

14 Causes of Growth Variation and Its Consequences for Fitness

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14.1. Introduction

The notion of fitness is central to evolutionary theory because (Darwinian) fitness of an individual or a particular genotype is defined as the contribution of that individual or genotype to the next generation (Falconer 1981). Patterns of avian growth are highly variable within species and populations, and therefore the question arises of what consequences variation in growth had (and still has) on fitness. It is generally assumed that avian growth of various taxonomic groups or populations is adapted to their specific environmental conditions. By this statement, one implies that variation in growth, at least in the past was present (chapter 13), was partly heritable, and affected fitness.

The fitness of an individual can be partitioned into the primary fitness characters, namely, survival probability, developmental time, and fertility (Istock 1983). The variation in primary fitness characters determines the potential for natural selection (Istock 1983) because phenotypic selection occurs when the phenotypic values of a trait correlate with fitness. In other words, a trait that correlates with fitness is under selection (Arnold and Wade 1984; Fig. 14.1). Traits not correlated with fitness characters are neutral. The large number of studies on growth variation in wild birds gives the us opportunity to investigate in natural populations how the variability of traits relates to fitness, a need that has often been expressed (e.g., Istock 1983; Endler 1986).

Intraspecific variation in growth rate of offspring can influence the parental fitness that results from the current breeding attempt (a) by affecting the probability of survival of the offspring between hatching and fledging and (b) by affecting the survival or fertility of the offspring after fledging. On the one hand, as a result of their longer exposure to predation, the probability of survival before fledging may be reduced if slower-growing nestlings fledge later than faster-growing ones. On the other hand, slow growth can reduce the probability of starvation by reducing the metabolic requirements of the nestling. Depending on the form that growth takes in a particular taxonomic group (Fig. 14.2), slow-growing nestlings may reach lower values of fitness-linked traits such as fledging mass or linear body size than fast-growing nestlings. Selection may act on fledging mass or linear size or both. Differences in selection pressures may also lead to the evolution

of different growth trajectories in different populations or species.

In this chapter we show first, that considerable variation in growth is common to many precocial and altricial bird species and, second, that this variation is correlated with variation in relative fitness. We give examples of studies that deal both with environmental and with internal (largely genetic) factors that cause variation in growth. We then address the consequences of this variation by reviewing studies that document natural selection on growth by means of mortality differences in the nest, differences in fledgling survival, differential recruitment into the breeding population, or differential fertility. Because variation in growth rate can be adaptive under specific conditions, some hypotheses on the adaptive value of this variation are discussed. Variation in final body size can be amplified by sibling competition during growth or diminished by compensatory or targeted growth (chapter 12). We only briefly discuss the connection between growth and final body size at this point; variation in final body size always implies variation in some aspect of growth. Final body size is often under natural selection, and variation in final body size among sexes within a species might be adaptive. However, it is often impossible to distinguish between selection on the growth trajectories per se or selection only on final body size.

Traits close to fitness or primary fitness characters themselves are assumed to express little or no heritable variation because of a strong directional selection on fitness (Fisher's theorem of natural selection; Istock 1983). We discuss the consequences of the almost ubiquitous variation in growth rates for evolutionary processes at the end of this chapter. When variation of growth affects survival probabilities or fertility rates, we ask whether there is a response to the selection for faster or slower growth.

The word *growth* is used throughout the chapter as a general term that includes different aspects of growth like growth rate, form of the growth curve, time to reach the asymptote. When we mean a specific aspect of growth, it is stated precisely. The same applies for the notion of body size. When specific studies are mentioned, the measured traits (e.g., body mass, and tarsus length) are given; otherwise *body size* refers to the generalized concept.

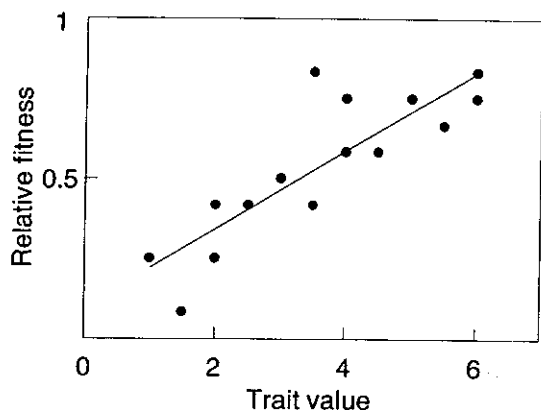
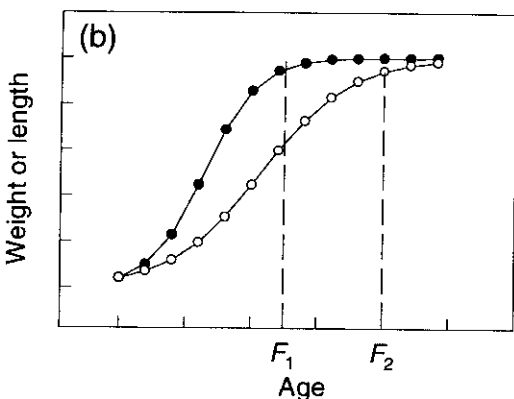
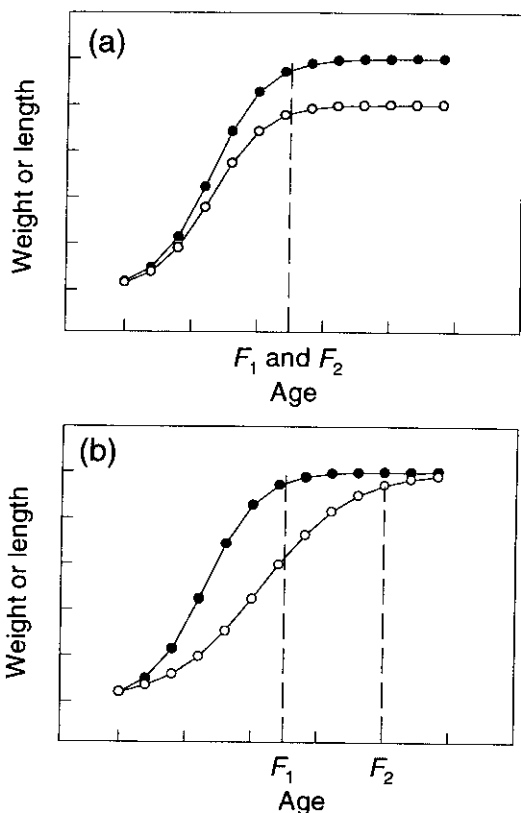


Fig. 14.1. Phenotypic selection occurs when the trait value correlates with the relative fitness (hypothetical example).



14.2. Variation of Growth in Birds

We restrict our overview to studies that document variation in growth and in final body size to *nondomesticated* birds. Some results are on free-living birds, others on captive birds. There is a large body of literature on factors that affect growth in domesticated birds that are also relevant to evolutionary biologists (see chapter 13). Here, we focus on the relationship between the length of the nestling period and selected aspects of growth (e.g., fledgling size as the asymptote). Studies that deal with adult size only, without further reference to the nestling period or growth, are discussed later (section 14.3). Our documentation of studies on growth variation is not exhaustive but exemplifies various causes of growth variation in various taxonomic groups of birds. We do not intend to discredit similar studies that are not mentioned here, but in general we give preference to more recent publications.

14.2.1. Observational studies

Several observational studies (Table 14.1) have documented cases of spatial or temporal differences among individuals or populations in growth rate or asymptotic body size. Some studies suggested that differences in food availability and quality are the cause of the differences in growth rates in different habitats, but the presumed causal factor has not been manipulated. By using multiple regression analyses, Bryant (1975) attempted to separate the direct effect of weather variables on nestling growth of house martins (*Delichon urbica*) from the effect of food availability. In little auk (*Alle alle*) chicks, Konarzewski and Taylor (1989) found a correlation between weather conditions and growth. The residuals given by the difference be-

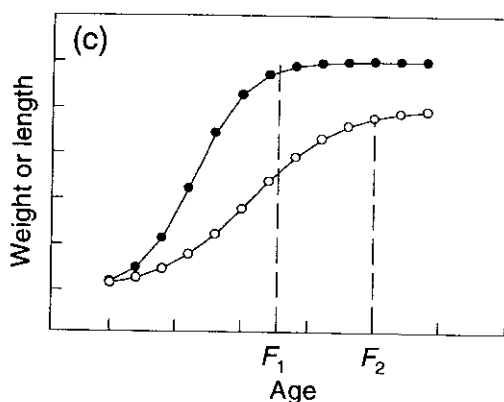


Fig. 14.2. In (a), the slower-growing nestlings grow with the same growth rate constant K toward a lower asymptote A . In (b), the slower-growing birds grow with a lower growth rate constant K toward the same asymptote A , and in (c), the slower-growing nestlings grow with a lower growth rate constant toward a lower asymptote. If a bird can fledge once it reaches, say, 90% of its asymptotic weight (or size, wing length etc.), the fast- and slow-growing nestlings will fledge at the same time (F_1 and F_2 in (a)), but not in (b) and (c). The slow growing birds (F_2) fledge later than the faster growing ones (F_1). Slower growth may therefore have a fitness cost arising from a prolongation of the nestling period through a higher risk of time-dependent nestling mortality in (b) and (c) but not in model (a). Slower growth may have a fitness cost arising from lower phenotypic values (body size at a given age) of a fitness-linked trait in (a) and (c) but not in (b). Open circles indicate depressed growth; filled circles, normal growth.

