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Acclimation

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Abstract

Acclimation refers to a physiological change in an individual stimulated by exposure to a different, often stressful, environment. As such it represents physiological phenotypic plasticity. This chapter reviews both early (1900 – 1960) and current research on arthropod acclimation, including: definitions, abiotic and biotic elicitors, types of acclimatory responses, tolerance and capacity acclimation, persistence and speed of response, confounding factors, including different experimental designs and metrics, graphic models, underlying physiological mechanisms, and possible adaptive value. Current acclimation research emphasizes molecular biology, environment-induced gene activation, passive vs. active responses, ecological and fitness consequence of acclimation, and its costs, adaptiveness, and evolution. Current studies attempt to integrate acclimation from genes-to-ecology, and relate acclimation to homeostatic physiology, phenotypic plasticity and stress studies. Understanding acclimation has numerous practical benefits.

Everything old is new again

Introduction

The current literature on phenotypic plasticity often proclaims the novelty of this exciting research area. However, like many fields of science, phenotypic plasticity actually has a long and diverse history, some of which has been nearly forgotten. During the early and mid 20th Century, as geneticists and evolutionary biologists worked to develop the initial ideas about phenotypic plasticity (Baldwin 1896, 1902, Morgan 1896a,b, Osborn 1897, Woltereck 1909, Johannsen 1911, Nilsson-Ehle 1914, Dobzhansky 1937, Clausen et al. 1940, Goldschmidt 1940, Waddington 1942, Schmalhausen 1949,

Bradshaw 1965), another group of scientists labored, largely beyond their view, on a sub-discipline of phenotypic plasticity: acclimation and acclimatization. Publishing in different journals, these physiologists, entomologists, and horticulturalists, produced a substantial body of literature that is underappreciated by modern workers on phenotypic plasticity (Pigliucci 1996). In this chapter, I hope to draw the attention of researchers to this prior work.

Acclimation and Acclimatization

Acclimation and acclimatization are forms of phenotypic plasticity. Acclimation refers to a change in the physiological phenotype of an individual following exposure to one or two well-defined environmental parameters such as temperature, osmolarity, or O_2 concentration, usually under controlled laboratory conditions. The analogous phenomenon in nature is acclimatization, which refers to a change in the physiological phenotype of an individual after exposure to different natural conditions.

It is interesting that despite the fact that around 10,000 papers have been published on acclimation, no one actually knows what it is (Lagerspetz 2006). Acclimatization was first applied to plants and insects that became more tolerant to freezing temperatures following pre-exposure to cold. As such, acclimatization implied the following:

1. The elicitor is a stressful (harmful) environmental factor.
2. The elicitor is an abiotic factor.
3. The elicitor stimulates a physiological change (as opposed to a morphological or behavioral change).
4. Acclimatization is beneficial (increases fitness) in that it allows the organism to better function or survive in the new environment. Hence, acclimatization allows individuals to adjust to a changing environment.
5. The elicitor is also the selective agent, i.e., the organism becomes more tolerant to the *same* factor that elicited the physiological change.
6. The response is anticipatory in that it prepares the animal for future environmental stress.
7. The response is gradual or delayed.
8. The response is medium- to long-lasting.
9. The effect is reversible.
10. The capacity for response is gene-regulated and has undergone natural selection.

Over the years, authors have offered numerous definitions of acclimation and acclimatization, few of which include all of the above criteria:

Habituation of an organism to different environmental conditions.
—Gordh 2001

A reversible physiological or morphological change evinced by one individual in response to some alterations in its environment.
—Morris 1992.

Acclimatization is the progressive physiological adjustment or adaptation by an organism to a change in an environmental factor, such as temperature . . . The adjustment can take place immediately or over a period of days or weeks . . . short-term responses include shivering or sweating in warm-blooded animals. —Rittner and McCabe 2004.

. . . the changes which take place in a process in an organism up to the time that the steady level is reached, after the organism has been transferred suddenly from one temperature to another within viable limits . . .
—Grainger 1958.

Physiological, emotional, and behavioral adjustments by an individual to changes in the environment. —Geller 2003.

Physiological or behavioral changes occurring within an organism, which reduces the strain or enhances endurance of strain caused by experimentally induced stressful changes in particular climatic factors. —IUPS (2001).

A physiological response involving sensory mechanisms detecting an environmental change and effecting a gene-regulated change in phenotypic expression. —Wilson and Franklin 2002b.

According to Prosser (1973), acclimation includes some morphological and behavioral changes, but not diapause, and represents "*. . . compensatory change in an organism under maintained deviation of a single environmental factor . . .*"

Williams et al. (2005) separate acclimation (short term) from longer-term phenotypic or developmental plasticity, such as when raising rodents under water-stress alters kidney structure or function.

