

# PHYSIOLOGICAL DIFFERENTIATION OF VERTEBRATE POPULATIONS

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## INTRODUCTION

. . . The foundation of most evolutionary theory rests upon inferences drawn from geographic variation or upon the verification of predictions made about it.

Gould & Johnston (120, p. 457)

The study of geographic variation occupies a central position in evolutionary biology . . . because geographic variation is ordinarily the smallest amount of evolution that can be detected in nature and because evolutionary theory, in its strongest form, applies only to small evolutionary change.

Arnold (7, p. 510)

### *The Importance of Population Differentiation*

Although studies of geographic variation are relatively common, the vast majority have dealt with morphometric or meristic traits (13, 120, 297, 327), allozymes (150, 233, 327), or most recently, mitochondrial DNA (9). The relative rarity of studies of geographic variation in physiological traits (see 42, 245, 312 for reviews of early studies) is somewhat surprising, considering that a major focus within vertebrate "physiological ecology," "comparative physiology," "environmental physiology," and "biophysical ecology" is the study of adaptation (14, 15, 44, 75, 102, 112, 156, 181, 244, 246, 298, 299). Of course, populations may show differentiation on other than large geographic scales, such as "microgeographic" (150, 188, 213, 233, 290),

temporal (164, 165, 213, 253, 278, Armitage, this volume) or altitudinal; the last has received considerable attention from vertebrate physiologists.

Why are population differences in physiology not studied more often? We suggest four reasons: (i) Physiological measurements require living organisms. Collecting from multiple populations is formidable enough without the additional difficulty of making physiological measurements. "Expeditionary physiology" is possible, but requisite equipment often is considerably less portable than that needed for sampling tissues or for obtaining study skins or skeletons. Moreover, physiological measurements can be quite time-consuming and require maintaining animals in a healthy state, sometimes for weeks or months, to achieve a common state of acclimation. (ii) Physiologists and evolutionary biologists often share little in the way of training, interests, perspectives, techniques, and study organisms. Population geneticists routinely study *Drosophila* because they are small and so can be bred in large numbers. Physiological ecologists rarely study *Drosophila* because they are small and hence intractable for most physiological measurements (but see 63, 137, 158, 166). Nonetheless, some studies of population differentiation in physiological traits have been done. Many involve invertebrates, including *Drosophila* (42, 63, 137, 158, 223, 233, 245, 312 refs. therein). Another cohort of researchers has come from a background in population genetics, having moved toward physiology in an attempt to discover the adaptive significance of population differences in allozymes (104, 137, 191, 223, 224, 243, refs. therein). (iii) To increase the likelihood of finding differences and exemplary cases of adaptation, comparative physiologists have tended to focus on species expected to display extremes in physiological function (102, 255). Recognizing problems introduced by rampant acclimatization, physiologists may have been inhibited from searching for relatively small population differences. Consequently, the focus on proximate mechanisms of coping with environmental change (i.e. acclimatization) drew more attention than the possibility of genetic differentiation among populations. (iv) "Typological thinking" still exists among many physiologists (102). (The coexistence of typological thinking and ardent adaptationism is somewhat surprising!)

### *Scope of This Review and Some Definitions*

We review population differences in physiological traits of vertebrates. As few physiological studies of natural variation allow direct inferences about genetics, we have not restricted ourselves to these. We avoid the issue of how to define a population and instead rely on each author's judgment. We have attempted to consider examples involving all physiological processes in all vertebrate classes except Chondrichthyes and Agnatha. We have excluded human examples, and our review reflects our particular physiological and taxonomic interests.

*Physiology* has to do with how organisms work. But where to draw lines between physiology on the one hand and behavior, morphology, or biochemistry on the other is not always clear (112, 245). For example, morphological (e.g. heart mass), biochemical (e.g. blood hemoglobin content, in vitro enzyme activity), and whole-animal performance traits (e.g. maximal sprint running speed) are routinely studied by "physiologists." We have therefore chosen to include certain morphological, biochemical, or performance measures wherever they seem closely tied to physiological function. Our holistic view is consistent with recent recommendations to "adopt and promulgate the definition of physiology as 'Integrative Biology'" (2). Studies relating growth or developmental rate to multilocus heterozygosity are reviewed elsewhere (104, 213, 223; refs. therein).

Many *life history traits* (e.g. fecundity, reproductive effort, growth rate, body size) are closely tied to physiology. However, we include only a few examples here, because variation in life history traits is reviewed extensively elsewhere (e.g. 27, 33, 82, 107, 118, 186, 200, 218, 226, 235, 253–255, 261, 289, 290; Godfray, this volume). The empirical validity of several well-known *biogeographic rules* pertaining to body size, proportions, and coloration (e.g. Allen's, Bergmann's, Gloger's) is highly questionable (39, 117, 139, 157, 173, 174, 252, 312, 327), and thorough "common garden" (60a) studies are rare (but see 77, 196, 252). Island populations also show characteristic patterns of gigantism or dwarfism (24, 25, 83, 226), but physiological correlates have not been studied. Variation in body size results partly from variation in growth rate, the genetic and physiological bases of which have been well studied in some domestic animals (99, 113, 256).

The term *adaptation* is used in two ways by physiologists (321). First, adaptation may have the traditional evolutionary meaning of genetic changes *in a population* occurring in response to either natural or artificial selection. Second, adaptation may refer to any change that occurs *within an individual* in response to changes in the environment, *and* that helps the organism function "better" under those changed conditions (e.g. 245). To quote Dejours (75, p. 14): "Adaptation consists in a change minimizing the physiological strain which results from a stressful environment." In the physiological literature, many authors are imprecise in their use of the word adaptation (321), and many are unclear as to whether they think observed population differences are in part genetically based or represent entirely acclimatization.

Nongenetic changes in physiology occurring during the lifetime of an individual generally are termed acclimation or acclimatization. *Acclimation* refers to changes that occur in response to change in any component of the environment in the laboratory. *Acclimatization* refers to the same, but as it occurs in nature. Most cases of acclimation or acclimatization are adaptive in the physiological sense (e.g. 55, 208), although physiologists have tended to

be too liberal in interpreting specific cases of physiological adaptation as evolutionarily adaptive (43, 102, 321). Nevertheless, a general capacity for acclimation or acclimatization is certainly adaptive in the evolutionary sense, and such capacity may itself be genetically based and subject to adaptive evolution (114, 115, 300).

Changes as a result of acclimation or acclimatization are generally reversible and are examples of *phenotypic plasticity* (131, 267, 300). Nongenetic adaptation buys time for individuals and for populations and "restores flexibility to physiological responses much as learning restores flexibility to behavior" (285, p. 401). As such, physiological adaptation is but one component of the overall "graded response" system that organisms may use when faced with changing environmental conditions, and nongenetic adaptive modifications may "prepare the way" for "subsequent evolutionary advance" (114, p. 100). Thus, phenotypic plasticity in response to environmental changes may reduce selection pressures and so "discourage the building up of geographic physiological races" (131, p. 53).