Table 14.1. Overview of studies reporting an environmental effect on the variation in postnatal growth. *A* indicates asymptote

Species	Presumed cause of variation	Affected growth parameter	Reference
Observational studies			
<i>Corvus corone</i>	Habitat	A; <i>K</i> of weight; <i>A</i> of tarsus	Richner (1989a)
<i>Cerorhinca monocerata</i>	Food provisioning	Slope of linear regression	Bertram, Kaiser, and Ydenberg (1980)
<i>Rissa tridactyla</i>	Food availability	A; <i>K</i> <i>A</i> /4 of weight	Barrett and Runde (1980)
<i>Fratercula arctica</i>	Food quantity and quality	A; <i>K</i> (logistic curve) of weight	Barrett et al. (1987)
<i>Delichon urbica</i>	Food abundance	Increase in weight	Bryant (1975)
<i>Tyrannus verticalis</i>	Food abundance	<i>K</i> of weight	Blancher and Robertson (1987)
<i>Megadyptes antipodes</i>	Food quality	Growth rate of logistic curve for weight	van Heezik and Davis (1990)
<i>Cephalophus columba</i>	Brood size and sequence of hatching	Slope of linear regression, asymptote	Emms and Verbeek (1991)
<i>Delichon urbica</i>	Rainfall and temperature	Increase in weight	Bryant (1975)
<i>Alle alle</i>	Precipitation, visibility and wind speed	Deviation of actual growth from predicted growth	Konarzewski and Taylor (1989)
<i>Parus major</i>	Rainfall	Deviation of actual growth from predicted growth	Keller and van Noordwijk (in press)
<i>Uria aalge</i>	Seasonal timing	<i>A</i> of weight	Hedgren and Linnman (1979)
<i>Parus major</i>	Same	<i>A</i> of weight and tarsus length	Gebhardt-Henrich and van Noordwijk (1991)
<i>Haematopus bachmani</i>	Parental quality	Weights after 14–16 days of age	Groves (1984)
<i>Rissa tridactyla</i>	Parental age	Increase of weights per day	Coulson and Porter (1985)
<i>Prunella modularis</i>	Mating system	6-day weights	Davies (1986)
<i>Megarops fuscatus</i>	Parasitism	Increase in body mass and tarsus length	Arendt (1985)

Experimental studies on free-living birds

<i>Corvus corone</i>	Food quantity	A for weight and tarsus	Richner (1992)
<i>Melospiza melodia</i>	Food quantity	Weight, tarsus length, and wing length on day 6	Smith and Arcese (1988)
<i>Tachycineta bicolor</i>	Exchange of eggs and nestlings	Weight increase, A of weight, 9th primary feather	Quinney, Hussell, and Ankney (19
<i>Delichon urbica</i>	Food quantity and quality	Weight, length of keel, and wing on day 20	Johnston (1993)
<i>Diomedea melonophris</i>	Cross-species exchange	Growth rate	Prince and Ricketts (1981)
<i>Diomedea chrysostoma</i>			
<i>Parus major</i>	Brood size	A of weight; weight increase	Gebhardt-Henrich and van Noordv (1994)
<i>Parus caeruleus</i>	Brood size	A of weight	Nur (1984)
<i>Parus major</i>	Presence of hen fleas	A of weight, and tarsus length	Richner, Oppliger, and Christe (19
<i>Parus major</i>	Hatching date	A of weight	Verhulst and Tinbergen (1991)
<i>Uria aalge</i>	Hatching date	Body masses after 12 days	Hedgren and Linnman (1979)
Experimental studies on captive birds			
<i>Corvus corone</i>	Food restriction	A of weight and tarsus; period to attain A	Richner, Schneider and Stirnimann
<i>Poephila guttata</i>	Protein content of food	K and A of weight, shape, etc.	Boag (1987)
<i>Sylvia atricapilla</i>	Diet quality	Gain of body mass and wing length	Berthold (1976)
<i>Aix sponsa</i>	Protein content of food	No effect	Brisbin, White, and Bush (1986a)
<i>Aix sponsa</i>	Amount of cadmium	Time to attain A of weight; shape of growth curve	Brisbin et al. (1986b)
<i>Anas platyrhynchos</i>	PCB intake	Shape of growth curve	Brisbin et al. (1986b)

tween actual growth and the growth predicted by the Richards curve (fitted to the nestlings' growth before the beginning of pre fledging weight recession) showed that the levels of precipitation were significantly correlated with the mean growth during the first five days, when chicks were still brooded by their parents. Visibility and wind speed were significant predictors for later growth. Whereas the amount of precipitation probably affected the thermoregulation of the wet chicks directly, visibility and wind speed most probably affected the ability of the parents to collect food (Konarzewski and Taylor 1989). A similar methodological approach, which additionally incorporated the mid-parent weight as the genetic component, was used by Keller and van Noordwijk (in press), who documented the influence of rainfall on daily growth in hole-nesting great tits (*Parus major*). In that study, rainfall had an effect on the feeding frequency of the parents rather than a direct effect on growth of the nestlings.

Food availability can correlate with the timing of breeding. In great tits, the timing of breeding often has an effect on fledgling weights, as peak abundance of the main food item, caterpillars on trees, is relatively short-lived (Perrins 1979; van Noordwijk et al. 1995). The form of the relationship between hatching date and fledgling weight may differ greatly among years, as documented in a four-year study on great tits (Gebhardt-Henrich and van Noordwijk 1991). The regression of fledgling weight on hatching date showed an optimum in the first year and was linear (a negative correlation between hatching date and fledgling weight) in both the second and the fourth years. The importance of the factor *hatching date* on *fledgling weight* differed as well. Hatching date had a significant effect on fledgling weight in the first and second years; had no significant effect in the third year; and was the most important factor on fledgling weight as well as on tarsus length in the fourth year. In the fourth year, food availability was estimated by the measurement of frass fall of caterpillars, the main prey during breeding (Gebhardt-Henrich 1990). A crash in caterpillar density during the breeding season in the fourth year led to a shorter duration of growth for both tarsus and body mass and significantly lowered the fledgling weights for late-hatched nestlings (Gebhardt-Henrich and van Noordwijk 1991, 1994).

When the parents' capacity to provide food to the brood is limited, the brood size might have an effect on nestling growth. For example, in American black oystercatchers (*Haematopus bachmani*), the chick's growth and survival was negatively correlated with brood size, which ranged from 1 to 3 chicks (Groves 1984). The opposite, that is, the better growth and survival of chicks from larger broods, was observed in the kittiwake, *Rissa tridactyla* (Coulson and Porter 1985). The researchers showed a significant effect of the experience of females on the chicks' growth and

concluded that parents' quality (in this case, parental age) was positively correlated with clutch size; therefore, the growth of the chicks increased with increasing clutch size. In other words, competent parents may be able to lay large clutches and rear the resulting chicks very well, while intrinsically poor parents may be limited in clutch size and in their ability to rear the resulting chicks. Parental age also correlated positively with chick's growth in the California gull, *Larus californicus* (Pugesek 1995). However, increased reproductive effort, not experience, was assumed to be the cause. The influence of parental behavior and some other aspect of investment into reproduction could not be separated in a study of snow petrels, *Pagodroma nivea* (Amundsen 1995). Parents that left their chicks alone earlier after hatching also laid smaller eggs, and these chicks were lighter than those attended by their parents.

All environmental causes of growth variation discussed so far are somehow related to food supply. In some studies, the quantity or quality of food was measured. In the others, differences in food supply appeared to cause variation in growth. In a comparative study of altricial birds, Saether (1994) showed that clutch size, as well as nestling growth rates, correlated significantly with the provisioning rate of the parents (after adjusting for body size). Based on the observational studies, food availability seems to be the most important environmental factor for postnatal growth (reviewed by Martin 1987).

Another factor that affects postnatal growth is parasitism. The increase in body mass and tarsus length of pearly-eyed thrashers (*Margarops fuscatus*) was significantly lower in nestlings that were naturally infected by botfly larvae (Arendt 1985). A negative influence on growth of the tarsus, as well as on increases in body mass, was also shown in pied flycatcher (*Ficedula hypoleuca*) nests that were naturally infested by mites and blowfly larvae (Merino and Potti 1995).

Other causes of growth variation include genetic diversity among individuals of a population or species (see chapter 13); sexual dimorphism of body size; and variation in egg sizes, which often has a genetic component itself (Schifferli 1973; O'Connor 1975; van Noordwijk et al. 1981; Galbraith 1988; Rhymer 1988). Synchronous hatching and sibling competition can cause variation in growth within broods (Schreiber 1976). For example, in the little blue heron (*Egretta caerulea*), late-hatched chicks grew significantly slower than their early-hatched siblings (Werschkul 1979). When the early-hatched siblings died, the late-hatched chicks increased their growth rates (expressed as the growth constant K of the logistic equation).

In sexually dimorphic birds, the maximum growth rate at the point of the inflection of the growth curve (g_{max}) for body mass and tarsus length generally differs among male and female nestlings. In all but one

species, the growth rate constants (K) did not differ among the sexes, and male and female chicks reached fledgling weight at the same time (Richner 1991). For example, the weight asymptote of the male boat-tailed grackle (*Quiscalus major*) is 65% larger than that of the female. However, fitting growth curves to the logistic equation yields identical rate constants of growth, indicating that the relative size increase is similar in the two sexes (Bancroft 1984). In absolute values, males have larger weight increases than females. In a comparative study of 31 species of sexually dimorphic birds, Teather and Weatherhead (1994) conclude that the relationship among asymptotic body mass, growth rate, and time to reach half of the asymptote is similar for both sexes.

Although most observational studies cannot always unravel the cause of growth variation because of unknown confounding factors, they can provide a basis for the formulation of testable hypotheses.