Huey and Berrigan (1996) suggest that acclimation is reversible, may be anticipatory *or* reactive, and may be induced by temperature and photoperiod, in time frames of minutes to months. They differentiate acclimation from labile (acute) effects, cross-generational effects, and developmental switches, in which, " *. . . the phenotype is fixed irreversibly by*

environmental conditions experienced during a critical phase of development." Examples of developmental switches might include permanent changes in adult body size, color, and bristle number.

As can be seen from the above, definitions of acclimation/acclimatization vary greatly and tend to be ambiguous and contradictory, leading to confusion. Does acclimation need to be adaptive? Must acclimatization be anticipatory (e.g., acclimatization of cold-tolerance *before* the onset of winter) or can it be responsive (e.g., induction of heat-shock proteins *after* heat-shock)? Can it be passive (i.e., not regulated by the organism) (e.g., Pigliucci 1996)? Must it be regulated by genes that are activated by the environment? What about cases where environmental stresses bypass genes and accomplish acclimation by *directly* influencing hormones or enzyme cofactors? Must acclimation be reversible? Are immediate physiological responses such as sweating included? How does acclimation differ from acute homeostasis? Can behavior, emotion, morphology, or life-history acclimate? Indeed, over the years, these terms have come to assume such breadth and imprecision, that they can encompass nearly all responses to the environment, such as the photoperiodic entrainment of circadian rhythms or the induction of aphids alates by crowding. However, restrictive definitions can be just as problematic. This is because, whether an environment-induced change is regulated or passive, immediate or delayed, permanent or reversible, physiological or behavioral, elicited by a stressful factor (such as cold) or an innocuous factor (such as photoperiod), such a change (1) still represents a modified phenotype and, hence, phenotypic plasticity, (2) places those individuals into a different selective regime, altering their evolutionary trajectory, (3) may be adaptive, and (4) may eventuate via similar physiological mechanisms (Schlichting and Smith 2002). In addition, whether an individual responds to cold by immediate shivering, moving into sunlight, erection of fur or feathers, vasoconstriction, thermogenesis, migration, diapause, gradual production of cold-adapted enzymes or lipids, or increased pelage, all of these altered phenotypes are similar in that they represent homeostasis or homeokinesis. Hence, a broader definition of acclimation can encompass these diverse and biologically relevant concepts, and this is the approach I use in this chapter. I will not attempt to provide a precise definition of acclimation, but will leave that problem to future workers.

Because acclimation and acclimatization are expressions of different physiological phenotypes in a single genotype after being exposed to different environments, they represent physiological phenotypic plasticity

(Huey and Berrigan 1996). As such they offer fertile ground for exploring all aspects of plasticity, including elicitors, signal transduction, effector systems, genetic control, population, geographic, and genetic variability of response, adaptive value, and evolution. Because physiologically plastic responses are typically more rapid than morphological responses, and because there are innumerable physiological systems, acclimation offers many experimental advantages to researchers. Because we now have a fair understanding of physiological control in organisms, the genetics underlying such physiology, and powerful new molecular tools, acclimation offers the opportunity to finally begin to understand what is happening during phenotypic modification *inside* the organism, which was previously considered a "black box." Laboratory acclimation studies have the advantage of precise control of all variables. In contrast, field acclimatization can be difficult to study, because conditions in nature are always changing, because individuals within natural populations vary in age, experience, and condition, and because of possible interactions among numerous factors. However, acclimatization has the advantage that it often can be directly linked to real fitness benefits in nature, such as when acclimatized insects withstand winter temperatures, but non-acclimatized insects die. Finally, understanding acclimation is essential for all experimental biologists, because both within- and trans-generational acclimation might influence their results (Falconer 1989, Garland and Adolph 1991).

Initial interest in acclimation and acclimatization originated for practical reasons: the need to induce winter hardiness or vernalization of seed germination or blooming in commercial plants, and the desire to understand the winter biology of pest insects. Hence, much of the initial research in this area was undertaken by applied entomologists and horticulturists. However, the field was soon subsumed by basic researchers (e.g., Davenport and Castle 1896, Parhon 1909). As a result, by mid-Century, scientists already had a good understanding of the environmental factors that triggered acclimation, the co-factors that influenced the response, the types and degree of responses possible, and the presumably adaptive nature of acclimation in a great diversity of taxa, including humans. The early workers in this area produced substantial observational and experimental data and theory (see Bělehrádek 1935, Prosser 1950, 1958a, 1961, 1973, H. Precht 1951, Bullock 1955, Fry 1958, Ingrid Precht 1967, H. Precht et al. 1973), and some simple graphical models (see H. Precht 1951, Smith 1951, H. Precht et al. 1973, Prosser 1973), much of which remains of value to current scientists.