## NATURE VERSUS NURTURE

Population differences in physiological traits may be due to genetic and/or environmental effects or their interaction. From a physiological perspective, any comparison showing (or failing to show) population differences may be of interest. Once population differences in physiology are discovered, they may be related to behavioral and ecological variation (a common goal of physiological ecologists) or to underlying mechanistic bases at lower levels of biological organization (a common goal of comparative physiologists and biochemists). From an evolutionary perspective, however, comparisons that allow conclusions regarding genetic differentiation are of prime importance for most phenotypic traits (300).

### *Special Problems Posed by Physiology*

Physiological traits are highly susceptible to a wide range of environmental factors (e.g. nutritional status, stress, acclimatization, early environmental effects, maternal effects); indeed, much of the physiological literature addresses these effects. For some traits, the magnitude of environmental effects can be quite large relative to the magnitude of genetic differences among populations; unfortunately, experimental data are rare (131, 132, 153, 155). When population differences in physiology are found in field-fresh animals, environmental effects are likely to be present (cf 300).

Seasonal variation in physiological traits has been documented innumerable times. Hence, populations might show differences simply because they are at different points on an annual cycle. Seasonal rhythms may be endogenous

and/or driven by environmental variables such as photoperiod (19, 40, 55, 78, 100, 138, 186, 194, 200, 218, 226, 242, 294, 326). The variety of traits that vary seasonally is surprising; examples include life history traits (253), gut morphology (271), and allozymes of blood proteins (214) and various enzymes (156). Physiological traits can vary on a daily basis as well; daily cycles in metabolic rates, body temperature, heat tolerance, blood pressure, and physical performance ability are well known (e.g. 43, 170, 240, 242). Problems due to annual and daily cycles are not always recognized by researchers.

Potential complications arising from acclimatization and other environmental effects often are dealt with by acclimating animals in the laboratory to standard conditions before measuring physiological traits. But not all environmental effects on physiological, morphological, or behavioral traits are reversible, particularly if they occur during early or critical periods of development (10–12, 75, 131, 136, 173, 174, 181, 199, 201, 209, 222, 235, 252, 268, 275, 300, refs. therein: but see 256). For example, diet can affect gut morphology and function in a variety of vertebrates (e.g. 12, 124, 181, 215, 271, refs. therein). Diet can even affect patterns of hibernation in small mammals (116). Nonreversible changes are troublesome for studies of population differences, because they are not eliminated by acclimation.

### *“Common Garden” Experiments—No Design is Ideal*

Although proximate environmental effects can confound population comparisons, few studies have used a “common garden” design (e.g. 60a, 251) to study physiological differences of vertebrate populations. The usual approach of acclimation to common laboratory conditions is not guaranteed to erase previous environmental influences. The next most common approach is to rear animals from birth (or near birth) in the laboratory, by collecting gravid females, eggs, or newborns from the wild. However, differences due to maternal (or paternal—11) effects may occur at any time during development, and in some cases prior to conception. Maternal effects may even persist for more than one generation (257); a well-known example involves litter size in *Mus musculus* (98, 99). Some parental effects might be partly controlled statistically by using parental traits (e.g. age, body mass, parity) as covariates in comparisons (e.g. 109, 110, 304).

As another way to eliminate possible maternal and other environmental effects, populations might be raised for multiple generations in captivity. Unfortunately, laboratory selection pressures, however unintentional, undoubtedly will differ from those in nature (10, 131) and may lead to changes in genetic composition. Consequently, comparisons among laboratory populations may not reliably reflect the genetic differences present in nature (e.g. 219). Incorporating time in captivity as a covariate may help to account for such effects (149, 219).

Thus, no "common garden" experimental design is ideal. In many cases, studying lab-reared offspring of field-collected adults is the best compromise. Comparisons of species may also be confounded by environmental effects. Biologists generally seem less concerned about this problem, however, and most interspecific comparative studies do not involve adequate common garden controls. This includes the vast majority of the classic studies cited in comparative physiology textbooks.

The disadvantage of genetic changes occurring over multiple generations in captivity (including the domestication process) can be turned into an advantage, as genetic drift and/or artificial selection can produce divergent (or convergent: 65) lines (populations) useful for a variety of purposes (e.g. 7, 11, 12, 21, 54, 63, 78, 81, 90, 96, 99, 113, 123, 166, 197, 198, 200, 211, 215, 239, 247, 256, 257, 259, 261, 266, 324).

## DOES PHYSIOLOGY VARY AMONG VERTEBRATE POPULATIONS?

### *Mammalia*

Many studies of population differences have involved *Peromyscus* or *Mus*, two speciose rodent genera that are easy to maintain in captivity and have short generation times. A thorough review of breeds of domestic mammals or of the quantitative genetics literature in general is beyond the scope of this review. Breed differences in physiology exist in domestic dogs (59, 108, refs. in 245, 324) and in cattle and sheep (refs. in 202, 203, 245, 322).

**GROWTH, REPRODUCTION, AND LIFE HISTORY TRAITS** Both migratory and nonmigratory (e.g. in Ngorongora Crater, Tanzania) populations of ungulates exist, and population differences in social structure may covary with habitat in some mammals. Reviews of population differences in reproductive characteristics of free-living mammals are available elsewhere (33, refs. in 40, 61, 62, 184, 218, 226). A variety of reproductive traits show geographic variation within species of *Peromyscus* (218). Millar (218, p. 196) concludes that "Little modification in basic reproductive and developmental patterns is evident within species that occupy diverse environments; differences in the timing of reproductive events constitute the major adaptation to different environments at the intraspecific level." Desjardins et al (78) have used artificial selection to alter the reproductive photoresponsiveness of deer mice, and Lynch et al (200) report differences in photoresponsiveness between two captive breeding stocks of the Djungarian hamster (see also 218). Comparisons of domestic mammals with their wild counterparts often show that the former are less seasonal in their reproduction (refs. in 40), and domestic *Rattus* and *Mus* are essentially aseasonal. Millar & Threadgill (219)

conclude that, in general, no major differences in reproductive and developmental patterns exist between wild, captive, and domesticated stocks of *Peromyscus*. This is not to say that *no* differences exist. The relationships of various reproductive traits to maternal mass differ among populations of captive-bred *Peromyscus* (96), and differences in offspring size and the trade-off between number and size of offspring "may represent nothing more than laboratory artifacts" (219, p. 1719). In a common garden experiment, cotton rat populations differed in their response to food restriction; Kansas dams, with larger litters, were more severely affected than were Tennessee dams (209).

Montane-mesic and lowland-xeric populations of *Marmota flaviventris* held under constant conditions in the lab for >25 months differ in the circannual rhythms of food consumption and body mass (317); in the field, population differences in growth rates and activity times occur (216; Armitage, this volume; refs. therein).