14.2.2. Experimental studies

Experimental studies in which the factor of interest is varied in a precise way and other sources of variation are controlled for or randomized in regard to the treatment offer a more straightforward approach for identifying the factors that affect growth. Experimental studies on the variation of growth in free-living birds that were randomly assigned to the treatment, as well as of studies of captive birds in which various sources of variation were experimentally controlled, are listed in Table 14.1.

Cross-fostering experiments, in which nestlings are reared by nonrelated foster parents, are an alternative experimental approach. These experiments allow the partitioning of genetic and environmental variance. The taxonomic level on which the experiment is conducted allows to determine different levels of genetic variance; for example, experiments may involve fostering among individuals of the same species within the same geographical region (e.g., Ricklefs and Peters 1981; Ricklefs 1984; Gebhardt-Henrich and van Noordwijk 1991; Smith and Wettermark 1995), exchanges between populations (e.g., James and NeSmith 1988; Rhymer 1992), or exchanges between species (Prince and Ricketts 1981; Shea and Ricklefs 1985).

Probably the most important environmental factor in the variation in avian growth rates is food availability (see preceding examples). Food availability during the growth of nestlings has been manipulated in field studies by provisions of extra-food (e.g., Smith and Arcese 1988; Richner 1992); by forcing females to lay a replacement clutch later in the season, when food availability has changed; or by manipulation of brood size. If parents cannot fully compensate for the experimentally modified brood size, nestlings from enlarged broods should get less food than nestlings from reduced broods. These approaches, however, are

not without problems. In some species, parent birds seem to counteract the effect of brood size manipulation by adjusting their workload to the new brood size. This might have been the case in a study of great tits, in which females with enlarged broods, if compared to their winter weights, lost more weight during the breeding season than females with reduced broods (Gebhardt-Henrich and van Noordwijk 1991). Also, forced replacement clutches that are laid later in the season may not be fully comparable to naturally late first clutches. When extra food is provided, it may be utilized to varying degrees beyond experimental control and could also be of different quality than natural food (e.g., Johnston 1993).

The presence of parasites or pollutants can be experimentally controlled in free-living, as well as in captive, birds. Influences of parasites and pollutants on growth have been shown in precocial and altricial species (Table 14.1; see Møller 1995).

In summary, variation in different aspects of growth, maximum growth rate, rate constant of growth, asymptote, and shape of the growth curve, was often demonstrated and seems to be common in various bird taxa with altricial and precocial young. Differences in the quantity and quality of food delivered to the chicks were identified as the major sources of variation.

14.2.3. Natural selection on growth rate

The assumption that natural selection drives the diversification of growth rates implies that the observed variation in growth must have consequences for fitness. Natural selection can occur at different stages of the life cycle. In this section, studies are arranged according to whether selection was demonstrated between hatching and fledging, whether it affected fledgling survival and recruitment into the breeding population, or whether it affected the future fertility of nestlings as adults. All studies were observational unless noted otherwise (Table 14.2).

Survival between hatching and fledgling

Lack (1968) hypothesized that growth rate is selected by the opposing forces of time-dependent mortality and parental energy supply to the growing chick. Bosque and Bosque (1995) tested this hypothesis by comparing island species that experience little or no nestling predation with closely related mainland species that do experience predation. They found a significant relationship among length of incubation period, postnatal growth rate, and predation rates, thus generally supported Lack's view (see chapter 11 for a detailed discussion). Here, we report a selection of recent studies that show that variation in growth rates affects mortality in the nest. In most cases, slowly growing nestlings within broods suffer higher mortality rates. Higher mortality may arise through the increased probability of starvation, stronger sibling com-

Table 14.2. Overview of studies reporting consequences of natural selection of postnatal growth on fitness.

Species	Growth parameter	Cause of selection	Reference
<i>Parus major</i>	Body mass on day 13	Survival	Smith et al. (1989)
<i>Vanellus vanellus</i>	Hatching size	Survival	Galbraith (1988)
<i>Anas platyrhynchos</i>	Hatching size	Resistance to cold	Rhymer (1988)
<i>Sterna paradisaea</i>	Growth rates	Resistance to cold	Klaassen and Bech (1992)
<i>Larus fuscus</i>	Weight increase	Survival	Bolton (1991)
<i>Egretta caerulea</i>	Growth rate	Starvation	Werschkul (1979)
<i>Egretta caerulea</i>	Body mass	Cainism	Werschkul and Jackson (1979)
<i>Turdus merula</i>	Mass on day 8	Survival	Magrath (1991)
<i>Megadyptes antipodes</i>	Growth rate	Survival	van Heezik and Davis (1990)
<i>Haematopus bachmani</i>	Mass on day 20	Survival	Groves (1984)
<i>Haematopus ostralegus</i>	Growth rate	Survival	Kersten and Brenninkmeijer (1995)
<i>Larus fuscus</i>	Growth rate	Starvation	Griffiths (1992)
<i>Larus fuscus</i>	Egg and hatching size	Survival	Bolton (1991)
<i>Anser caeruleus</i>	Growth rate	Survival	Cooke et al. (1995)
<i>Uria aalga</i>	Growth rate	Survival	Harris et al. (1992)
<i>Tyrannus verticalis</i>	K value of growth rate	Survival	Blancher and Robertson (1987)
<i>Parus major</i>	Asymptote of mass and tarsus	Survival	Garnett (1981)
<i>Ficedula hypoleuca</i>	Tarsus length	Survival	Alatalo and Lundberg (1986)
<i>Turdus merula</i>	Mass on day 8	Survival	Magrath (1991)
<i>Prunella modularis</i>	Mass on day 6	Survival	Davies (1986)
<i>Chen canagicus</i>	Prefledging mass	Survival	Schmutz (1993)
<i>Branta leucopsis</i>	Mass at 3 – 5 months	Survival	Owen and Black (1989)
<i>Sturnus vulgaris</i>	Mass on day 18	Survival	Krementz et al. (1989)
<i>Rissa tridactyla</i>	Weight gain (g/day)	Recruitment rate	Coulson and Porter (1985)
<i>Parus major</i>	Fledging weight	Recruitment rate	Tinbergen et al. (1987)
<i>Parus major</i>	Tarsus length	Clutch size	Haywood and Perrins (1992)
<i>Parus montanus</i>	Tarsus length	Survival	Thessing and Ekman (1994)
<i>Corvus corone</i>	Tarsus length	Aquisition of territory	Richner (1989a, 1992)
<i>Geospiza fortis</i>	Weight; wing length; bill length; width and depth	Survival	Boag and Grant (1989)
<i>Poephila guttata</i>	Asymptote of mass	Clutch size	Haywood and Perrins (1992)

petition, the higher rate of predation, or interaction among these factors. For example, the body mass of 13-day-old great tit nestlings was significantly correlated with survival to fledging, the lighter nestlings surviving less well (Smith et al. 1989). A positive correlation between growth rate and fledging success was also shown in oystercatchers, *Haematopus ostralegus* (Kersten and Brenninkmeijer 1995). Postfledging survival, however, was independent of growth rate or of fledging size.

Egg size often correlates with survival in the nest. Northern lapwing (*Vanellus vanellus*) hatchlings from larger eggs were larger, grew faster, and survived better during the first 10 days after hatching (Galbraith

1988). Galbraith assumed that chicks from larger eggs had larger reserves. In mallards, larger hatchlings could survive colder temperatures and starvation longer than smaller hatchlings (Rhymer 1988). The relationship between egg size and survival could also be due to a correlation with an unknown third factor. In a laboratory study Klaassen and Bech (1992) found that Arctic tern (*Sterna paradisaea*) chicks with growth rates less than 75% of normal were likely to die of hypothermia. Chicks of lesser black-backed gull (*Larus fuscus*) that increased in body mass faster had a greater chance to fledge successfully (Bolton 1991). As in northern lapwing, chicks hatching from larger eggs were larger and survived better. However, because the

last egg of a clutch tended to be the smallest, this might be the effect of hatching sequence rather than size (Bolton 1991).

Sibling competition may cause starvation of the more slowly growing chicks resulting in high mortality rates for the smaller nest mates, for example, in the little blue heron (Werschkul 1979). The extreme case is *cainism*, in which bigger siblings sacrifice their smaller nest mates for the sake of their own success in growth (Werschkul and Jackson 1979).

In contrast, sibling competition does not seem to be present in various asynchronously hatching birds; for example in yellow-eyed penguins (*Megadyptes antipodes*), the first and second chicks to hatch did not differ in growth rates, and chicks that grew faster (skull, tail, and flippers) had even lower survival rates than their more slowly growing nest mates (van Heezik and Davis 1990). Asynchronous hatching and the possible lack of sibling competition is also known in parrots, for example, in the budgerigar, *Melopsittacus undulatus* (Stamps et al. 1985). In blue herons (*Ardea herodias*), sibling competition is determined by the size of the food items (Mock et al. 1987).

It has been suggested, that a trade-off between growth rate and energy supply may guide the evolution of postnatal growth because faster growth rates can make nestlings more susceptible to starvation (Lack 1968; Ricklefs 1969a; Griffiths 1992; see chapter 11). For example, in lesser black-backed gulls, starvation was the most common cause of the death of nestlings. The faster-growing males had lower survival rates because of their higher susceptibility to starvation (Griffiths 1992). Klaassen et al. (1994) estimated that nestlings of common terns (*Sterna hirundo*) would need 30% less energy if the average growth rate were reduced by 50%. In contrast to the effect on the total metabolic rate, reduced growth rates had little effect on the resting metabolic rate of Arctic tern chicks (Klaassen and Bech 1992).