Elicitors

By the 1960's researchers had a good understanding of the environmental factors that elicited acclimation in animals. These included temperature (Robinson 1928, Bullock 1955), oxygen level (Wigglesworth 1954), osmotic pressure and salinity (Haas and Strenzke 1957, Kinne 1958, Waddington 1959, Oglesby 1965), humidity (Breitenbrecher 1918, Giersberg 1928), water pressure and density (Bardenfleth and Ege 1916, Damant 1924), food type (Knox et al. 1956, Knox 1958), food quality (Gambaro 1954, Hughes 1960, de Wilde 1962), food quantity (Dreyer 1932), food moisture level (Okay 1953, 1956), and, if one ignores Criteria 1 and 5 (above), photoperiod (Yeates 1954, Hoar and Robertson 1959, de Wilde 1962, Müller 1970), light intensity (Herrstroem 1949, Lees 1955), light color (Kogure 1933), and crowding (Iwao 1962, Uvarov 1966, Rowell 1970) (see also Precht 1951, Bullock 1955, Prosser 1961, Rowell 1971) (Table 1). Subsequently, toxins, pH, CO_2, lunar cycles, and tidal cues were shown to induce long-lasting changes in physiological state (Husain and Mathur 1936a, Prosser 1973, Hill and Wyse 1976, Nicolas and Sillans 1989).

In most cases, exposure to an elicitor stimulates the organism to alter its physiology such that it subsequently shows a different physiological response to that *same* factor, such as when exposure to cold temperature induces low-temperature tolerance or alteres temperature-specific metabolic rates in individuals (Bullock 1955, Prosser 1958a). In nature, these same eliciting factors often serve as selective agents, capable of directly or indirectly lowering fitness. In other cases, the eliciting factor induces a change in physiological response to a *different* factor, such as when changes in photoperiod induce improved cold-tolerance (Danilevskii 1965), or when changes in humidity alter body color in grasshoppers and walking sticks (Giersberg 1928, Faure 1932, 1933, Key 1954), which alters thermoregulation, and hence, thermal physiology (Buxton 1924, Hill and Taylor 1933), as well as antipredatory defense (Rowell 1971). In such cases, the elicitor is not the selective agent, but serves as a proxy (token) stimulus for that agent and cues the individual to adaptively alter its physiology such that it is more resistant to the selective agent. In some cases the elicitor can be far removed from the harmful factor. Hughes (1960) noted a two-step elicitation process, whereby photoperiod altered plant chemistry, which subsequently triggered pupal diapause in feeding cabbage root fly larvae.

In some cases, such as with photoperiod, the insect has evolved specific structures to detect the elicitor and transfer that information to effector systems. In other cases, there may be no formal sensing of the environmental

Table 1 Examples of the progressive steps during acclimation. Examples include physiological, physio-morphological, and physio-behavioral responses, and their assumed fitness consequences. HSPs = heat shock proteins. SCP = supercooling point.

Step 1	*Step 2*	*Step 3*	*Step 4*	
Elicitor	*Physiological response*	*Physio-ecological outcome*	*Fitness consequence*	*Reference*
Cold	↑ Glycerol titer	↓ Supercooling point	↑ Survival in cold	Salt 1958, 1959
Cold	Change in enzymes	↑ Metabolic rate and activity	↑ Survival in cold	Marzusch 1952
Heat	↑ Heat-shock proteins	↑ Thermal protein stability	↑ Survival in heat	Feder and Hofmann 1999
Low O_2	↑ Hemoglobin titer	↑ Tissue O_2 concentration	↑ Survival at low O_2 levels	Wigglesworth 1938
Low O_2	↑ Tracheal growth	↑ Tissue O_2 concentration	↑ Survival at low O_2 levels	Locke 1958
High salinity	↑ Papillae growth	↑ Osmoregulation	↑ Survival at high salinity	Waddington 1959
Short photoperiod	↑ Diapause	↑ SCP or ↑ freeze tolerance ↓ Metabolic rate	↑ Winter survival	de Wilde 1962 Danilevskii 1965
Thermoperiod	↑ HSPs and polyols	↑ Protein stability in cold	↑ Survival in cold	Wang et al. 2006
Low humidity	↓ Temperature preference ↓ Phototropism	↓ Body temperature and ↓ Desiccation	↑ Survival in dry	Breitenbrecher 1918 Franenkel and Gunn 1961
Low humidity	↑ Unsaturated lipids	↑ Membrane fluidity in cold	↑ Survival in cold	Holmstrup et al. 2002
Food toxins	↑ P450 enzymes	↑ Diet detoxification	↑ Growth and survival on diet	Berenbaum 2002

factor. Instead, a new phenotype is produced via direct, passive, biophysical effects.

What Changes during Acclimation?

Acclimation can alter physiology, morphology, behavior, and/or life history. However, because the latter traits are simply extensions of physiology, all acclimation is physiological.