Latitudinal clines in pupping data exist in a number of pinniped species (107, 295), but their genetic basis, if any, is unknown. For some species, variation in the date of birth is apparently cued by photoperiod acting through the mechanism of delayed implantation (294). Similar phenomena occur in other Carnivora such as weasels (186).

**THERMAL BIOLOGY, THERMOREGULATION, AND RESTING METABOLISM** Acclimation and acclimatization of mammalian thermoregulatory variables in response to temperature and/or photoperiod have been studied extensively (55, 71, 132, 138, 245, 322). For example, changes in response to cold exposure may include fur growth, increased resting metabolic rate, increased body temperature, shifts in critical temperatures, increased sensitivity to norepinephrine-induced nonshivering thermogenesis, increased amounts of brown fat, changes in masses of internal organs, increases in  $\text{Na}^+$ ,  $\text{-K}^+$ -ATPase activity, and increased food consumption. Interestingly, changes induced by acclimation may differ substantially from those seen under natural acclimatization. Some seasonal cycles persist when animals are held in the lab under constant conditions (12, 71, 132, 138, 201, 317). However, we know of no longitudinal studies (following individuals) of natural seasonal variation in thermoregulatory parameters.

The lability of mammalian thermoregulatory traits indicates that common garden approaches are extremely important for population comparisons. Moreover, several studies demonstrate that environmental factors acting early in life may have large and lasting influences on thermoregulatory traits of mammals (11, 12, 136, 199, 201).

Much of the earlier work on geographic differences in thermoregulation of rodents is in Russian, and some provides evidence that geographic population

differences may in part be genetically based (132). Unfortunately, many of the earlier studies on population differences are difficult to interpret, because (i) combinations of wild caught and laboratory born (sometimes to females captured while gravid) animals are studied, (ii) metabolic rate is expressed per gram (metabolic rate generally does not scale as  $[\text{body mass}]^{1.00}$ ), and (iii) statistical analyses are lacking or inadequate. Some of the relevant studies completed since Hart's review (132) are discussed below, and many suffer from the same problems. "Thermal conductance," used to describe the relationship between heat production and ambient temperature below the thermal neutral zone, is misleading but still in common use.

Body temperature appears to show little among-population variation, and whether basal metabolic rate (BMR) shows climatic adaptation within species of small mammals is still controversial (39, 132, 312). MacMillen & Garland (204), analyzing a multispecies sample of 31 *Peromyscus* populations taken from the literature, found a significant partial regression (after accounting for body mass effects) of basal metabolic rate (BMR) on environmental temperature: populations from hotter habitats tended to have lower BMRs. Neither latitude, precipitation nor "desert index" added significantly to the predictive equation.

Thompson (296) shows significant subspecific differences in BMR and heat loss coefficient (a.k.a. "thermal conductance") in harvest mice (*Reithrodontomys megalotis*). The subspecies differ also in propensity to enter shallow daily torpor, consistent with previous reports for this species and suggestions for *Peromyscus* subspecies. [Populations of pygmy possum (*Cercartetus nanus*) may also differ in torpor patterns (F. Geiser, personal communication).] Chaffee (54) artificially selected for tendency to hibernate in hamsters.

Two populations of golden spiny mice born and bred in the laboratory differ in nonshivering thermogenesis and possibly in thyroid status (32). Subsequently, Haim & Borut (128) reported differences in ability to maintain body temperature when exposed to 6°C and in resting O<sub>2</sub> consumption below 20°C, but not in O<sub>2</sub> consumption within the thermal neutral zone or in thermal conductance; these animals were acclimated to common conditions for at least one month. Two populations of bushy-tailed gerbil acclimated to common conditions for at least three weeks show differences in resting O<sub>2</sub> consumption and body temperature when measured at 6°C, but not within the thermal neutral zone (35°C); nor did thermal conductance differ (129). Desert and mesic striped mice differ in resting oxygen consumption, body temperature, and thermal conductance after three weeks of laboratory acclimation (130).

For field-fresh animals, Hulbert et al (167) showed differences in plasma thyroxine levels among coastal, desert, and "intermediate" populations of several species of California rodents. These differences were greatly reduced



after 10 weeks in captivity. Minimal and summit metabolism, measured after 2–5 weeks in captivity, apparently did not differ among populations, although sample sizes were small. For all three physiological traits, desert populations tend to show the lowest values.

Scheck (263) studied laboratory-reared  $F_1$  offspring of wild-caught adult cotton rats from northern Kansas and south-central Texas. Kansas animals have a lower BMR, lower critical temperatures (both upper and lower), and lower thermal conductance, but body temperatures and evaporative water loss (EWL) are similar. Scheck (263) interpreted these lower values in Kansas animals as adaptive in the evolutionary sense and possibly permissive for northward range expansion within the last century. However, Scheck (264) found no differences between the two populations in the development of thermoregulatory abilities in 1–18 day old  $F_2$  animals. Finally, the populations differ in growth rates, and Kansas animals have lower metabolic rates at 10°C and increased pelage insulation (265). In one of the most thorough common garden studies, Derting & McClure (77) studied cotton rats from laboratory-bred populations representing seven distinct geographic locations. Unfortunately, the focus of this study was on correlations between BMR and indices of production; the significance of population differences is not clearly reported, nor is it clear whether population differences in BMR exist after accounting for differences in body mass.

Nevo (232) and colleagues have studied geographic variation among 12 populations of mole rats (*Spalax ehrenbergi*) from Israel. These populations comprise four chromosomal forms that are considered to “represent four sibling species at final stages of speciation” (149). Population and/or species differences in BMR, nonshivering thermogenesis in response to noradrenaline, thermoregulation, heart and respiration rates, and hematological characteristics (6, 232) have been demonstrated, although origin (wild-captured or lab-born) and length of captivity are not clearly stated in many of these papers. Many of the traits studied covary with environmental characteristics in a way that has been interpreted as adaptive and possibly related to speciation (6, 232).

Berry and colleagues have extensively studied population variation in *Mus musculus* (now termed *Mus domesticus*) (24, 172). Many physiological differences have been demonstrated, but not with common garden experiments. Berry et al (25, p. 73) suggest that many of the observed “large inter-island differences can be attributed primarily to ‘instant sub-speciation’ produced by each colonization depending on a probable small number of effective founders.” Perhaps the most sophisticated study of geographic variation in thermoregulatory traits of small mammals is that of Lynch (196). *Mus musculus* were captured from populations in five states, representing a thermal cline along the eastern United States (Maine to Florida). Mice were bred in the

laboratory, and their  $F_1$  offspring were tested. Populations show significant differences in body temperature and amount of brown adipose tissue, but not in a clinal pattern expected from thermal conditions (see also 12, 172). This lack of evolutionarily adaptive clinal variation was related to previous studies of the quantitative genetics of these and other traits. Because the physiological traits show very low heritabilities, they were not predicted to show adaptive clinal variation (196). Nest building behavior and body mass, on the other hand, show relatively high heritabilities and, as predicted, show apparently adaptive clinal variation. Strain differences in resting or basal oxygen consumption have not been clearly demonstrated in *Mus musculus* (159, 198, 239), in part owing to inappropriate corrections for body size effects.