Although nestling predation is a common phenomenon (e.g., Ricklefs 1969a; Albano 1992; Westneat 1992; Martin 1992; Morton et al. 1993), the relationship of growth rate, nestling period, and time-dependent mortality has not yet been clearly resolved. Some studies demonstrate a link between growth rate and nestling period (e.g., Vinuela and Bustamante 1992; Bosque and Bosque 1995) and, assuming a constant risk of nest predation, show with some plausibility that growth rate is related to nestling predation (see chapter 11). There may also be an interaction between slow growth and predation because slow-growing chicks not only stay longer in the nest but may also become more vulnerable to predation in other ways. The slow-growing broods are the more hungry broods and hungry chicks beg more than well-fed chicks, so it is possible that the hungry chicks attract more predators (Martin 1992). During periods of low food abundance, the par-

ents of slowly growing broods may be absent for longer foraging periods (Coulson and Johnson 1993) and thereby facilitate nest predation. Slow growth and reduced fledging size may also be caused by the conflict of allocating time to foraging or to defence of the nest.

Fledgling survival

In many altricial species, nestling mortality is rather low while a significant rate of mortality occurs soon after fledging (Perrins 1979). It has often been found that heavier or larger fledglings survive better. For example in great tits, heavier and/or bigger fledglings (based on the weight or tarsus length when 15 days old) were later more often recaptured than smaller fledglings (Perrins 1965; Garnett 1981; Tinbergen 1987; Smith et al. 1989), suggesting higher mortality rates for lighter and/or smaller fledglings. The body mass of 15-day old great tits is often considered to be the fledgling mass, even though fledging occurs about a week later. Changes in body mass after day 15 are small and nonsystematic (van Noordwijk et al. 1988; Richner et al. 1993). Similarly, in pied flycatchers, offspring with longer tarsi had higher survival rates after fledging (Alatalo and Lundberg 1986). The body mass of 8-day old blackbirds (*Turdus merula*) was positively correlated with fledging success and survival during the first month after fledging (Magrath 1991), and 6-day old dunnocks (*Prunella modularis*) with higher body masses had higher postfledging survival (Davies 1986). In European starlings (*Sturnus vulgaris*) both body mass at 18 days and date of fledging affected postfledging survival (Krementz et al. 1989).

Only a few studies considered precocial species. In precocial emperor goose (*Chen canagicus*), the post-fledging survival of goslings was also positively correlated with their pre-fledgling body mass (Schmutz 1993). In barnacle geese (*Branta leucopsis*), gosling survival was correlated with body mass independently of age (Owen and Black 1989). Precocial chicks of American black oystercatchers that were heavy on day 20 survived better to the first flight than lighter chicks. However, postfledging survival was not affected by the chick's weight at day 20 (Groves 1984).

In at least two studies smaller juveniles had higher survival rates than larger juveniles. Price and Grant (1984) observed that in some years selection acted against large juveniles in one species of Darwin's finches, probably because smaller individuals required less food during food shortages. Juvenile song sparrows (*Melospiza melodia*) with long tarsi suffered higher mortality (Schluter and Smith 1986), but in the same study, females with longer tarsi had more young later, thus, on the average, compensating for higher mortality rates as juveniles.

Some studies show no effect of growth or fledgling

size on survival. No correlation between the maximum growth rate and the first year of survival was found in Ipswich sparrows (*Passerculus sandwichensis*) during the years of a decline in population (Ross and McClaren 1981). Similarly, postfledging survival was independent of fledgling mass in both sparrow hawks, *Accipiter nisus* (Newton and Moss 1986) and puffins, *Fratercula arctica* (Harris and Rothery 1985).

Recruitment rate and future fertility

The fitness of an individual may be measured as the number of offspring that survive and later reproduce themselves. Variation in the recruitment rate of the offspring, which is the probability for a fledgling to breed in the next reproductive season, can be one of the largest components of the overall variation in reproductive success (for great tit see Tinbergen et al. 1987; van Noordwijk and van Balen 1988; for Florida scrub jay see Fitzpatrick and Woolfenden 1988). In those studies the local recruitment rate, that is, recruitment into the studied breeding population, was measured, although the emigration of successful recruits could not be assessed. However, in great tits it was shown that for fairly closed island populations with low migration rates (van Noordwijk and van Balen 1988) emigrated juveniles are often faced with lower chances of survival and recruitment than local juveniles. In semiprecocial kittiwakes, the recruitment rate to the natal colony was positively correlated with weight increases of chicks (Coulson and Porter 1985).

In great tits, the local recruitment rate is positively correlated with the fledgling weight up to a certain weight (Tinbergen et al. 1987; Gebhardt-Henrich and van Noordwijk 1991). For larger fledglings there is no further increase in the local recruitment rate (Tinbergen et al. 1987), and a large fledgling size may even result in a decrease (Fig. 14.3.a and b). In the study by Gebhardt-Henrich and van Noordwijk, fledgling weights were significantly influenced by brood size manipulations. For different nestling weight classes, the probabilities to return the following spring as breeders were significantly different. The same trend held for tarsus length but was not significant (Fig. 14.3 c and d). The study by Tinbergen and Boerlijst (1990) is exceptionally detailed as it shows both the correlation between body mass two weeks after hatching and survival to the following breeding season, as well as nonlinear relationship between the two for each sex separately.

In great tits, the body mass on day 15 after hatching affected future fertility because body mass itself was positively correlated with later clutch sizes (Haywood and Perrins 1992). In a laboratory study, the asymptotic body mass of zebra finches (*Poephila guttata*) was related to the amount of food they were fed by their parents during growth (Haywood and Perrins 1992). As in great tits, the average clutch size

produced by these females later in life correlated positively with their asymptotic body mass as nestlings.

In summary, fledgling body size measurements (body mass and tarsus length) may affect survival and recruitment rates. The variation in fledgling size seems to be the most important component of the variation of fitness. Since higher growth rates generally result in higher fledgling masses, it is difficult to distinguish the selection target. An additional problem emerges in the case of observational studies because lower growth rates may be caused simultaneously by poor-quality habitats and poor-quality parental phenotypes breeding there (Bolton 1991). A poor habitat can either lower the growth rate or reduce survival of the fledglings or both. However, the growth rate is not necessarily tied to the survival rate. Harris et al. (1992) showed for semiprecocial common murre (*Uria aalge*) that when chicks grew well, fledgling survival was also high. However, because in some particular years growth rate was not correlated with survival of the chicks, they concluded that growth rate per se could not be the cause of the variation in survival.

Parental care often extends into the period after the young have fledged. Good parents could cause nestlings to grow fast and also ensure their increased survival once their young have fledged. Parental quality probably influenced recruitment rates in kittiwakes because chicks in natural broods of three survived better than those in broods of two (Coulson and Porter 1985).

Adaptive value of variation in growth rates

As shown in the previous sections, variation in post-natal growth rates is ubiquitous and often has consequences for the fitness of the individual. Variation in growth may be caused by poor environmental conditions, thus reflecting phenotypic plasticity rather than adaptation to specific environmental conditions. However, under certain circumstances, variation itself can be adaptive. The ability to rear a certain number of offspring depends to some extent on the availability of food during the nestling period. If food availability could be predicted during egg laying, clutch size could be adjusted optimally (Lack 1954; Ricklefs 1965; O'Connor 1977). If food availability is not predictable, brood reduction, flexible growth rates, or both might be advantageous (O'Connor 1977, 1978).

From the viewpoint of the parents, brood reduction is favored if the parents achieve higher overall fitness by raising a reduced brood than by attempting to bring up the whole brood. Intra-brood variation in growth rates will in these circumstances be adaptive because it leads to a size spread within the brood that, in the case of a food shortage, enables the parents to sacrifice one or a few young before over investing in them. Size differences can be established by egg size variation and/or hatching asynchrony (O'Connor 1977), leading to sibling competition (Groves 1984) with competitive

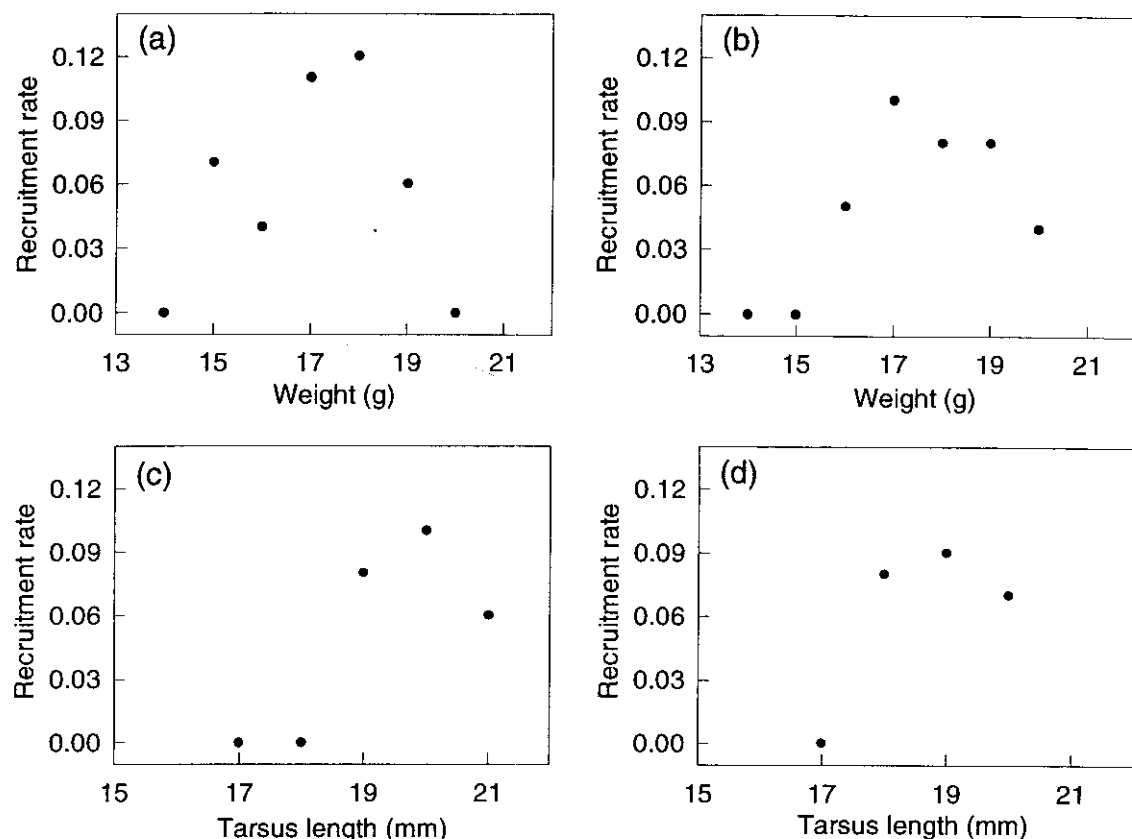


Fig. 14.3. Great tit nestlings in different weight classes (15-day weights) have significantly different recruitment rates: (a) 1986; (b) 1987. Nestlings with small tarsi have lower recruitment rates: (c) 1986; (d) 1987.