Early studies documented a great variety of acclimating traits (Fig. 1, Table 1), including biochemical traits such as enzyme concentrations (Carlsen 1953, Knox et al. 1956, Knox 1958), membrane permeability (Oglesby 1965), O_2-binding capacity of blood, synthesis of thermal-adaptive lipids (homeoviscous adaptation) (Fraenkel and Hopf 1940, Munson 1953, Fast 1970), Q_{10} (Bělehrádek 1935, Agrell 1947, Edwards 1958), and enzyme activity rates (Mutchmor and Richards 1961, Prosser 1962), with resulting alterations in concentrations of numerous organic molecules (Fox 1955, Precht et al. 1955, Mews 1957). Performance traits could also acclimate, including: supercooling points, the ability to survive freezing, nerve output and conductance, heartbeat rate (Thompson 1937, Perttunen and Lagerspetz 1956), buoyancy (Damant 1924), digestive functions (Applebaum et al. 1964), metabolic rate (Fig. 2) (Sayle 1928, Agrell 1947, Lühmann and Drees 1952, Dehnel and Segal 1956), blood coagulation (Numanoi 1938, Dean and Vernberg 1966), and tolerance to extreme temperatures, salinities, humidities, and oxygen levels (Bodenheimer and Klein 1930, Wigglesworth 1933, 1938, Bělehrádek 1935, Prosser 1950, Baldwin 1954, Baldwin and House 1954, Benthe 1954, Bullock 1955, Fox 1955, Kerkut and Taylor 1957, 1958, Maynard Smith 1957, Straub 1957, Tribe and Bowler 1968) (Table 1; Fig. 1). For example, a short exposure to 37.5°C triples survival time of *Drosophila* pupae at 42.5°C (Milkman 1962).

Fig. 1 Each graph represents a reaction norm showing acclimation (phenotypic plasticity) when insects of the same genotype are maintained under two or more different environments. Examples include acclimation to temperature (a-d), O_2 level (e), and osmolarity (f), as evinced by changes in survival (tolerance) (a & b), supercooling point (c), behavior (d), chemical titer (e), and morphology (f). a) Mortality of *Anagasta* (*Ephestia*) *kuhniella* moth pupae when exposed to –15°C, after pre-conditioning for 4 h at various temperatures. After Atwal (1960a). b) Mortality of adult *Dahlbominus fuscipennis* wasps when exposed to 43°C for 3 h, with or without a prior 2-h heat shock at 36°. After Baldwin (1954). c) Supercooling points for *Bracon cephi* wasp larvae pre-conditioned at various temperatures in the laboratory. Control larvae collected outside in August. After Salt (1959). d) Percentage of male *Blattella germanica*

Fig. 1 Contd. ...