Ringtail cats (*Bassariscus astutus*) from a desert population show lower BMR and other thermoregulatory differences when compared to animals from a mesic habitat (58). Similar differences exist among breeds of cattle and sheep (322). Wild piglets show higher resistance to cold than do domestic piglets, apparently owing to both higher oxygen consumption (heat production) and extra pelage (106).

Variation in resting metabolic rate may have a variety of functional bases at lower levels of biological organization, but little information is available concerning population differences within species (but see 167 on thyroid function). Strain differences in body temperature, and a circadian dependence of these differences, have been demonstrated in *Mus musculus* (64). Mice selected for large and small size differ in a variety of ways, including the amount of brown adipose tissue, "strongly suggesting that much of the decreased efficiency of the small lines is due to heat production by brown fat" (198, p. 299). Strain differences in amount of brown adipose tissue and in glucose utilization (measured in vitro) have also been demonstrated for mice (159). In vitro preparations of calf muscles reveal breed differences in oxygen consumption, owing to the  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase-independent component of respiration (cf 71), and in rate of protein synthesis, but not in the  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase-dependent component of respiration (123).

In summary, the available data, although relatively abundant, are too fraught with difficulties to allow firm conclusions regarding the prevalence, let alone the adaptive significance, of genetically based population differences in basal metabolic rate. One pattern that does seem to recur is that desert populations of small mammals often have relatively low resting metabolic rates (e.g. 58, 204, cf 158). Some studies suggest that differences in organismal metabolic rate may be more prevalent outside as opposed to inside the thermal neutral zone.

EXERCISE PHYSIOLOGY AND ADAPTATION TO ALTITUDE Adaptation to altitude and hypoxia has been studied intensively by vertebrate physiologists,

especially in mammals (56, 57, 133–135, 282, 321). Following considerable earlier work on *Peromyscus maniculatus* (reviews in 55, 132), M. A. Chappell, J. P. Hayes, & L. R. G. Snyder studied both BMR and maximal oxygen consumption ( $\dot{V}O_2\text{max}$ ) of this species in detail (see below). Significant differences in both exercise- and cold-induced  $\dot{V}O_2\text{max}$  exist among laboratory-bred populations of *Peromyscus maniculatus*, and cold acclimation (three months at 3°C) increases both measures (135). For animals measured within two days of capture, in situ, Hayes (133) found no differences in cold-induced  $\dot{V}O_2\text{max}$  rates for a high- and a low-altitude *P. maniculatus* population. At times of the year when the thermal environment was similar (i.e. summer at high altitude and winter at low altitude), Hayes (134) found differences in BMR but not  $\dot{V}O_2\text{max}$  between field-fresh high- and low-altitude *P. maniculatus*.

Chappell & Snyder (57) have shown that  $\alpha$ -chain hemoglobin haplotypes affect blood oxygen affinity ( $P_{50}$ ) and both exercise- and cold-induced  $\dot{V}O_2\text{max}$  in *Peromyscus maniculatus*. Alternate  $\alpha$ -globin haplotypes are strongly correlated with altitude, and the effects on  $\dot{V}O_2\text{max}$  of the high- and low-altitude hemoglobin genotypes are in the direction expected if natural selection is maintaining the polymorphism. The foregoing work (56, 57, 133–135; see also 282) is one of the best-documented cases of adaptive variation at the protein level in a vertebrate (see also 228, 270 on feral *Mus*). Interestingly, hemoglobin loci may be affected by selection for body size in *Mus musculus* (113).

Geographic variation in swimming ability among the 12 populations of Israeli mole rats mentioned above (6, 232) appears to correlate “with the extent and level of flooding and free-standing water” (149, p. 29). Djawdan (80) reports no significant difference in treadmill running endurance for field-fresh kangaroo rats (*Dipodomys merriami*) from two sites in California. Laboratory rats raised under common conditions show strain differences in exercise  $\dot{V}O_2\text{max}/\text{unit body mass}$  (20).

Breed differences in muscle fiber composition exist in rabbits (234), dogs (280), and horses (280). A variety of characteristics, such as long legs, a large relative muscle mass, and a high percentage of muscle fibers with high myosin ATPase activity, distinguish greyhounds from other dog breeds (280, 324). Various morphological, physiological, and biochemical differences also correlate with athletic abilities among breeds of horses (280).

OSMOREGULATION AND WATER BALANCE Grubbs (125) reports a lack of difference in water turnover rates of free-living rodents from three adjacent sites in agricultural fields and undisturbed habitat. Ward & Armitage (318) report apparently adaptive differences in urine volume and concentration between montane-mesic and lowland-xeric populations of yellow-bellied mar-

mots held in the laboratory. Water restriction did not reduce evaporative water loss (EWL) in these populations, although it does in some small mammals. Limited data suggest site differences in water influx for yellow-bellied marmots in the field (216; Armitage, this volume). Desert ringtail cats show lower EWL than does a mesic population (58). Population differences in urine concentrating ability, correlated with habitat aridity, occur in bats (18; refs. therein). Possible variation in kidney function in mole rats (6, 232) is currently under study (E. Nevo., in litt.). Differences in water turnover rates among breeds of domestic ungulates are reviewed elsewhere (202, 203, 322); feral island and domestic goats can also differ (87).

**OTHER** Kavaliers & Innes (182, 183; refs. therein), using a combination of laboratory-reared and wild-captured *Peromyscus maniculatus*, demonstrate population differences in opioid-mediated analgesia and locomotor activity, induced by physical restraint, exposure to scent of conspecifics, exposure to predators, or peripheral administration of opiate agonists and antagonists. According to these workers, the pattern of population differences can be interpreted in an adaptive context in relation to differential selection pressures on mainland and island populations of small mammals, thus encouraging further "pharmaco-ecological" studies. Relevant to these findings, strain differences in opioid activity and a variety of related behaviors are known in laboratory mice and rats.

### *Aves*

Poultry strains often differ in such physiological traits as growth rate, metabolism, water balance, blood characteristics, and disease resistance (e.g. 90, 91, 99, 211).

**LIFE HISTORY TRAITS AND ANNUAL RHYTHMS** Hormonal cycles governing reproduction might be expected to vary with latitude, because the relationship between the optimal time for breeding and proximate cues (e.g. photoperiod) is likely to vary. In a common annual photoperiod regimen (48°N), redpolls from populations at 65° and 48°N latitude differ in (i) the timing of their circadian activity rhythm with respect to the daily solar cycle, (ii) the timing and extent of night activity, (iii) the date of postnuptial molt, and (iv) the pattern of seasonal change in body weight (242). Domesticated or semi-domesticated stocks of several bird species "have lost, to varying degrees, the mechanisms of their feral progenors [sic] for the use of environmental information in the control of reproductive function . . ." (326, p. 66).

