G K. 1993. Genetic, environmental, and interactions on growth an distress response of Chinook salmon (*Oncorhynchus tshawytscha*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* 50:435-442.

Hedhammar A A. 1973. Overnutrition and skeletal development: an experimental study in Great Dane dogs. [MSc thesis]. Cornell University, Ithaca.

Herms D A, Mattson W J. 1992. The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67:283-335.

Hill R W. 1992. The altricial/precocial contrast in the thermal relations and energetics of small mammals. In T E Thomas, T H Horton, editors. *Mammalian Energetics*. Ithaca: Comstock. pp 122-157.

Hill A M, Sinars D, M., Lodge D M. 1993. Invasion of an occupied niche by the crayfish *Orconectes rusticus*: potential importance of growth and mortality. *Oecologia* 94:303-306.

Hunter J R. 1981. Feeding ecology and predation of marine fish larvae. In R Lasker editor. *Marine Fish Larvae: Morphology, Ecology, and Relation to Fisheries*. Seattle: Washington Sea Grant Program. pp 33-79.

Iwasa Y. 1991. Pessimistic plant: optimal growth schedule in stochastic environments. *Theoretical Population Biology* 40:246-268.

Janz N, Nylin S, Wedell N. 1994. Host plant utilization in the comma butterfly: sources of variation and evolutionary implications. *Oecologia* 99:132-140.

de Jong T J. 1995. Why fast growing plants do not bother about defence. *Oikos* 74:545-548.

Kajiura L, Rollo C D. 1994. A mass budget for transgenic "Supermice" engineered with extra rat growth hormone genes: evidence for energetic limitation. *Canadian Journal of Zoology* 72:1010-1017.

Kemp P, Bertness M D. 1984. Snail shape and growth rates: evidence for plastic shell allometry in *Littorina littorea*. *Proceedings of the National Academy of Science, USA* 81:811-813.

Kirpichnikov V S, Ilyasov J I, Shart L A, Vikhman A A, Ganchenko M V, Ostashevsky A L, Simonov V M, Tikhonov G F, Tjurin V V. 1993. Selection of Krasnodar common carp (*Cyprinus carpio* L.) for resistance to dropsy: principal results and prospects. *Aquaculture* 111:7-20.

Klassen M, Drent R. 1991. An analysis of hatchling resting metabolism: in search of ecological correlates that explain deviations from allometric relations. *Condor* 93:612-629.

Korner C, Menendez-Riedl S P. 1989. The significance of developmental aspects in plant growth analysis. In H Lambers, et al., editors. *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants*. The Hague, The Netherlands: SPB Academic. pp 141-157.

Kozlowski J. 1992. Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *TREE* 7:15-19.

Lachmansingh E, Rollo C D. 1994. Evidence for a trade-off between growth and behavioural activity in giant "Supermice" genetically engineered with extra growth hormone genes. *Canadian Journal of Zoology* 72:2158-2168.

Lack D A. 1968. *Ecological Adaptations of Breeding in Birds*. London: Methuen.

Lambers H, Poorter H. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* 23:187-261.

Langham N P. 1983. Growth strategies in marine terns. *Studies in Avian Biology* 8:73-83.

Law B S. 1991. Ontogenetic habitat shift in the Eastern Australian water skink (*Eulamprus quoyii*)? *Copeia* 1992:1117-1120.

Leamy L. 1984. Morphometric studies in inbred and hybrid house mice. V. directional and fluctuating asymmetry. *American Naturalist* 123:579-593.

Leamy L, Atchley W. 1985. Directional selection and developmental stability: evidence from fluctuating asymmetry of morphometric characters in rats. *Growth* 49:8-18.

Leary R F, Allendorf F W, Knudsen K L. 1985. Inheritance of meristic variation and the evolution of developmental stability in rainbow trout. *Evolution* 39:308-314.

Lerdau M, Litvak M, Monson R. 1994. Plant chemical defense: monoterpenes and the growth-differentiation balance hypothesis. *TREE* 9:58-61.

Leterrier C, Nys Y. 1992. Composition, cortical structure and mechanical properties of chicken tibiotarsi: effects of growth rate. *British Poultry Science* 33:925-939.

Levins R. 1969. Thermal acclimation and heat resistance in Drosophila species. *American Naturalist* 103:483-499.