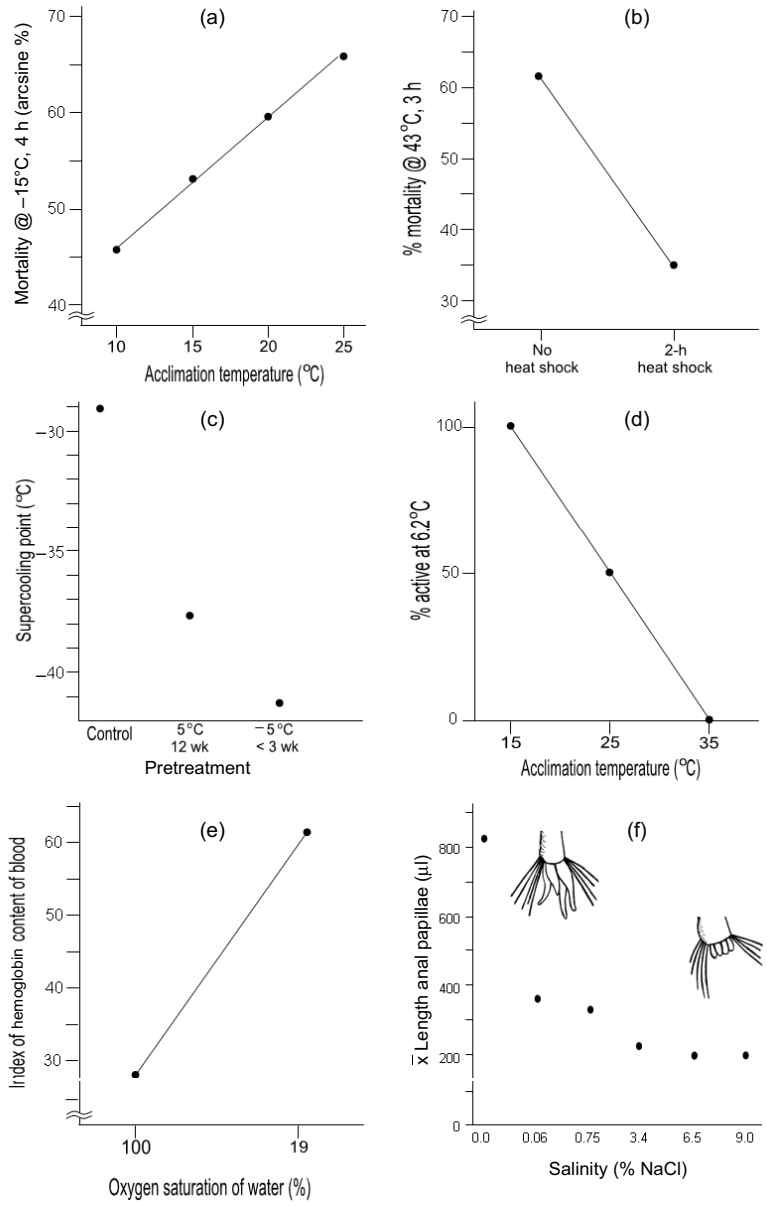

Fig. 1 Contd. ...

roaches active (not in cold-torpor) at 6.2°C after pre-conditioning at various temperatures. After Colhoun 1954). e) Relative hemoglobin content of the blood of *Chironomus* midge larvae from well-aerated and poorly aerated water. After Fox (1955). f) Length of anal papillae of *Culex pipiens* mosquito larvae reared in water of different salinities. After Wigglesworth (1938).

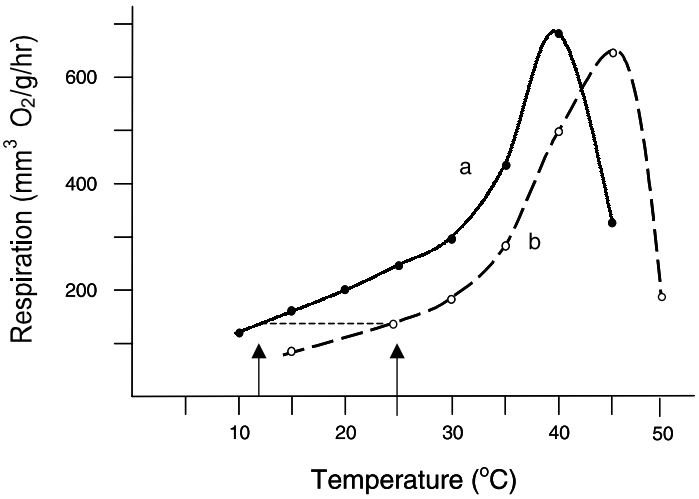

Fig. 2 Metabolic rates of *Melasoma populi* chrysomelid beetles tested at various acute temperatures, for a) insects acclimated to 12°C, and b) insects acclimated to 25°C. Horizontal dotted line at points where acclimation temperature = test temperature, shows temperature compensation in O_2 consumption. After Marzusch (1952).

Environmentally induced diapause and estivation (as opposed to developmentally programmed) are forms of acclimatization of great importance to insects, and are largely responsible for their success and distribution. Various environmental cues trigger diapause and estivation, inducing manifold coordinated physiological changes that make the individual more resistant to the temperature-, food-, and water-stresses of seasonal environments (Lees 1955, Maynard Smith 1957, Salt 1961, Müller 1970). Diapause dramatically alters physiological phenotype. For example, diapausing cecropia silkworm pupae (Saturniidae) consume 1.4% of the O_2 of non-diapausing caterpillars (Schneiderman and Williams 1953), and diapausing *Bracon* wasp larvae can survive temperatures as low as –47°C (Salt 1959).

Many morpho-physiological traits also acclimate, such as number and size of tracheae and tracheoles in *Rhodnius* and *Tenebrio* (Wigglesworth 1954, Locke 1958), diameter of nephridial canals in polychaete worms (Jones 1967), size of anal papillae in midges, mosquitoes, and *Drosophila* (Pagast 1936, Wigglesworth 1938, Harnisch 1951, Haas and Strenzke 1957, Waddington 1959) (Fig. 1f), surface area in hydra (Kinne 1958), buoyancy and size of air sacs and swimbladders in aquatic and marine organisms (Bardenfleth and Ege 1916, Damant 1924, Prosser 1973), body color in

insects (Knight 1924, Giersberg 1928, 1929, Atzler 1930, Faure 1932, Husain and Mathur 1936a,b, Key and Day 1954a,b, Ergene 1956), number of mitochondria in cold-acclimated roaches (Thiessen and Mutchmor 1967), hemocyte number in *Galleria* wax moths (Marek 1970), and, in vertebrates, increased pelage or fat (Yeates 1954, Hill and Wyse 1976).