asymmetries within broods. Computer simulations with and without modeled sibling competition show that it significantly increases the variance in nestling sizes and generates runts, which might die during poor conditions or catch up if conditions are again favorable (van Noordwijk 1988a). Thus intrabrood variation in growth rates may be a consequence of an adaptive parental strategy to reduce brood size efficiently.

From the viewpoint of the surviving nestlings, the death of a sibling implies a loss of inclusive fitness and will only be favored if a survivor's individual fitness, plus its inclusive fitness, is higher with brood reduction than without. In this case, siblicidal behavior may evolve, and intrabrood variation in growth rates may be a consequence of adaptive siblicidal strategies. From the viewpoint of the nestling that potentially dies, its death is favored only if the gain in inclusive fitness through the surviving kin is higher than the potential gain in individual fitness, plus inclusive fitness, when surviving itself. Since the genetic relatedness with a sibling is only half of the relatedness of a nestling to itself, the latter condition will not be easily fulfilled, particularly in small broods. Each nestling will strive for survival, and sibling competition will consequently select for maximum growth rates.

Sibling competition is viewed as a significant factor in the evolution of avian growth rates (Werschkul 1979; Werschkul and Jackson 1979; Ricklefs 1982, 1993).

Variation of growth rates among nestlings within broods, as occurs, for example, through hatching asynchrony, has been shown to increase parental efficiency in cattle egrets (*Bubulcus ibis*), expressed as the number of chicks per brood that survived to 25 days of age per daily volume of delivered food (Mock and Ploger 1987). Parental efficiency in experimentally synchronized three-chick broods was only 55% of that in which hatching asynchrony was experimentally controlled to correspond closely to natural hatching intervals (Mock and Ploger 1987). Finally, several bird species (e.g. rock pigeon, *Columba livia*) have overlapping clutches that is, a new clutch is initiated before the last brood has fledged. In this case, nestlings from two overlapping clutches are of different ages with different instantaneous growth rates and food demands. Thus rearing small, overlapping clutches instead of one large clutch may reduce the peak demand of parental care and enable the parents to raise more offspring (Burley 1980). This can be seen as an extreme form of hatching asynchrony.

Flexible growth rates of the whole brood may be

adaptive when food availability fluctuates stochastically. Flexible growth rates can then ensure survival during food shortages (O'Connor 1977). For example, nestling white-fronted bee eaters (*Merops bullockoides*) can reduce growth rates during food shortages and recover as soon as food is abundant again. During the retardation of growth, energy requirements are reduced and the chances of survival are increased (Emlen et al. 1991; see chapter 12).

Ricklefs (1968) further considered the adaptive value of lowering the growth rate of the brood as a whole if it allows the rearing of extra young on a given food supply. As this implies the prolongation of the nestling period, lowering the growth rate is beneficial only if there is no time-dependent mortality. At equilibrium, the fitness benefits arising from the extra young will be balanced by the costs of the additional risk of mortality (or other negative factors) that arise from the longer nestling period.

Finally, at a given brood size and food abundance, variation in growth rates of offspring will be correlated with variation in parental effort. As recently shown experimentally (e.g., Gustafsson and Sutherland 1988), parental effort affects future adult survival and fecundity, for example, through a trade-off between effort and parasitism (reviewed by Gustafsson et al. 1994; Richner et al. 1995), and these costs to parents will affect the upper limit of growth rates of nestlings. Thus for iteroparous species there will be a further selective force acting on growth rate, which will tend to maximize the lifetime reproductive success of the parents.

14.3. Body Size Variation in Birds

So far, all the studies we have discussed here addressed variation in growth, including variation in the asymptotic size. In the following section we discuss studies that demonstrate the causes and consequences of variation in adult body size when nestling growth was not studied.

Adult birds of the same species may be of different size in different habitats. Such variation may have both a genetic and an environmental component. In great tits (Ulfstrand et al. 1981), males in a deciduous forest (good habitat) had longer wings and bills than those in the coniferous forest. Since females in coniferous forests had the same wing length as those in deciduous forests, the researchers concluded that the cause for the size difference was not food availability per se but the fact that smaller males were forced into the suboptimal habitat by larger males. Habitat selection does not exclude the presence of genetic variation in body size, however, which has been demonstrated repeatedly for many bird species, for example, for great tits (Garnett 1981; van Noordwijk et al. 1988; Gebhardt-Henrich and van Noordwijk 1991), for star-

lings (Ricklefs and Peters 1981), for tree swallows, *Tachycineta bicolor* (Wiggins 1989), and for Darwin's finches, *Geospiza* ssp. (Grant and Grant 1989).

14.3.1. Natural selection on body size

Body size variation has been found to affect fitness either directly or indirectly when acting through fitness components of other life history traits. Within a social group, a large body size may affect social rank (dominance), and social rank is known to affect survival or reproductive success in a number of species. For example, within the same age class of male carrion crows (*Corvus corone*), bigger males were significantly more successful than smaller males (Richner 1989b). Body size affected the time that the crows had access to a food patch and also correlated with the length of a feeding bout. The fitness of small crows was reduced since only the birds above a certain tarsus length could acquire a breeding territory (Richner 1989a), which is a prerequisite for breeding.

Direct effects of body mass on survival were already documented in the classical study of Bumpus (1899), who showed that large individuals of house sparrows (*Passer domesticus*) had a better chance to survive a heavy storm than smaller individuals (but see Buttemer 1992). Also, large Darwin's finches survived a drought better than smaller Darwin's finches (Boag and Grant 1981). In very cold winters, overwinter survival of great tits correlated with male body size (Lehikoinen 1986), but no selection differentials could be measured in females. Sex-related effects may complicate the interpretation of the outcome of selection on body size.

Several studies report selection on body size through differences in fertility. In pied flycatchers, clutch size increases with the female's tarsus length, except for females with very long tarsi (Alatalo and Lundberg 1986). Female song sparrows with long tarsi and short beaks have more young than those with short tarsi, but juveniles with long tarsi suffer increased mortality (Schluter and Smith 1986). In the long-billed curlews (*Numenius americanus*), Redmond (1986) found an interaction between female body size and environmental conditions during the prelaying stage. In good years, when food patches were close to the breeding area, larger females started egg laying earlier and their eggs were larger than those of smaller females. In contrast, in a poor year, when curlews had to fly long distances to food patches, larger females laid later and laid smaller eggs. The selective advantage of egg size is not known, but in the unfavorable year earlier clutches had higher survival rates than later clutches (Redmond 1986). In precocial snow geese (*Chen caerulescens*) adult summer-body weight in correlated negatively with the date of laying in the following spring (Cooke et al. 1995). Breeding early is advantageous in this species.

14.4. Connection between Growth Rate and Final Body Size

One may now ask whether and how growth rate and final body size are interrelated. To study this connection, Smith and Arcese (1988) provided some nests of song sparrows with extra food during growth. Although extra food provisioning influenced early growth rates, no correlation was found between early growth and final body size. In contrast, carrion crow chicks that were hand-raised under restricted food conditions remained permanently and significantly smaller than hand-raised chicks under *ad libitum* feeding (Richner et al. 1989). These studies are difficult to compare because in one case additional food was provided and in the other case food was restricted. It also appears that the ability and degree of compensatory growth, and thus the connection between growth rate and final body size, depends on the environmental conditions: under good conditions, compensation of an earlier growth depression may be possible; under poor conditions, it is not (Schifferli 1973; Gebhardt-Henrich and van Noordwijk 1994). Regardless, compensatory growth cannot cancel selection during the early ages. It may dampen the selection pressure on growth rates but cannot prevent it. The degree to which variation in growth rate will lead to variation in final body size is addressed in chapter 12 in more detail.

14.5. Unresolved Questions

Interspecific variation in postnatal growth rates are commonly interpreted as an adaptation to the species' environment (e.g., Lack 1968; Case 1978; chapters 11 and 16). As pointed out before, patterns of growth are seemingly adapted to ecological factors, especially the food supply during the growth period. The notion of adaptive growth rates implies that selection has been acting on heritable variation in growth rates. Selection on growth rates and final body size has been shown in several studies on various taxonomic groups, encompassing mostly altricial and much fewer precocial species. Evidence for an evolutionary response to selection on growth rates is less clear, and one may also ask what kind of evolutionary response can be expected from known variation in growth rates and natural selection on growth.