Levinton J S. 1983. The latitudinal compensation hypothesis: growth data and a model of latitudinal growth differentiation based upon energy budgets. I. interspecific comparison of Ophryotrocha (Polychaeta: Dorvilleidae). *Biological Bulletin* 165:686-698.

Lonsdale D J, Levinton J S. 1985. Latitudinal differentiation in copepod growth: an adaptation to temperature. *Ecology* 66:1397-1407.

Loomis W E. 1932. Growth-differentiation balance vs. carbohydrate-nitrogen ratio. *Proceedings of the American Society of Horticultural Sciences* 29:240-245.

Lynch M, Arnold S J. 1988. The measurement of selection on size and growth. In B Ebenman, L Persson, editors. *Size-Structured Populations*. Berlin: Springer-Verlag. pp 47-59.

Lyndon R F. 1990. *Plant Development: the Cellular Basis*. London: Unwin Hyman.

MacArthur R H, Wilson E O. 1967. *The Theory of Island Biogeography*. Princeton: Princeton University Press.

Macdonald B A, Thompson R J. 1988. Intraspecific variation in growth and reproduction in latitudinally differentiated populations of the giant scallop *Placopecten magellanicus* (Gmelin). *Biological Bulletin* 175:361-371.

Macnair M R. 1987. Heavy metal tolerance in plants: a model evolutionary system. *TREE* 2:354-359.

Martin T E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* 18:453-487.

Martin T E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141:897-913.

Martin T. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101-127.

Martin T E, Li P. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73:579-592.

McClure P A, Randolph J C. 1980. Relative allocation of energy to growth and development of homeothermy in the eastern wood rat (*Neotoma floridana*) and hispid cotton rat (*Sigmodon hispidus*). *Ecological Monographs* 50:199-219.

McGraw J B, Wulff R D. 1983. The study of plant growth: a link between the physiological ecology and population biology of plants. *Journal of Theoretical Biology* 103:21-28.

McGraw J B, Chapin F S. 1989. Competitive ability and adaptation to fertile and infertile soils in two Eriophorum species. *Ecology* 70:736-749.

Meyer-Rochow V B, Ingram J R. 1993. Red-white muscle distribution and fibre growth dynamics: a comparison between lacustrine and riverine populations of the Southern smelt *Retropinna retropinna* Richardson. *Proceedings of the Royal Society of London, B* 252:85-92.

Millar J S, Hickling G J. 1990. Fasting endurance and the evolution of mammalian body size. *Functional Ecology* 4:5-12.

Mittelbach G G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology* 65:499-513.

Mowatt J, Myerscough P J. 1983. Ecological differentiation between species of Scribbly gum [Eucalyptus informal subseries Haemastominae (MATK) Pryor & Johnson] and Angophora in seedling responsiveness to mineral nutrients. *Australian Journal of Botany* 31:645-656.

Neal B R. 1990. Observations on the early post-natal growth and development of *Tatera leucogaster*, *Aethomys chrysophilus* and *A. namaquensis* from Zimbabwe, with a review of the pre- and post-natal growth and development of African Muroid rodents. *Mammalia* 54:245-270.

Neat F, Fowler K, French K, Partridge L. 1995. Thermal evolution of growth efficiency in *Drosophila melanogaster*. *Proceedings of the Royal Society of London, B* 260:73-78.

Niewiarowski P H, Roosenburg W. 1993. Reciprocal transplant reveals sources of variation in growth rates of the lizard *Sceloporus undulatus*. *Ecology* 74:1992-2002.

Niklas K J. 1994. Size-dependent variations in plant growth rates and the "3/4-power rule". *American Journal of Botany* 81:134-144.

Nur N. 1984a. Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. *Oecologia* 65:125-137.

Nur N. 1984b. The consequences of brood size for breeding blue tits I. adult survival, weight change and the cost of reproduction. *Journal of Animal Ecology* 53:479-496.

Odum H T, Pinkerton R C. 1955. Time's speed regulator: the optimum efficiency for maximum power output in physical and biological systems. *American Scientist* 43:331-343.

Olson J M. 1992. Growth, the development of endothermy, and the allocation of energy in Red-winged Blackbirds (*Agelaius phoeniceus*) during the nestling period. *Physiological Zoology* 65:124-152.