White-crowned sparrow (*Zonotrichia leucophrys*) populations differ in migration distance, timing of reproduction, and number of broods per year. Correspondingly, populations have different patterns of seasonal change in

gonad size and plasma levels of luteinizing hormone and steroid hormones (326).

**THERMAL BIOLOGY, THERMOREGULATION, AND RESTING METABOLISM**  
As in mammals, acclimation, acclimatization, and seasonality of avian thermoregulatory variables have been studied intensively; seasonal change in plumage insulation is especially common (55, 138, 208). Interspecific geographic variation in avian SMR has been documented (319), but intraspecific data on wild species are limited (208). Strain differences occur in chickens (99, 211).

In North America, northern populations of the introduced house sparrow have lower lethal temperatures, reduced thermal conductance, and higher resting and existence metabolic rates than do southern birds (29, 30, 163, 185). On the other hand, gross energy intake, metabolized energy, body temperature, and EWL do not vary geographically (29, 163). No common garden studies have been attempted. Some other species show similar patterns. Montane rufous-collared sparrows have broader thermal neutral zones than do those from the lowlands; however, birds from these populations do not differ in BMR or in the threshold  $O_2$  level at which metabolic rate is reduced (52). House finches from colder environments can remain homeothermic at low air temperatures longer than do their conspecifics from warmer climates (74). However, house finches from California and Colorado do not differ in standard metabolic rate, measured at several seasons and temperatures (72). A desert subspecies of horned larks shows lower  $O_2$  consumption and lower body temperatures, when measured at  $45^\circ C$ , than does a mesic, inland subspecies (301).

American goldfinches from Michigan and Texas increase their fat content during the winter, whereas individuals from southern California do not (73). Starlings likewise vary geographically in winter lipid levels and in several other body composition traits related to thermoregulation (31). In Gambel's white-crowned sparrow, however, the rate and degree of premigratory fattening do not vary with latitude, although northern populations begin to fatten at an earlier date (187).

**EXERCISE PHYSIOLOGY** Both migratory and nonmigratory populations exist within many bird species, including, formerly, the whooping crane. Long-distance migrants of the white-crowned sparrow show greater increases in hematocrit at the time of spring migration than do birds from a population that migrates only short distances (326). Montane and lowland populations of several bird species differ in heart size, lung size, and various hematological variables, usually in the expected (physiologically adaptive) direction (51, 86).

**OSMOREGULATION AND WATER BALANCE** Domesticated mallards are more tolerant to salt and have a developmentally more flexible salt gland than do wild mallards (268). Similarly, mallards found along the Greenland coast have larger salt glands than do those found inland in Europe (Stresemann 1934, cited in 268). In several species of phalacrocoracids, marine and freshwater populations differ in the size of nasal gland depressions (272). In three species of cormorants, marine birds have smaller nasal glands, whereas in imperial shags, marine birds have larger depressions; double-crested cormorant populations did not differ. Salt gland size and function can acclimate (268).

Salt marsh populations of the savannah sparrow have enhanced osmoregulatory abilities, including higher plasma and ureteral osmolalities, urine sodium concentrations, and tolerance of saline drinking water, compared with upland populations (17, 119). Anatomical modifications of the kidney may underlie these functional differences (119, cf 18). Desert horned larks have lower EWL than do inland valley birds, but they do not differ in rate of water consumption or ability to survive without water (301). Chickens from different strains differ in water intake and urine production (90, 91).

**EGGS** Intraspecific variation in the physiology of bird eggs and embryos is frequently studied in the laboratory. Montane coot embryos have lower oxygen consumption rates than do lowland embryos (50). However, red-winged blackbird embryos from different elevations have similar  $O_2$  consumption and incubation periods (51a).

Eggs of red-winged blackbirds, robins, cliff swallows, barn swallows, domestic fowl, and the native chicken of India have lower gas conductances at high elevations (48, 237, 249, 283, 316). This would counteract the greater diffusivity of water vapor at high elevations. However, conductance increases with elevation in coot eggs (50), which would compensate for reduced oxygen availability but compound the problem of water loss. In Andean chickens, eggshell conductance first decreases with altitude, then increases (192), suggesting that the conflicting demands of water loss and  $O_2$  requirements are resolved differently at different elevations. Pigeons from a dry habitat lay eggs with reduced gas conductance (5). Finally, black-billed magpie eggs show no consistent altitudinal variation in conductance (287).

Several workers have transferred birds from high to low elevations, or vice versa, to determine whether females can alter eggshell characteristics. In one instance, hens increased egg conductances by 30%, roughly the magnitude of among-population differences seen in wild birds (248). However, no consistent changes occurred in several other studies of quail, finches, and domestic fowl (49, 193). Hence, it is an open question whether altitudinal variation in eggshell gas conductances represents maternal adjustments or genetic differentiation among populations.

OTHER In marsh wrens, a population difference in the ability to learn songs is correlated with a difference in the sizes of brain regions involved in song learning (45).

## *Reptilia*

GROWTH AND REPRODUCTION Reptiles often show population differences in life history traits, including field growth rates, but the genetic basis of population differences is rarely studied (4, 82). Lab-reared hatchlings show population differences in growth rate in the lizard *Sceloporus undulatus* (103). Similarly, reciprocal field transplant experiments suggest genetic differences between populations of *S. undulatus* (P. H. Niewiarowski, W. M. Roosenburg, personal communication). Sinervo & Adolph (1, 273, 274; Sinervo & Adolph, in preparation) found population differences in the thermal sensitivity of growth rate in lab-reared *S. occidentalis*, but not in *S. graciosus*.

Reptilian reproductive cycles vary among populations in the wild, often in relation to latitude (e.g. 82, 194, 217, 225; refs. therein); however, we know of no common garden studies. Previous reports of population differences in degree of placentation in the lizard *Sceloporus aeneus* (127) actually involve two separate sibling species (127a).

THERMAL BIOLOGY AND THERMOREGULATION Reptile populations frequently differ in body temperatures ( $T_b$ ) during field activity; in most cases, this probably reflects environmental differences (8, 240). However, preferred  $T_b$  may differ between populations of the lizard *Lacerta vivipara* (310), and between some populations of *Sceloporus occidentalis* (273) but not others (320).

Critical thermal limits are frequently studied in reptiles; these are generally measured as the upper (CTMax) and lower (CTMin)  $T_b$  at which an animal loses its righting response. Traditionally, thermal physiology was thought to be evolutionarily conservative (i.e. relatively invariant within species and even genera; 69, 146). This view is supported by studies of lizards which found no significant population differences in critical thermal limits or other thermal physiological traits (69, 141, 146, 147, 307, 311). Similarly, eastern and western Canadian populations of the turtle *Chrysemys picta* (at the same latitude) do not differ in a variety of traits related to freeze-tolerance, including survival times, temporal changes in glucose concentration, supercooling points, and changes in lactate levels (in hatchlings, dug from overwintering sites, often in a frozen state; K. B. Storey, personal communication). On the other hand, CTMax and/or CTMin does vary geographically in several species of lizards (141, 143–145, 303, 325) and turtles (169).