Strong directional selection on postnatal growth might not necessarily lead to an evolutionary response. Variation in growth rates has to be (at least partially) heritable to elicit an evolutionary change. In contrast to final body size, the heritability estimates of growth rate are small or not significantly different from zero (Smith and Wettermark 1995; chapter 13). It seems that the shape of the growth curve in different taxonomic groups (sheep, poultry, and mice) does not display genetic variation, whereas the variation in the timing of growth often has a genetic basis (Kirkpatrick

and Lofsvold 1992). Therefore, an evolutionary response to the selection on growth might be limited. One reason for low heritabilities of growth rates could be that if selection consistently favored faster growth, bird species would all grow at maximum speed and the genetic variance in growth rates would have largely disappeared. Variation in growth rates among and within species would then reflect internal constraints (e.g., Ricklefs 1969b, 1973; chapter 11).

Variation in final body size has been found to be heritable in many studies on various species (e.g., great tits: Garnett 1981; van Noordwijk et al. 1988; song sparrows: Smith and Zach 1979; Smith and Dhondt 1980; Darwin's ground finches: Boag 1983; Price et al. 1984). Evolutionary change in body size dimensions was shown in medium ground finches, *Geospiza fortis* (Grant and Grant 1995). Survivors of a drought were larger than nonsurvivors, particularly in weight and wing length. In this well-studied population, heritabilities, including genetic correlations of the traits, were known. Indeed, when the next generation was measured, predicted and observed responses to selection matched well (Grant and Grant 1995). In contrast, no directional selection on body size could be demonstrated in a study on long-billed curlews (Redmond 1986). The height of vegetation determined whether small or large long-billed curlews were selected, and selection pressures on body size fluctuated over the years. A specific but variable range of body sizes within the population probably persisted. One problem with weight as a measure of body size is that it includes an overall size component, as well as a measure of condition. So far, the effects of the two components of weight on selection have not been separated. We do not know exactly whether postfledging mortality correlates with condition or with size.

Most often, the genetic system underlying the measured trait is unknown. Natural selection might act on an (unknown) correlated trait instead of the one that is being measured. In this case, the response to selection cannot be predicted (van Tienderen and de Jong 1994, and references therein). Based on studies concerning fledgling mass in great tits (van Noordwijk 1988b), tarsus length in collared flycatchers, *Ficedula albicollis* (Alatalo et al. 1990) and willow tits, *Parus montanus* (Thessing and Ekman 1994), these researchers argue that natural selection acted on the environmental component of the variation. This is, the fitness of a *genetically small* bird is different from the fitness of a bird that is of the same size because of environmental causes. When selection is acting on an environmentally but not genetically correlated trait, the consequences on fitness of genetic variation of growth could be different from those caused by environmental variation. We do not know how common this is, and it is basically a problem of understanding the system and identifying the traits under selection. If poor environ-

mental conditions affected both the phenotype and its fitness regardless of the genotype, the fitness of the same genotype under good and poor conditions would be different (see Price et al. 1988).

To avoid these problems to some degree, organisms can be experimentally separated from their environment. Let us, for example, assume that growth has a significant parental component, but there is no genetic correlation between the degree of parental care and the growth and final size of the young. This parental care can be generalized to consist of breeding in a better habitat by good-quality parents, providing a lot of good-quality food during the nestling period and good care after their offspring fledge. Nestlings provided with good parental care will grow fast and enjoy increased future survival and fertility. Natural selection acts on the provision of good parental care but not on growth or body size. The investigator will find a positive correlation between growth and body size and fitness and falsely predict an increase in growth rates and body size if these traits were heritable.

Experimental procedures can avoid these problems to some extent. In a study by Richner et al. (1989), chicks of carrion crows were hand-raised apart from their parents, and the correlation between body size (tarsus length) and dominance status was still present. This suggests that body size per se was the selection criterion and not parental influences correlated with body size. However, other traits (e.g., disease resistance) could be correlated with body size and might have been important for dominance. This example serves to illustrate how difficult it would be to exclude all possible confounding factors in order to demonstrate convincingly on which trait selection was acting.

Observational field studies have demonstrated correlations between environmental variables and growth; experimental studies, in which environmental variables have been manipulated sometimes identified the cause of the variation in growth. Missing are further investigations into the mechanisms of how the environmental variable affects growth and how that affects the fitness of the individual. This has rarely been done and is probably only possible through an integrated effort, including the study of physiological, ecological, and genetic aspects of growth.

References

- Alatalo, R.V., and A. Lundberg. 1986. Heritability and selection on tarsus length in the pied flycatcher (*Ficedula hypoleuca*). *Evolution* 40:547–583.
- Alatalo, R.V., L. Gustafsson, and A. Lundberg. 1990. Phenotypic selection on heritable size traits: Environmental variance and genetic response. *Amer. Nat.* 135:464–474.
- Albano, D.J. 1992. Nestling mortality of Carolina chickadees breeding in natural cavities. *Condor* 94:371–382.
- Amundsen, T. 1995. Egg size and early nestling growth in the snow petrel. *Condor* 97:345–351.
- Arendt, W.J. 1985. *Philornis* ectoparasitism of pearly-eyed thrashers. I. Impact on growth and development of nestlings. *Auk* 102:270–280.
- Arnold, S.J., and M.J. Wade. 1984. On the measurement of natural and sexual selection: Theory. *Evolution* 38: 709–719.
- Bancroft, G.T. 1984. Growth and sexual dimorphism of the boat-tailed grackle. *Condor* 86:423–432.
- Barret, R.T., T. Anker-Nilssen, F. Rikardsen, K. Valde, N. Røv, and W. Vader. 1987. The food, growth and fledgling success of Norwegian puffin chicks *Fratercula arctica* in 1980–1983. *Orn. Scand.* 18:73–83.
- Barret, R.T., and O.J. Runde. 1980. Growth and survival of nestling kittiwakes *Rissa tridactyla* in Norway. *Orn. Scand.* 11:228–235.
- Berthold, P. 1976. Über den Einfluss der Nestlingsnahrung auf die Jugendentwicklung, insbesondere auf das Flügelwachstum, bei der Mönchsgrasmücke (*Sylvia atricapilla*). *Vogelwarte* 28:257–263.
- Bertram, D.F., G.W. Kaiser, and R.C. Ydenberg. 1991. Patterns in the provisioning and growth of nestling rhinoceros auklets. *Auk* 108:842–852.
- Blancher, P.J., and R.J. Robertson. 1987. Effect of food supply on the breeding biology of western kingbirds. *Ecology* 68:723–732.
- Boag, P.T. 1983. The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galápagos. *Evolution* 37:877–894.
- Boag, P.T. 1987. Effects of nestling diet on growth and adult size of zebra finches (*Poephila guttata*). *Auk* 104: 155–166.
- Boag, P.T., and P.R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. *Science* 214:82–86.
- Bolton, M. 1991. Determinants of chick survival in the lesser black-backed gull: Relative contributions of egg size and parental quality. *J. Anim. Ecol.* 60:949–960.
- Bosque, C., and M.T. Bosque. 1995. Nest predation as a selective factor in the evolution of development rates in altricial birds. *Amer. Nat.* 145:234–260.
- Brisbin, L.I., Jr., G.C. White, and P.B. Bush. 1986a. PCB intake and the growth of waterfowl: Multivariate analyses based on a reparameterized Richards sigmoid model. *Growth* 50:1–11.
- Brisbin, L.I., Jr., G.C. White, P.B. Bush, and L.A. Mayack. 1986b. Sigmoid growth analyses of wood ducks: The effects of sex, dietary protein and cadmium on parameters of the Richards model. *Growth* 50:41–50.
- Bryant, D.M. 1975. Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. *Ibis* 117:180–216.
- Bumpus, H.C. 1899. The elimination of the unfit as illustrated by introduced sparrow, *Passer domesticus*. *Biol. Lect. (Woods Hole Marine Biol. Station)* 6:209–226.
- Burley, N. 1980. Clutch overlap and clutch size: Alternative and complementary reproductive tactics. *Amer. Nat.* 115: 223–246.
- Buttemer, W.A. 1992. Differential overnight survival by Bumpus' house sparrows: An alternate interpretation. *Condor* 94:944–954.
- Case, T.J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Quart. Rev. Biol.* 53:243–282.
- Cooch, E.G., D.B. Lank, A. Dzubin, R.F. Rockwell, and F. Cooke. 1991a. Body size variation in lesser snow geese:

- Environmental plasticity in gosling growth rates. *Ecology* 72:503–512.
- Cooch, E.G., D.B. Lank, R.F. Rockwell, and F. Cooke. 1991b. Long-term decline in body size in a snow goose population: Evidence of environmental degradation? *J. Anim. Ecol.* 60:483–496.
- Cooke, F., R.F. Rockwell, and D.B. Lank. 1995. The snow geese of La Pérouse Bay. *Natural Selection in the Wild*. Oxford Ornithology Series 4. Oxford University Press, Oxford.
- Coulson, J.C., and M.P. Johnson. 1993. The attendance and absence of adult kittiwakes *Rissa tridactyla* from the nest site during the chick stage. *Ibis* 135:372–378.
- Coulson, J.C., and J.M. Porter. 1985. Reproductive success of the Kittiwake *Rissa tridactyla*: The roles of clutch size, chick growth rates and parental quality. *Ibis* 127:450–466.
- Davies, N.B. 1986. Reproductive success of dunlocks *Prunella modularis*, in a variable mating system. I. Factors influencing provisioning rate, nestling weight and fledgling success. *J. Anim. Ecol.* 55:123–138.
- Emlen, S.T., P.H. Wrege, N.J. Demong, and R.E. Hegner. 1991. Flexible growth rates in nestling white-fronted bee-eaters: A possible adaptation to short-term food shortage. *Condor* 93:591–597.
- Emms, S.K., and N.A.M. Verbeek. 1991. Brood size, food provisioning and chick growth in the pigeon guillemot *Cephus columba*. *Condor* 93:943–951.
- Endler, J.A. 1986. *Natural Selection in the Wild*. Monographs in Population Biology 21. Princeton University Press, Princeton, N.J.
- Falconer, D.S. 1981. *Introduction to Quantitative Genetics*. 2nd ed. Longman, London.
- Fitzpatrick, J.W., and G.E. Woolfenden. 1988. Components of lifetime reproductive success in the Florida scrub jay. In *Reproductive Success* (T.H. Clutton-Brock, ed.). University of Chicago Press, Chicago, pp. 305–320.
- Gadallah, F.L., and R.L. Jefferies. 1995. Forage quality in brood rearing areas of the lesser snow goose and the growth of captive goslings. *J. Appl. Ecol.* 32:276–287.
- Galbraith, H. 1988. Effects of egg size and composition on the size, quality and survival of lapwing *Vanellus vanellus* chicks. *J. Zool. Lond.* 214:383–398.
- Garnett, M.C. 1981. Body size, its heritability and influence on juvenile survival among great tits, *Parus major*. *Ibis* 123:31–41.
- Gebhardt-Henrich, S.G. 1990. Temporal and spatial variation in food availability and its effects on fledgling size in the great tit. In *Population Biology of Passerine Birds* (J. Blondel, A. Gosler, J.-D. Lebreton, and R. McCleery, eds.). Springer Verlag, Heidelberg, pp. 175–185.
- Gebhardt-Henrich, S.G., and A.J. van Noordwijk. 1991. Nestling growth in the great tit I. Heritability estimates under different environmental conditions. *J. Evol. Biol.* 3: 341–362.
- Gebhardt-Henrich, S.G., and A.J. van Noordwijk. 1994. Nestling growth in the great tit. Environmental influences on the expression of genetic variances during growth. *Funct. Ecol.* 8:469–476.
- Grant, B.R., and P.R. Grant. 1989. Natural selection in a population of Darwin's finches. *Amer. Nat.* 133:377–393.
- Grant, P.R., and B.R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 49:241–251.
- Griffiths, R. 1992. Sex-biased mortality in the lesser backed gull *Larus fuscus* during the nestling stage. *Ibis* 134: 237–244.
- Groves, S. 1984. Chick growth, sibling rivalry, and chick production in American black oystercatchers. *Auk* 101: 525–531.
- Gustafsson, L., A. P. Møller, and J. Merilä. 1995. Genotype-by-environment interactions and environmental gradients in the barn swallow and the collared flycatcher. I. Morphological traits. In press.
- Gustafsson, L., D. Nordling, M.S. Andersson, B.C. Sheldon, and A. Qvarnström. 1994. Infectious diseases, reproductive effort and the cost of reproduction in birds. *Phil. Trans. Roy. Soc. Series* 346B: 323–331.
- Gustafsson, L., and W. Sutherland. 1988. The cost of reproduction in the collared flycatcher. *Nature Lond.* 335:813–817.
- Harris, M.P., D.J. Halley, and S. Wanless. 1992. The post-fledgling survival of young guillemots *Uria aalge* in relation to hatching date and growth. *Ibis* 134:335–339.
- Harris, M.P., and P. Rothery. 1985. The post-fledgling survival of young puffins *Fratercula arctica* in relation to hatching date and growth. *Ibis* 127:243–250.
- Haywood, S., and C.M. Perrins. 1992. Is clutch size in birds affected by environmental conditions during growth? *Proc. R. Soc. Lond.* 249B:195–197.
- Hedgren, S., and A. Linnman. 1979. Growth of Guillemot *Uria aalge* chicks in relation to time of hatching. *Orn. Scand.* 10:29–36.
- Heezik van, Y., and L. Davis. 1990. Effects of food variability on growth rates, fledgling sizes and reproductive success in the yellow-eyed penguin *Megadyptes antipodes*. *Ibis* 132:354–365.
- Istock, C.A. 1983. The extent and consequences of heritable variation for fitness characters. In *Population Biology: Retrospect and Prospect* (C.R. King and P.S. Dawson, eds.). Columbia University Press, New York, pp. 61–96.
- James, F.C., and C. NeSmith. 1988. Nongenetic effects in geographic differences among nestling populations of red-winged blackbirds. *Acta Congr. Int. Orn.* 19(2): 1424–1433.
- Johnston, R.D. 1993. Effects of diet quality on the nestling growth of a wild insectivorous passerine, the house martin *Delichon urbica*. *Funct. Ecol.* 7:255–266.
- Keller, L., and A.J. van Noordwijk. In press. Effects of local environmental conditions on nestling growth in the great tit (*Parus major*). *Ardea*.
- Kersten, M., and A. Brenninkmeijer. 1995. Growth, fledging success and postfledging survival of juvenile oystercatchers *Haematopus ostralegus*. *Ibis* 137:396–404.
- Kirkpatrick, M., and D. Lofsvold. 1992. Measuring selection and constraint in the evolution of growth. *Evolution* 46:954–971.
- Klaassen, M., and C. Bech. 1992. Resting and peak metabolic rates of Arctic tern nestlings and their relation to growth rate. *Physiol. Zool.* 65:803–814.
- Klaassen, M., B. Habekotté, P. Schinkelshoek, E. Stienen, and P. van Tienen. 1994. Influence of growth rate retardation on time budgets and energetics of arctic tern *Sterna paradisaea* and common tern *S. hirundo* chicks. *Ibis* 136:197–204.
- Konarzewski, M., and J.R.E. Taylor. 1989. The influence of weather conditions on growth of little auk *Alle alle* chicks. *Orn. Scand.* 20:112–116.
- Krementz, D.G., J.D. Nichols, and J.E. Hines. 1989. Post-fledging survival of European starlings. *Ecology* 70: 646–655.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Clarendon, Oxford.

- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- Lacombe, D., D.M. Bird, and K.A. Hibbard. 1994. Influences of reduced food availability on growth of captive American kestrels. *Can. J. Zool.* 72:2084–2089.
- Larsson, K., and P. Forslund. 1991. Environmentally induced morphological variation in the barnacle goose, *Branta leucopsis*. *J. Evol. Biol.* 4:619–636.
- Lehikoinen, E. 1986. Dependence of winter survival on size in the great tit *Parus major*. *Orn. Fenn.* 63:10–16.
- Lindholm, A., G. Gauthier, and A. Desrochers. 1994. Effects of hatch date and food supply on gosling growth in arctic-nesting greater snow geese. *Condor* 96:898–908.
- Magrath, R.D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *J. Anim. Ecol.* 60:335–351.
- Martin, T.E. 1987. Food as a limit on breeding birds: A life-history perspective. *Ann. Rev. Ecol. Syst.* 18:453–487.
- Martin, T.E. 1992. Interaction of nest predation and food limitation in reproductive strategies. *Curr. Orn.* 9:163–197.
- Merino, S., and J. Potti. 1995. Mites and blowflies decrease growth and survival in nestling pied flycatchers. *Oikos* 73:95–103.
- Mock, D.W., T.C. Lamey, C.F. Williams, and A. Pelletier. 1987. Flexibility in the development of heron sibling aggression: An intraspecific test of the prey-size hypothesis. *Anim. Behav.* 35:1386–1393.
- Mock, D.W., and B.J. Ploger. 1987. Parental manipulation of optimal hatch asynchrony in cattle egrets: An experimental study. *Anim. Behav.* 35:150–160.
- Møller, A.P. 1990. Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. *Ecology* 71:2345–2357.
- Møller, A.P. 1995. Parasitism and the evolution of host life history. In *Coevolutionary Biology of Birds and Their Parasites* (D.H. Clayton and J. Moore, eds.). Oxford University Press, Oxford.
- Morton, M.L., K.W. Sockman, and L.E. Peterson. 1993. Nest predation in the mountain white-crowned sparrow. *Condor* 95:72–82.
- Newton, I., and D. Moss. 1986. Post-fledgling survival of sparrowhawks *Accipiter nisus* in relation to mass, brood size and brood composition at fledgling. *Ibis* 128:73–80.
- Nisbet, I.C.T., J.A. Spendlow, and J.S. Hatfield. 1995. Variation in growth rate of roseate tern chicks. *Condor* 97:335–344.
- Noordwijk, A.J. van. 1988a. Sib competition as an element of genotype-environment interaction for body size in the great tit. In *Population Genetics and Evolution* (G. de Jong, ed.). Springer Verlag, Heidelberg, pp. 124–137.
- Noordwijk, A.J. van. 1988b. Two-stage selection in which the first stage only reduces the environmental variation in body size in the great tit. In *Acta of the Congress of International Ornithologists*. Vol. 19, no. 2 (H. Ouellet, ed.). University of Ottawa Press, Ottawa, pp. 1408–1415.
- Noordwijk, A.J. van, L.C.P. Keizer, J.H. van Balen, and W. Scharloo. 1981. Genetic variation in egg dimensions in natural populations of the great tit. *Genetica* 55:221–232.
- Noordwijk, A.J. van, J.H. van Balen, and W. Scharloo. 1988. Heritability of body size in a natural population of the great tit (*Parus major*) and its relation to age and environmental conditions during growth. *Gen. Res. (Cambridge)* 51:149–162.
- Noordwijk, A.J. van, R.H. McCleery, and C.M. Perrins. 1995. Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *J. Anim. Ecol.* 64:451–458.
- Noordwijk, A.J. van, and J.H. van Balen. 1988. The great tit, *Parus major*. In *Reproductive Success* (T.H. Clutton-Brock, ed.). University of Chicago Press, Chicago, pp. 119–135.
- Nur, N. 1984. The consequences of brood size for breeding blue tits II. Nestling weight, offspring survival and optimal brood size. *J. Anim. Ecol.* 53:497–517.
- O'Connor, R.J. 1975. Initial size and subsequent growth in passerine nestlings. *Bird-Banding* 46:329–340.
- O'Connor, R.J. 1977. Growth strategies in nestling passerines. *Liv. Bird* 16:209–238.
- O'Connor, R.J. 1978. Brood reduction in birds: Selection for fratricide, infanticide, and suicide? *Anim. Behav.* 26:79–96.
- Owen, M., and J.M. Black. 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. *J. Anim. Ecol.* 58:603–617.
- Perrins, C.M. 1965. Population fluctuations and clutch size in the great tit, *Parus major* L. *J. Anim. Ecol.* 34:601–647.
- Perrins, C.M. 1979. *British Tits*. William Collins, Glasgow.
- Price, T.D., and P.R. Grant. 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. *Evolution* 38:483–494.
- Price, T.D., P.R. Grant, and P.T. Boag. 1984. Genetic changes in the morphological differentiation of Darwin's ground finches. In *Population Biology and Evolution* (K. Wöhrmann and V. Loeschke, eds.). Springer, Heidelberg, pp. 49–66.
- Price, T.D., M. Kirkpatrick, and S.J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. *Science* 240:798–799.
- Prince, P.A., and C. Ricketts. 1981. Relationship between food supply and growth in albatrosses: An interspecies chick fostering experiment. *Orn. Scand.* 12:207–210.
- Pugesek, B.H. 1995. Offspring growth in the California gull: Reproductive effort and parental experience hypothesis. *Anim. Behav.* 49:641–647.
- Quinney, T.E., D.J.T. Huxell, and C.D. Ankney. 1986. Sources of variation in growth of tree swallows. *Auk* 103:389–400.
- Redmond, R.L. 1986. Egg size and laying date of long-billed curlews *Numenius americanus*: Implications for female reproductive tactics. *Oikos* 46:330–338.
- Rhymer, J.M. 1988. The effect of egg size variability on thermoregulation of mallard (*Anas platyrhynchos*) offspring and its implications for survival. *Oecologia* 75:20–24.
- Rhymer, J.M. 1992. An experimental study of geographic variation in avian growth and development. *J. Evol. Biol.* 5:289–306.
- Richner, H. 1989a. Habitat-specific growth and fitness in carrion crows (*Corvus corone corone*). *J. Anim. Ecol.* 58:427–440.
- Richner, H. 1989b. Phenotypic correlates of dominance in carrion crows and their effects on access to food. *Anim. Behav.* 38:606–612.
- Richner, H. 1991. The growth dynamics of sexually dimorphic birds and Fisher's sex ratio theory: Does sex-specific growth contribute to balanced sex ratios? *Funct. Ecol.* 5:19–28.
- Richner, H. 1992. The effect of extra food on fitness in breeding carrion crows. *Ecology* 73:330–335.
- Richner, H., P. Christe, and A. Oppliger. 1995. Paternal investment affects malaria prevalence. *Proc. Nat. Acad. Sci. U.S.A.* 92:1192–1194.