Oniki Y, Ricklefs R E. 1981. More growth rates of birds in the humid new world tropics. *International Journal of the British Ornithologists' Union* 123:349-354.

Osenberg C W, Werner E E, Mittelbach G G, Hall D J. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. *Canadian Journal of Fisheries and Aquatic Sciences* 45:17-26.

Osmond C B, Austin M P, Berry J A, Billings W D, Boyer J S, Dacey J W H, Nobel P S, Smith S D, Winner W E. 1987. Stress physiology and the distributions of plants. *BioScience* 37:38-48.

Palmer A R. 1981. Do carbonate skeletons limit the rate of body growth? *Nature* 292:150-152.

Pandian T J. 1987. Fish. In T J Pandian, F J Vernberg, editors. *Animal Energetics: Bivalvia trhough Reptilia*. New York: Academic Press. pp 358-467.

Parrish J A D, Bazzaz F A. 1985. Ontogenetic shifts in old-field annuals. *Ecology* 66:1296-1302.

Partridge L, Barrie B, Fowler K, French V. 1994. Evolution and development of body size and cell size in *Drosophila melanogaster* in response to temperature. *Evolution* 48:1269-1276.

Peebles E D, Marks H L. 1991. Effects of selection for growth and selection diet on eggshell quality and embryonic development in Japanese quail. *Poultry Science* 70:1474-1480.

Persson L, Greenberg L A. 1990. Juvenile competitive bottlenecks: the perch (*Perca fluvatilis*)-roach (*Rutilus rutilus*) interaction. *Ecology* 71:44-56.

Peters R H. 1983. *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.

Petraitis P S. 1995. The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). *Ecology* 76:1337-1346.

Polak M, Trivers R. 1994. The science of symmetry in biology. *TREE* 9:122-124.

Polis G A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *American Naturalist* 123:541564.

Poorter H. 1989. Interspecific variation in relative growth rate: on ecological causes and physiological consequences. In H Lambers, et al., editors. *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants*. The Hague, The Netherlands: SPB Academic. pp 45-68.

Poorter H, Remkes C. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83:553-559.

Posthuma L. 1990. Genetic differentiation between populations of *Orchesella cincta* (Collembola) from heavy metal contaminated sites. *Journal of Applied Ecology* 27:609-622.

Posthuma L, Hogervorst R F, Joosse E N G, Van Straalen N M. 1993. Genetic variation and co-variation for characteristics associated with cadmium tolerance in natural populations of the springtail *Orchesella cincta* (L.). *Evolution* 47:619-631.

Priede I G. 1985. Metabolic scope in fishes. In P Tytler, P Calow, editors. *Fish Energetics: New Perspectives*. Baltimore: The Johns Hopkins University Press. pp 33-66.

Primack R B, Hall P. 1990. Costs of reproduction in the pink lady's slipper orchid: a four-year experimental study. *American Naturalist* 136:638-656.

Redfern C P F. 1994. Variation in the developmental timing of flight-feather growth in nestling birds. *International Journal of the British Ornithologists' Union* 136:72-78.

Reekie E G, Bazzaz F A. 1992. Cost of reproduction as reduced growth in genotypes of two congeneric species with contrasting life histories. *Oecologia* 90:21-26.

Reimchen T E. 1991. Trout foraging failures and the evolution of body size in stickleback. *Copeia* 1991:1098-1104.

Reznick D. 1982. Genetic determination of offspring size in the guppy (*Poecilia reticulata*). *American Naturalist* 120:181-188.

Reznick D. 1983. The structure of guppy life histories: the tradeoff between growth and reproduction. *Ecology* 64:862-873.

Rhymer J M. 1992. An experimental study of geographic variation in avian growth and development. *Journal of Evolutionary Biology* 5:289-306.

Ricklefs R E. 1969. Preliminary models for growth rates in altricial birds. *Ecology* 50:1031-1039.

Ricklefs R E. 1973. Patterns of growth in birds. II. growth rate and mode of development. *International Journal of the British Ornithologists' Union* 115:177-201.

Ricklefs R E. 1976. Growth rates of birds in the humid new world tropics. *International Journal of the British Ornithologists' Union* 118:179-207.