Sex is determined by egg incubation temperature in some reptiles (41). The threshold temperature for a 1:1 sex ratio varies geographically in the turtles

*Chrysemys picta* and *Graptemys pseudogeographica* (41); surprisingly, southern populations have slightly lower threshold temperatures.

**RESTING METABOLISM** Both acclimation and acclimatization of resting metabolic rate have been demonstrated in various reptiles (22, 42, 303). In the tropical skink *Mabuya striata*, high-elevation lizards can acclimate their resting metabolic rate to temperature, whereas low-elevation lizards cannot (238).

In *Sceloporus occidentalis* and *S. malachiticus*, lizards from high elevations have higher resting rates of  $O_2$  consumption ( $\dot{V}O_2$ ); lab-reared *S. malachiticus* show the same pattern, suggesting a genetic basis (16). Similarly, Tsuji (302, 303) found latitudinal differences in the pattern of seasonal change in standard metabolic rate (SMR) and the direction of seasonal acclimation of SMR in *S. occidentalis*. The dependence of resting  $\dot{V}O_2$  on partial pressure of  $O_2$  differs between high- and low-altitude *S. occidentalis* (281). On the other hand, *S. occidentalis* from different elevations do not differ in minimum  $\dot{V}O_2$ ; differences in 24-hr  $O_2$  consumption were attributed to behavior rather than physiology (148, 177). Two New Jersey populations of *S. undulatus* do not differ in SMR (V. Pierce, H. B. John-Alder, personal communication). Whiptail lizards (*Cnemidophorus hyperythrus*) show interhabitat differences in field metabolic rates (measured by doubly-labeled water; 180). Painted turtles (*Chrysemys picta*) from a Canadian population accumulate less lactate when submerged in anoxic water than do those from Alabama (305).

**EXERCISE PHYSIOLOGY** Sprint speeds differ among lizard populations in at least eight species, mainly iguanids (69, 112, 146, 164, 165, 274–277, 279, 309; D. B. Miles, personal communication; J. Herron & B. S. Wilson, personal communication). Usually, populations at lower altitudes or latitudes are faster. Differences sometimes depend on age class or reproductive condition (see also 112). In *Sceloporus occidentalis*, sprint speeds of gravid females vary among populations, whereas those of nongravid females do not (277); in lab-reared hatchlings, sprint performance on various substrates varies among populations, paralleling field habitat use (276). By experimentally manipulating egg size in *S. occidentalis*, Sinervo & Huey (274, 275) showed that among-population differences in hatchling sprint speed, but not stamina, are largely due to differences in egg size; variation in stamina presumably reflects additional physiological differences (cf 111). Thermal sensitivity of sprint performance (e.g. optimal temperature) typically does not vary (or varies only slightly) among lizard populations (69, 146, 307, 309, 311).

Two New Jersey populations of *Sceloporus undulatus* show no differences



in treadmill endurance or in  $\dot{V}O_2\text{max}$  (V. Pierce, H. B. John-Alder, personal communication). Neither duration of maximal activity nor amount of lactate formed differs between two populations of *S. occidentalis* from different elevations (23). Population differences in locomotor performance occur in garter snakes (36, 37). Hydric conditions during incubation can affect locomotor performance of turtles (222).

Hemoglobin concentrations, erythrocyte counts, and/or hematocrits are higher in high-elevation populations in some lizard species but not in others (154, 281, 320). Similarly, erythrocyte count varies latitudinally in the turtle *Sternotherus odoratus* (168).

**OSMOREGULATION AND WATER BALANCE** Hertz & colleagues have studied intraspecific variation in evaporative water loss (EWL) rates and dehydration resistance in several species of *Anolis* lizards. Variation with altitude occurs in some species but not in others (142, 144). Similarly, Hillman et al (153) found among-population differences in EWL rate in two *Anolis* species, but not in *A. cristatellus* (152). Desert, montane, and coastal populations of the lizard *Uta stansburiana* have similar EWL rates (210, refs therein). EWL rates can acclimate rapidly, and the magnitude of acclimation effects can be several times as great as the difference between populations (153).

Estuarine populations of the water snake *Nerodia fasciata* have (i) lower rates of water and sodium influx, (ii) a lower rate of water efflux, and (iii) less skin permeability to water and sodium, compared to freshwater animals (88); however, these populations may comprise separate species (93). Hatchling snapping turtles (*Chelydra serpentina*) from saline water grow faster in saline water, but more slowly in fresh water, than do yearlings from a freshwater population (89).

**OTHER** In captivity, two *Sceloporus occidentalis* populations differ in blood osmolality, protein content, and hematocrit, and in plasma corticosterone levels in response to handling (K. Dunlap, personal communication). Garter snake populations sympatric with the toxic newt *Taricha granulosa* are more resistant to tetrodotoxin (37); resistance was measured as degree of locomotor impairment. The potential for multiple paternity may also differ among garter snake populations (269, refs. therein).

## *Amphibia*

**GROWTH, REPRODUCTION, AND LIFE HISTORY TRAITS** Larval growth and developmental rates are strongly temperature-sensitive and density-dependent (27, 300). Hence, variation observed in the field may reflect proximate

environmental effects (27). Because amphibian eggs are easy to collect and rear, a number of common garden or transplant experiments have been conducted (300). Berven & colleagues have documented genetic differences in the temperature dependence of larval differentiation rate and size at metamorphosis in two frog species (*Rana sylvatica*, *R. clamitans*) and measured heritabilities in some populations (26–28). In a seminatural common garden setting, populations of the salamander *Ambystoma maculatum* differ in larval survival, rate of metamorphosis, and activity (105). Temperature sensitivity of early development varies geographically in a number of other amphibians (3, 38, 94, 313); populations from colder environments are almost invariably cold-adapted. On the other hand, population differentiation is absent in some species (140, 227, 313, 314). Some previously described differences among populations of "*Rana pipiens*" (227) actually represent interspecific differences (151).

**THERMAL BIOLOGY AND THERMOREGULATION** As in reptiles, most cases of body temperature variation in nature probably represent environmental variation. However, montane *Bufo boreas* select higher  $T_b$  than do lowland toads (46).

Thermal tolerance (e.g. critical thermal maximum—CTMax) acclimates in response to both temperature and photoperiod, and varies diurnally, seasonally, and geographically in amphibians (34, 35, 42, 84, 245). Geographic variation in CTMax, and/or its acclimation rate, is common in frogs (34, 35, 160, 220, 221) and salamanders (70, 162), particularly in wide-ranging species (34, 35). However, larval and neotenic adult *Ambystoma tigrinum* from desert and mountain ponds have similar CTMax (76); likewise, two populations of the frog *Acris crepitans* do not differ in CTMax (122).