Behavio-physiological traits can also acclimate (Thorpe 1963), including preferred temperatures in ants (Herter 1924), beetles (Bodenheimer and Schenkin 1928, Miller 1969), mites (Henschel 1929), ticks (Totze 1933), and wireworms (Campbell 1937), preferred humidity in roaches (Krijgsman 1930, Gunn and Cosway 1938), preferred light intensity in ground beetles (Herrstroem 1949), low and high temperature thresholds for activity (Bělehrádek 1935, Mellanby 1939, Colhoun 1954, McLeese and Wilder 1958), circadian rhythms (Hoffmann 1957, Papi and Parrini 1957), feeding rates (Breitenbrecher 1918, Chapman 1957), and rates of locomotion (Gunn and Hopf 1942, Fry and Hart 1948). For example, nymphal snow scorpionflies, *Boreus hiemalis*, prefer 34°C in summer, but 10°C in winter (Herter 1953). In many insects, including some cockroaches, grasshoppers, beetles, earwigs, lice, flies, and Thysanura, pretreatment with low humidity or dry food alters temperature- or light-preference (Herter 1924, Henke 1930, Bodenheimer 1931, Gunn 1931, 1934, Jack 1939, van Heerdt 1946, Jakovlev and Krüger 1954, Heeg 1967). For example, Colorado potato beetles, *Leptinotarsa*, kept in low humidity for 8 d, refused to feed, became positively geotactic and negatively phototactic, burrowed into the soil, and remained there until it rained (Breitenbrecher 1918). Those kept at high humidity remained active, negatively geotactic and positively phototactic. Photoperiod alters salinity preferences in sticklebacks (Baggerman 1957). Even learning may acclimate to temperature, as suggested when adult *Tenebrio molitor* beetles became more adept at learning after acclimating to a cold temperature (Alloway 1969). Likewise, life history properties such as rate of reproduction (Dick 1937), growth and development rate (Parker 1930, Uvarov 1966), number of instars (Hunter-Jones 1958, Farrow 1975), and time to oviposit can be said to acclimate (Ryan 1941, Elens 1953, Pantyukhov 1962). Finally, Kinne (1958) and Uvarov (1966) give examples of apparent trans-generational acclimation in amphipods and locusts, respectively.

One problem with the early rush to document acclimating traits was a failure to differentiate cause and effect. The process of acclimation proceeds through at least four steps (Table 1): (1) An environmental factor (elicitor) stimulates (2) a complex series of physiological changes that (3) alters an ecophysiological relationship, which (4) alters fitness. For example, exposure to cold and/or short day lengths may induce antifreeze

production, which prevents nucleation and lowers freezing temperature, which increases cold-tolerance and hence, winter survival. These steps are mechanistically linked, but not conceptually equivalent. For example, physiologists claim that acclimation alters capacity *or* tolerance (resistance) (Precht 1958, Prosser 1961). But capacity acclimation usually refers to changes in rates such as changes in rate of synthesis, nerve firing, heartbeat, metabolism, behavior, etc., and hence represents Steps 2 or 3 (Table 1). Tolerance usually refers to the ability to survive a specific environmental condition, such as an extremely high or low temperature or osmolarity, and hence represents Step 4. Furthermore, tolerance normally applies to extreme conditions, whereas capacity normally refers to adjustments within normal or mid-ranges of environmental factors (Prosser 1967). However, tolerance and capacity are linked in complex ways. A desynchronization of compensation across all functions may reduce tolerance, and intolerance of a single function or organ can alter lower- or higher-level compensation.

A second major problem with early acclimation studies was insufficient knowledge of the transcriptional, biochemical, and physiological mechanisms underlying acclimation (Step 2). Although researchers identified bits and pieces of the complex physiological cascades effecting acclimation (i.e., concentration changes in specific hormones, enzymes, organic compounds, etc.), most early research documented only inputs (the eliciting factors) and outputs (i.e., changes in capacity or tolerance). What happened in-between often remained clouded. For example, referring to rudimentary flow-diagrams explaining acclimation, Knox (1958) stated, "*… they permit us to express a relationship while remaining ignorant of the nature of the relation and even the nature of the parts affected.*"

Although early workers lacked the tools to elucidate complete pathways, they recognized that acclimation represented not just changes in single traits, but complex cascades involving numerous branching and interacting physiological pathways (see Mechanisms, below). Because complex physiological traits, such as metabolic rate, represented aggregates of multiple underlying systems and processes, it was clear that acclimation proceeded at multiple levels and in multiple systems simultaneously. As such, adaptation was apparent at the enzyme, membrane, organelle, cell, tissue, and whole-animal levels (Bullock 1955, Precht 1958, Prosser 1958a, 1961, Thiessen and Mutchmor 1967, Spencer-Davis and Tribe 1969). Each different level, organelle or tissue might or might not acclimate tolerance or capacity in a different way. Thus, demonstrating acclimation in whole tissues or animals is quite different from knowing which of many possible

underlying traits actually acclimated to produce the complete effect (Das and Singh 1974). Likewise, interaction of multiple simultaneous processes confounded understanding. For example, studying high-temperature tolerance in *Drosophila*, Maynard-Smith (1957) found evidence of two kinds of acclimation (developmental and physiological) occurring simultaneously in the same individual. Acclimation was also sometimes confused with developmental changes in physiology (Davison 1971).