Ricklefs R E. 1979a. Adaptation, constraint, and compromise in avian postnatal development. *Biological Reviews* 54:269-290.

Ricklefs R E. 1979b. Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern , and Japanese Quail. *The Auk* 96:10-30.

Ricklefs R E. 1992. The roles of parent and chick in determining feeding rates in Leach's stormpetrel. *Animal Behaviour* 43:895-906.

Ricklefs R E, Marks H L. 1985. Anatomical response to selection for four-week body mass in Japanese quail. *Auk* 102:323-333.

Ricklefs R E, Webb T. 1985. Water content, thermogenesis, and growth rate of skeletal muscles in the European starling. *Auk* 102:369-376.

Ricklefs R E, Shea R E, Choi I-H. 1994. Inverse relationship between functional maturity and exponential growth rate of avian skeletal muscle: a constraint on evolutionary response. *Evolution* 48:1080-1088.

Riddell C. 1981. Skeletal deformities in poultry. *Advances in Veterinary Science and Comparative Medicine* 25:277-310.

Riha V F, Berven K A. 1991. An analysis of latitudinal variation in the larval development of the Wood Frog (*Rana sylvatica*). *Copeia* 1991:209-221.

Robertson H A. 1988. Interspecific variation in growth of British pigeons Columbidae. *International Journal of the British Ornithologists' Union* 130:261-267.

Roff D A. 1984. The evolution of life history parameters in teleosts. *Canadian Journal of Aquatic Sciences* 41:989-1000.

Roff D A. 1988. The evolution of migration and some life history parameters in marine fishes. *Environmental Biology of Fishes* 22:133-146.

Roff D A. 1991. Life history consequences of bioenergetic and biomechanical constraints on migration. *American Zoologist* 31:205-215.

Roff D A. 1992. *The Evolution of Life Histories: Theory and Analysis*. New York: Chapman & Hall.

Sacher G A, Staffeldt E F. 1974. Relation of gestation time to brain weight for placental mammals: Implications for the theory of vertebrate growth. *American Naturalist* 108:593-615.

Saunders R L, Farrell A P, Knox D E. 1992. Progression of coronary arterial lesions in Atlantic salmon (*Salmo salar*) as a function of growth rate. *Canadian Journal of Fisheries and Aquatic Sciences* 49:878-884.

Schael D M, Rudstam L G, Post J R. 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). *Canadian Journal of Fisheries and Aquatic Sciences* 48:1919-1925.

Serafin J A. 1982. The influence of diet composition upon growth and development of Sandhill cranes. *Condor* 84:427-434.

Shaver G R, Melillo J M. 1984. Nutrient budgets of marsh plants: efficiency concepts and relation to availability. *Ecology* 65:1491-1510.

Shaw J. 1988. Genetic variation for tolerance to copper and zinc within and among populations of the moss, *Funaria hygrometrica* Hedw. *New Phytologist* 109:211-222.

Shine R. 1988. The evolution of large body size in females: a critique of Darwin's "fecundity advantage" model. *American Naturalist* 131:124-131.

Sibly R, Calow P. 1985. Classification of habitats by selection pressures: a synthesis of life-cycle and r/K theory. In R Sibly, R H Smith, editors. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*. Oxford: Blackwell Scientific. pp 75-90.

Sibly R, Calow P, Nichols N. 1985. Are patterns of growth adaptive? *Journal of Theoretical Biology* 112:553-574.

Sibly R, Calow P. 1986. *Physiological Ecology of Animals: An Evolutionary Approach*. Boston: Blackwell Scientific.

Sinervo B, Adolph S C. 1994. Growth plasticity and thermal opportunity in *Sceloporus* lizards. *Ecology* 75:776-790.

Smiley J T, Rank N E. 1986. Predator protection versus rapid growth in a montane leaf beetle. *Oecologia* 70:106-112.

Smith C C. 1976. When and how much to reproduce: the trade-off between power and efficiency. *American Zoologist* 16:763-774.

Smoker W W. 1986. Variability of embryo development rate, fry growth, and disease susceptibility in hatchery stocks of chum salmon. *Aquaculture* 57:219-226.

Snow A A, Whigham D F. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). *Ecology* 70:1286-1293.

Snyder R J. 1991. Migration and life histories of the threespine stickleback: evidence for adaptive variation in growth rate between populations. *Environmental Biology of Fishes* 31:381-388.