Several temperate frog species are amazingly freeze-tolerant. Although one might expect freeze tolerance to vary in wide-ranging species, K. B. Storey (personal communication) has found no differences among wood frogs (*Rana sylvatica*) from northern Ontario, southern Ontario, the middle United States, and even South Carolina: populations build up similar levels of glucose as a cryoprotectant, store similar amounts of glycogen in their livers, and possess the same nucleating proteins in their blood. Likewise, *R. sylvatica* varies latitudinally in heat tolerance but not in cold tolerance (207).

A few studies have compared thermal physiology at the tissue or cell level in amphibians. Thermal properties of cells and tissues from the frog *Rana ridibunda* do not differ between populations living in hot springs versus cool water (306). However, temperature tolerance of tissues from the frog *Limnodynastes tasmaniensis* differs with latitude (284).

**RESTING METABOLISM** SMR is higher in montane than in lowland toads (*Bufo boreas*), under several thermal and acclimation conditions; however,

active metabolic rates are similar (47). Oxygen consumption rate, and its response to temperature, varies with latitude and altitude in the frog *Hyla regilla* (176).

**EXERCISE PHYSIOLOGY** Populations of the poison-arrow frog *Dendrobates pumilio* differ in aerobic capacity for locomotion and in degree of toxicity, but not in anaerobic capacity (288). Florida and New Jersey populations of the frog *Hyla crucifer* do not differ in sprint swimming abilities or in muscle contractile properties (except for twitch tension at low temperatures) (179). Populations of *Hyla regilla* differ in erythrocyte count and hemoglobin concentration per cell (176), and two populations of *Rana pipiens* differ in levels of liver and muscle glycogen, but not blood glucose (101). Hellbender populations differ in a variety of hematological characteristics (178).

**OSMOREGULATION AND WATER BALANCE** In the laboratory, Puerto Rican *Eleutherodactylus coqui* from low-elevation rehydrate faster than do highland frogs (308). Similarly, in the frog *Hyla versicolor*, desiccation tolerance differs between mesic and xeric habitats (250). Two Illinois populations of the frog *Acris crepitans* differ slightly in desiccation rates (122), as do several populations of *Hyla regilla* (175) and two populations of *Bufo arenarum* (53).

**OTHER** Vocalization characteristics (call duration, pulse rate) vary among populations of *Rana pipiens* (85). Changes in serum proteins at metamorphosis differ between two populations of the salamander *Dicamptodon ensatus* (236). Connecticut *Rana sylvatica* show population differences in acid tolerance of embryos and tadpoles; breeding studies suggest a genetic basis for the latter but not the former (241).

### *Osteichthyes*

**GROWTH, REPRODUCTION, AND LIFE HISTORY TRAITS** A number of fish species show polymorphism, with relatively discrete morphs differing genetically and in such life history variables as growth and developmental rates (97, 206, 290, 293). Geographic variation in life history traits, including size-specific fecundity, occurs in many species (e.g. 235, 253–255, 290), and biogeographic “rules” may exist for fishes (252). Genetically based differences in growth rate occur among strains of various species of fishes, some of which have been produced by artificial selection (e.g. 81, 247). Differences in developmental and growth rates occur among hatchery strains of trout (refs. in 81) and may correlate positively with multilocus heterozygosity (104). We do not consider the general problem of stock discreteness and differentiation in marine fishes (see 290 for some refs.).

Reznick et al (253, 254) perturbed a natural population of guppies to test

the effects of predation on life history evolution. Correlated population differences in mating preferences and coloration exist in guppies (161). The Atlantic silverside shows genetic variation for temperature-dependent sex determination (65).

The marine killifish *Fundulus heteroclitus* can show "clinal" geographic variation (Canada to Florida) in frequencies of alleles at several loci (79, 243, 244). Allelic isozymes of lactate dehydrogenase-B (LDH-B) are functionally nonequivalent, and relative catalytic efficiencies are reversed at different temperatures. Oxygen consumption of embryos, developmental rate, and hatching time all differ among allelic isozyme LDH-B genotypes, which differ also in erythrocytic ATP concentrations and blood oxygen affinity (see below). Developmental rate also correlates with allelic variation at the malate dehydrogenase-A and glucose phosphate isomerase-B loci. Population differences in the amount of LDH-B<sup>b</sup> appear to be due both to acclimatization and genetic adaptation (68).

**THERMAL BIOLOGY AND THERMOREGULATION** Population differences in optimum temperatures for development (fastest development) exist in fishes (refs. in 10). Thermal tolerance (e.g. critical thermal maximum) acclimates in response to both temperature and photoperiod, and shows daily, seasonal, and geographic variation in fishes (42, 131, 212, refs. therein). A thorough common garden experiment demonstrated significant differences in both the limits and the range of thermal and oxygen tolerance between two pupfish populations, and showed intermediate values for hybrids (155). Apparently adaptive changes in allele frequencies have occurred rapidly in mosquitofish inhabiting areas receiving thermal effluent from a nuclear power plant (195, 258, 278; see also 188, 224).

Koehn (190) presented data suggesting thermally adaptive geographic variation in esterase alleles in the freshwater *Catostomus clarkii*; subsequent studies suggesting temperature-dependent selection in relation to population differences in allozyme frequencies have been reviewed elsewhere (79, 191, 243, 244, 290). The thermal stability of tissues from *Cobitis taenia* and *Carassius auratus* does not differ between populations living in hot springs versus cool water (306). Temperature acclimation of fish may result in changes in ATP concentrations in erythrocytes (244) and in amounts of various enzymes; changes in allozyme or isozyme expression are less common (68, 156).

**RESTING METABOLISM** Oxygen consumption of (relatively) inactive fishes is subject to acclimation and acclimatization, although some studies have shown a lack of acclimation (42, 245). Seasonal variation is apparently more common in adult than in juvenile fishes (19). Studies of population dif-

ferences are uncommon, although differences among hatchery strains have been documented (refs. in 81). Cave-dwelling populations of *Astyanax fasciatus* do not differ from surface-dwelling populations in average daily metabolic rate (323).

**EXERCISE PHYSIOLOGY** Seasonal changes in blood parameters occur in some fishes but not in others (42, 121). Seasonal variation in swimming performance has been reported (262), and activities of various enzymes important for swimming performance may change before or during migration (126). Acclimation to low temperature of swimming performance has been demonstrated in fishes (41, 260). Nelson (229) reported acclimation to pH of critical swimming speed in perch; however, more than two years of aquarium housing alone had no effect.