It also became evident that numerous traits could be altered by a single elicitor (Anderson and Mutchmor 1971, Precht 1973a,b). For example, a pre-exposure to high temperature can not only adaptively alter metabolic and behavioral capacity (compensation), but can improve heat tolerance and resistance to oxygen, salinity, and toxic stresses (Precht 1973b). In some cases of acclimation, entire suites of co-adaptive traits are altered in synchrony, an example of phenotypic integration (see Canfield and Greene, this Volume). Diapause and estivation represent phenotypic integration, whereby much of the insect's physiology and behavior are altered, starting with temperature, light, and geotactic preferences, and alterations in concentrations of numerous biomolecules, such as enzymes, polyols, amino acids, peptides, proteins, charbohydrates, and lipids, leading to changes in growth, development, metabolic rate, and resistance to temperature extremes, dehydration, lowered O_2, and starvation (Schneiderman and Williams 1953, Lees 1955, Prosser 1961, 1973).

The manifold effects of single environmental factors are seen in the response of some grasshoppers to moisture. In response to humidity, *Locusta* grasshoppers alter both body color and starvation resistance (Rowell 1971). Dry conditions induce brown forms that are more starvation-resistant in dry conditions, and moist conditions induce green forms that are more resistant in moist conditions (Albrecht 1964, 1965). Likewise, darker cuticle is generally more desiccation-resistant (Needham 1974) and shields against harmful UV radiation (Burtt 1981). Both low RH and food moisture can lower temperature preference in grasshoppers and thus reduce evaporative water loss (Jakovlev and Krüger 1954, Laudien 1973). Even activity levels can be altered, given that the brown morph of *Locustana pardalina* is more active than the green morph (Pick and Lea 1970).

Early researchers noted that insect species and stages varied greatly in the ability to acclimate, and many species showed no acclimation (Dreyer 1932, Mellanby 1940a, Salt 1956, Atwal 1960a,b). For example, some Orthoptera alter body color in response to temperature, humidity, food moisture, background color, crowding, etc. (Rowell 1971). However, in regard to color-polymorphic Tetrigidae, Nabours (1929) frustratingly

proclaimed, "…*neither excessive humidity, temperature, aridity, acidity, salinity, sunlight through glass or direct, darkness, color of soil, food, excreta, starvation, fungus disease, parasitism, nor any other observable feature of the environment has ever changed color pattern to any appreciable extent.*" Keister and Buck (1974) even suggested that insects in general had poor ability for respiratory compensation in comparison to other taxa.

Early researchers quickly discovered that different traits varied greatly in pattern of acclimation (Fig. 3). Many traits show no acclimation (Nabours 1929, Dryer 1932, Atwal 1960a, Keister and Buck 1961), and some traits

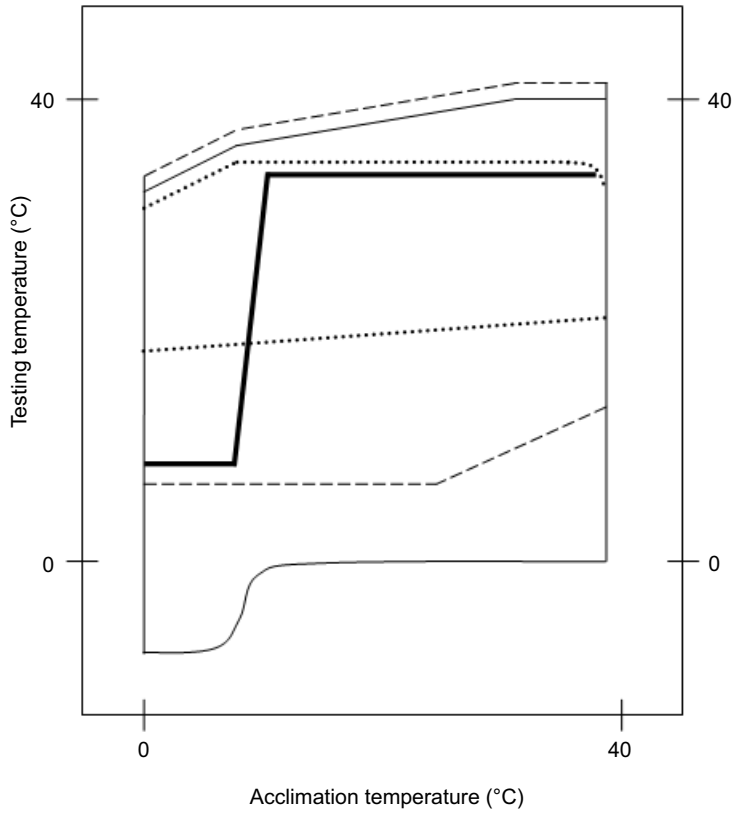

Fig. 3 Hypothetical tolerance polygon showing the potential complexity of acclimation in a genetically identical population of male or female adult insects. Horizontal axis gives temperature at which animal was acclimated. Vertical axis gives temperature at which animal was tested, subsequent to acclimation. Graph shows four functions, each acclimating differently. Areas bounded by similar lines represent zone of tolerance (ability to tolerate specific combinations of acclimation and test temperatures). **Thin solid line:** 1-d survival at test temperature. **Dashed**