- Richner, H., A. Oppliger, and P. Christe. 1993. Effect of an ectoparasite on reproduction in great tits. *J. Anim. Ecol.* 62:703–710.
- Richner, H., P. Schneider, and H. Stürnimann. 1989. Life-history consequences of growth rate depression: An experimental study on carrion crows (*Corvus corone corone* L.). *Funct. Ecol.* 36:17–624.
- Ricklefs, R.E. 1965. Brood reduction in the curve-billed thrasher. *Condor* 67:505–510.
- Ricklefs, R.E. 1968. On the limitation of brood size in passerine birds by the ability of adults to nourish their young. *Proc. Nat. Acad. Sci. U.S.A.* 61:847–851.
- Ricklefs, R.E. 1969a. An analysis of nestling mortality in birds. *Smith. Contr. Zool.* 9:177–210.
- Ricklefs, R.E. 1969b. 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. *Ibis* 115:177–210.
- Ricklefs, R.E. 1982. Some considerations on sibling competition and avian growth rates. *Auk* 99:141–147.
- Ricklefs, R.E. 1984. Components of variance in measurements of nestling European starlings *Sturnus vulgaris* L. in southeastern Pennsylvania. *Auk* 101:319–333.
- Ricklefs, R.E. 1993. Sibling competition, hatching asynchrony, incubation periods and lifespan in altricial birds. *Curr. Orn.* 11:199–276.
- Ricklefs, R.E., and S. Peters. 1981. Parental components of variance in growth rate and body size of nestling European starlings (*Sturnus vulgaris*) in eastern Pennsylvania. *Auk* 98:39–48.
- Ross, H.A., and I.A. McClaren. 1981. Lack of differential survival among young Ipswich sparrows. *Auk* 98:495–502.
- Saether, B.-E. 1994. Food provisioning in relation to reproductive strategy in altricial birds: A comparison of two hypotheses. *Evolution* 48:1397–1406.
- Samuel, M.D., D.R. Goldberg, D.B. Thomas, and P. Sharp. 1995. Effects of *Mycoplasma anatis* and cold stress on hatching success and growth of mallard ducklings. *J. Wildl. Dis.* 31:172–178.
- Schiffnerli, L. 1973. The effect of egg weight on the subsequent growth of nestling great tits *Parus major*. *Ibis* 115:549–558.
- Schluter, D., and J.N.M. Smith. 1986. Natural selection on beak and body size in the song sparrow. *Evolution* 40:221–231.
- Schmutz, J.A. 1993. Survival and pre-fledgling body mass in juvenile emperor geese. *Condor* 95:222–225.
- Schreiber, R.W. 1976. Growth and development of nestling brown pelicans. *Bird Band.* 47:19–39.
- Sedinger, J.S., and P.L. Flint. 1991. Growth rate is negatively correlated with hatch date in black brant. *Ecology* 72:496–502.
- Shea, R.E., and R.E. Ricklefs. 1985. An experimental test of the idea that food supply limits the growth rate in a tropical pelagic seabird. *Amer. Nat.* 126:116–122.
- Smith, H.G., H. Källander, and J.A. Nilsson. 1989. The trade-off between offspring number and quality in the great tit *Parus major*. *J. Anim. Ecol.* 58:383–401.
- Smith, H., and K.-J. Wettermark. 1995. Heritability of nestling growth in cross-fostered European starlings *Sturnus vulgaris*. *Genetics* 141:657–665.
- Smith, J.N.M., and P. Arcese. 1988. Effects of supplemental food on growth and adult size in the song sparrow. *Acta Congr. Int. Orn.* 19(2):1416–1423.
- Smith, J.N.M., and A.A. Dhondt. 1980. Experimental confirmation of heritable morphological variation in a natural population of song sparrows. *Evolution* 34:1155–1158.
- Smith, J.N.M., and R. Zach. 1979. Heritability of some morphological characters in the song sparrow. *Evolution* 33:460–467.
- Stamps, J., A. Clark, P. Arrowood, and B. Kus. 1985. Parent-offspring conflict in budgerigars. *Behaviour* 94:1–40.
- Teather, K.L., and P.J. Weatherhead. 1994. Allometry, adaptation, and the growth and development of sexually dimorphic birds. *Oikos* 71:515–525.
- Thessing, A., and J. Ekman. 1994. Selection on the genetical and environmental components of tarsal growth in juvenile willow tits (*Parus montanus*). *J. Evol. Biol.* 7:713–726.
- Tienderen, P.H. van, and G. de Jong. 1994. A general model of the relation between phenotypic selection and genetic response. *J. Evol. Biol.* 7:1–12.
- Tinbergen, J.M. 1987. Population biology of the great tit (*Parus major*) and related species. Progress Report. Institute for Ecological Research, pp. 5–18.
- Tinbergen, J.M., and M.C. Boerlijst. 1990. Nestling weight and survival in individual great tit (*Parus major*). *J. Anim. Ecol.* 59:1113–1127.
- Tinbergen, J.M., J.H. van Balen, P.J. Drent, A.J. Cavé, J.A.L. Mertens, and J. den Boer-Hazewinkel. 1987. Population dynamics and cost-benefit analysis. *Neth. J. Zool.* 37:180–213.
- Ulfstrand, S., R.V. Alatalo, A. Carlson, and A. Lundberg. 1981. Habitat distribution and body size of the great tit *Parus major*. *Ibis* 123:495.
- Verhulst, S., and J.M. Tinbergen. 1991. Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major*. *J. Anim. Ecol.* 60:269–282.
- Vinuela, J., and J. Bustamante. 1992. Effect of growth and hatching asynchrony on the fledging age of black and red kites. *Auk* 109:748–757.
- Werschkul, D.F. 1979. Nestling mortality and the adaptive significance of early locomotion in the little blue heron. *Auk* 96:116–130.
- Werschkul, D.F., and J.A. Jackson. 1979. Sibling competition and avian growth rates. *Ibis* 121:97–102.
- Westneat, D.F. 1992. Nesting synchrony by female red-winged blackbirds—effects on predation and breeding success. *Ecology* 73:2284–2294.
- Wiggins, D.A. 1989. Heritability of body size in cross-fostered tree swallow broods. *Evolution* 43:1808–1811.