Population differences in swimming performance between coastal and interior coho salmon are apparently genetically based, related to differences in body form, and possibly related to differences in the energetic demands of migration and/or predation (292). Similarly, Couture & Guderley (67) compared field-fresh fish from populations in two rivers differing in flow and temperature and hence in the difficulty of migration. As predicted, the population of anadromous cisco with greater swimming requirements during migration show higher aerobic capacity in their swimming musculature, whereas the whitefish population do not, possibly because whitefish are larger and so are less affected by flow differences. Field-captured adult anadromous and resident freshwater sticklebacks also differ in swimming performance (293). Lab-reared anadromous and nonanadromous *Oncorhynchus nerka* differ in critical swimming speeds (291), and some hatchery-reared strains of trout exhibit poor swimming performance (95).

Perch from a naturally acidic lake are less (negatively) affected by soft, acid water than are fish from a circumneutral lake, although the former do not have higher absolute critical swimming speeds (229). Hematocrit, hemoglobin, and mean corpuscular hemoglobin content also differ between perch populations from acidic and alkaline waters, but red blood cell numbers and volume, and buffering capacity of white muscle, do not (230, 231). Seasonal variation also occurs in buffering capacity and in some hematological variables.

In the killifish, erythrocytic ATP concentration correlates with LDH-B genotype, and this may be causally related to differences in critical swimming speed among LDH-B genotypes (79, 243, 244). Other possible allozymic correlates of population differences in swimming performance of fish have been reported by investigators (refs. in 292).

Population differences in hemoglobin concentrations and in red cell Hb-phosphate ratio exist in some air-breathing fishes and may correlate with

habitat oxygen level (121). Wells (321) cautions against excessive adaptationism in interpreting patterns of variation in fish hemoglobins.

**OSMOREGULATION AND pH TOLERANCE** Measures of osmotic tolerance undergo acclimation and acclimatization in fishes (42). Racial differences in osmotic tolerance such as the ability to develop in saline waters occur in sticklebacks and correlate with differences in scalation (refs. in 10, 131, 245, 312). Common garden experiments indicate population and family differences in salinity tolerance in juvenile chinook salmon; the former but not the latter are largely a function of body size differences (289).

Strains of brook trout differ in pH tolerance (92, 259, 286), and yellow perch exhibit "ecotypes" with respect to low pH and oxygen concentration (205, 229–231).

**OTHER** Genetic differences in gas retention by swimbladders exist between two populations of lake trout (171). Cave-dwelling populations of *Astyanax fasciatus* differ from populations living in surface waters in the structure of the lateral line system and of the eye (323). Genetically based population differences in disease resistance occur in salmonids (290).

Two populations of pumpkinseeds, living in lakes with and without snails, differ in handling time (a measure of physiological performance) when feeding on snails, and in the motor patterns of one muscle, but not of several others (315). McLeese & Stevens (215) report differences between two strains of rainbow trout in relative caecal mass and in trypsin activity; moreover, one strain apparently produced a new trypsin isozyme in response to cold acclimation, whereas the other did not. E. D. Stevens (in litt.) also reports population differences, including "clear latitudinal gradients," "in the number of pyloric caeca and their function."

## CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

Based on the examples reviewed here, physiological traits do indeed vary among populations. Unfortunately, few studies have been designed to indicate whether observed differences are to any extent genetic in origin, but those that have often suggest genetic differentiation. On the other hand, the extensive literature on physiological acclimation and acclimatization cautions that any population differences observed in the absence of proper common garden controls may not be genetically based.

To overcome this constraint, we need more common garden studies of physiological differentiation (e.g. 1, 27, 77, 155, 183, 196, 209, 218, 251, 252, 273, 274, 289). In addition, physiologists need to study more than two

or a few populations (cf 241). Studies of several different types of traits (e.g. morphometric, biochemical, hormonal, organismal) would allow us to determine whether "physiology" is to any extent fundamentally different in terms of microevolution (cf 110, 131, 196, 212). Questions asked routinely of morphometric traits should be asked of physiological traits. How common are physiological clines (63, 158, 196, 295)? Do physiological traits show character displacement? How much of the among-population variation of animals in nature is genetically versus environmentally based? What is the range and scope of acclimation/acclimatization in physiological traits, as compared with the magnitude of genetically based differentiation seen among populations? We encourage more studies that use common garden designs and test a priori hypotheses based on quantitative genetic or other information (e.g. 158, 196). On a more topical note, the study of population differentiation in physiological traits will be important for understanding the ecological and evolutionary implications of global warming (e.g. 21, 166, 188, 278) and of other changes wrought by human activities, such as acid rain and lake acidification (cf 205, 229–231, 241, 259, 286) and other types of pollution.

Another virtually unexplored area is the year-to-year repeatability of population differences in physiological traits (253), although some studies are now in progress with lizards (164, 165) and with snakes (S. J. Arnold & A. F. Bennett, personal communication). Multiyear studies of the physiology of single populations (other than humans) are more common but still quite rare (cf 66, 118; Armitage, this volume). Thus, long-term studies of populations should be encouraged (82, 165, 254, 278).

Regardless of their origin (genetic or environmental), population differences in physiological (or in any) traits cannot be assumed to be "adaptive." Demonstration of adaptive significance requires further work, often including experimental manipulations and comparative studies (e.g. 27, 43, 44, 56, 60, 68, 102, 112, 137, 156, 191, 196, 224, 232, 233, 243, 251, 254, 273, 276, 278, 279, 282, 285, 300, 315, 321). Notwithstanding, studies reporting an apparent lack of adaptation among populations are in the minority (cf 251). On the other hand, the predilection of comparative physiologists for choosing extreme species for comparison (15, 44, 75, 102, 156, 181, 298) may have led to a bias in our data base and hence in our view regarding the commonness of physiological adaptation to the environment (43, 60, 102, 251, 321). A close matching at the population level is perhaps much less likely, in part due to the homogenizing effects of gene flow. Moreover, patterns of (co)variation among populations may differ fundamentally from those among species (e.g. 82, 112, 255). As well, we may expect to find multiple, rather than single optimal, solutions to adaptive problems (that is, specific answers to general physiological questions; 14, 15), especially as chance differences in the initial genetic constitution of populations may predispose them to different responses to uniform selection (63).

With more and more practitioners employing quantitative genetic (e.g. 21, 36, 63, 78, 109, 110, 166, 196, 261, 273, 304), population/biochemical genetic (104, 191, 243), and rigorous comparative (111a, 112) analyses, it has been rumored that a new field of "evolutionary physiology" is at hand (cf 44, 43, 102). Soon, it would seem, Dobzhansky's 1949 statement (267, p. xv) that "Among the major subdivisions of modern biology only physiology and biochemistry still remain largely unaffected by evolutionary ideas, doubtless to mutual detriment," or Prosser's (246, p. 4) statement that "evolutionists pay little attention to physiology, and most physiologists have only a superficial knowledge of evolution," will no longer ring true. We believe that an important thrust of this new evolutionary physiology will be studies of population differentiation. To quote Prosser (245, pp. 254-255; and cf 208), there exists "an immediate need for the description of phenotypic and genotypic variation of physiological characters within . . . species . . . according to history and distribution of natural populations. . . ."

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