Southwood T R E. 1988. Tactics, strategies and templets. *Oikos* 52:3-18.

Spitze K. 1991. *Chaoborus* predation and life-history evolution in *Daphnia pulex*: temporal pattern of population diversity, fitness, and mean life history. *Evolution* 45:82-92.

Stearns S C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51:3-47.

Stearns S C. 1980. A new view of life-history evolution. *Oikos* 35:266-281.

Stearns S C. 1983. A natural experiment in life-history evolution: field data on the introduction of mosquitofish (*Gambusia affinis*) to Hawaii. *Evolution* 37:601-617.

Stearns S C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Tarburton M K. 1987. An experimental manipulation of clutch and brood size of white-rumped swiftlets *Aerodramus spodiopygius* of Fiji. *Internationl Journal of the British Ornithologists' Union* 129:107-114.

Taylor D R, Aarson L W, Loehle C. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* 58:239-250.

Thompson D W. 1942. *On Growth and Form.* [Abridged Edition 1992]. Cambridge: University Press.

Trevelyan R, Read A F. 1989. Nest predation and the evolution of avian reproductive strategies: a comparison of Australian and New Zealand birds. *Oecologia* 81:274-278.

Tuomi J. 1992. Toward integration of plant defence theories. *TREE* 7:365-367.

van der Meijden E, van der Waals-Kooi R E. 1979. The population ecology of *Senecio jacobaea* in a sand dune system. *Journal of Ecology* 67:131-153.

van der Meijden E, Wijn M, Verkaar H J. 1988. Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51:355-363.

Van Heezik Y, Davis L. 1990. Effects of food variability on growth rates, fledging sizes and reproductive success in the Yellow-eyed Penguin *Megadyptes anitpodes*. *International Journal of the British Ornithologists' Union* 132:354-365.

Van Valen L. 1962. A study of fluctuating asymmetry. *Evolution* 16:125-142.

Videler J J. 1993. *Fish Swimming*. New York: Chapman & Hall.

Weatherley A H, Gill H S. 1987. *The Biology of Fish Growth*. London: Academic Press.

Weatherley A H, Gill H S, Lobo A F. 1988. Recruitment and maximal diameter of axial fibres in teleosts and their relationship to somatic growth and ultimate size. *Journal of Fish Biology* 33:851-859.

Webb D R, McClure P A. 1989. Development of heat production in altricial and precocial rodents: implications for the energy allocation hypothesis. *Physiological Zoology* 62:1293-1315.

Welty J C, Baptista L. 1988. *The Life of Birds*. Fourth Edition. New York: Saunders College Publishing.

Werner E E. 1988. Size, scaling, and the evolution of complex life cycles. In B Ebenman, L Persson, editors. *Size-Structured Populations*. Berlin: Springer-Verlag. pp 60-81.

Wieser W. 1991. Limitations of energy acquisition and energy use in small poikliotherms: evolutionary implications. *Functional Ecology* 5:234-240.

Wieser W, Forstner H, Medgyesy N, Hinterleitner S. 1988. To switch or not to switch: partitioning of energy between growth and activity in larval cyprinids (Cyprinidae: Teleostei). *Functional Ecology* 2:499-507.

Wilson J B. 1988. The cost of heavy-metal tolerance: an example. *Evolution* 42:408-413.

Winemiller K O, Rose K A. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Science* 49:2196-2218.

Wood C C, Foote C J. 1990. Genetic differences in the early development and growth of sympatric sockeye salmon and kokanee (*Oncorhynchus nerka*), and their hybrids. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2250-2260.

Wroot A J, Wroot S A., Murie, J O. 1987. Intraspecific variation in postnatal growth of Columbian ground squirrels (*Spermophilus columbianus*). *Journal of Mammalogy* 68:395-398.

Yamasaki K, Itakura C. 1988. Bone lesions in clinically normal and in lame pigs. *Journal of Comparative Pathology* 98:415-432.

Ydenberg R C. 1989. Growth-mortality trade-offs and the evolution of juvenile life histories in Alcidae. *Ecology* 70:1494-1506.

Young T P. 1985. *Lobelia telekii* herbivory, mortality, and size at reproduction: variation with growth rate. *Ecology* 66:1879-1883.