Fig. 3 Contd. ...

exhibit reverse acclimation (Precht 1951, Marzusch 1952, Kirberger 1953, Roberts 1953). Different enzyme systems, tissues, and functions acclimate differently under the same experimental treatment (Edwards 1957, Precht 1958, Free and Spencer-Booth 1960, Prosser 1961, Anderson and Mutchmor 1971, Sømme 1972, Das and Singh 1974). For example, in the same animal, anabolic and energy-producing enzyme systems often acclimate to cold, whereas catabolic enzyme systems do not (Marzusch 1952, Mutchmor 1967, Hazel and Prosser 1970). In eels, metabolic rate of head muscles acclimated differently to temperature than that of tail muscle (Schultze 1965). In *Periplaneta americana*, different regions of the nervous system respond differently to changes in temperature (Kerkut and Taylor 1957). Even different regions of individual cells can apparently acclimate: Chatfield and coworkers (1953) examined compensatory increases in nerve conduction in the long nerve that runs the length of the leg in herring gulls, acclimated to cold vs. warm temperatures. In cold-acclimated gulls, the distal portion of the nerve (in the thin distal portion of the leg) became cold-acclimated, but the proximal portion of the nerve (in the thicker, partially feathered and warmer tibial region of the leg) did not.

Speed of Change

Early work on acclimation demonstrated inter- and intraspecific variation in rate of acclimation to the same conditions, and great variation within

Fig. 3 Contd. ...

line: Ability to move (= torpor temperature) (1-min exposure). **Dotted line:** Temperature allowing oogenesis (or other function such as spermogenesis or molting). **Bold solid line:** Temperature preference. Note that animals cannot survive below 0°C or above 38°C, unless first acclimated. Also note that each function (survival, activity, and oogenesis) exhibits a different thermal capacity, with survival possible over a wide temperature range, behavior over a medium temperature range, and oogenesis over a narrow temperature range. Hence, at extreme temperatures, activity and survival are possible, but not oogenesis. Each function acclimates differently, and, in this example, the high and low limits for each function acclimate differently. For example, low-temperature (< 0°C) survival only acclimates following exposure to low temperatures. In contrast, high-temperature survival generally rises gradually across all acclimation temperatures. Survival acclimates beneficially to both heat and cold. In contrast, there is little beneficial acclimation for oogenesis, suggesting that there are overriding thermal constraints for that function. Indeed, acclimation at high temperatures reduces the subsequent ability to complete oogenesis at high temperatures (downward curved line). Note high-temperature survival and activity change gradually and in unison with increasing acclimation temperature, but temperature preference and low-temperature survival switch dramatically at about 10°C acclimation temperature.

individuals in the rates of acclimation to different factors (Mellanby 1939, Prosser 1958a). Each different enzyme system, tissue, and function acclimated at a different speed (Mellanby 1939, 1940a,b). For example, Meats (1973) claimed that *Dacus tryani* fruit flies could acclimate "immediately" to changes in temperature. A 2-h-long, 36°C high-temperature shock immediately doubles the amount of time that *Dahlbominus* wasps can withstand 43°C (Baldwin 1954, Baldwin and Riordan 1956). *Periplaneta* roaches begin to acclimate metabolic rates to heat in 4 h (Dehnel and Segal 1956). In *Blattella* roaches, the same cold-exposure increases cold-activity within a few hours, but lowers super-cooling only after several days (Colhoun 1960). *Tribolium confusum* requires only a few hours to increase cold-resistance (survival) (Sømme 1968), ~ 60 h to acclimate O_2 consumption, ~ 17 d for full behavioral acclimation (locomotion) to cold, and 38 d for ATPase acclimation (Anderson and Mutchmor 1971). Brine shrimp, *Artemia*, may take up to three weeks to acclimate to low O_2 levels by increasing hemoglobin levels (Bowen et al. 1969).

Because acclimation often involves numerous physiological systems, the rate at which the whole tissue or organism can acclimate is limited by the acclimation speed of the slowest step (Bullock 1955). In addition, speed of acclimation varies with direction of change and high vs. low levels of a particular environmental factor (Prosser 1973). For example, some animals acclimate faster to warm than to cold temperatures (Prosser 1973). Also, as in the case of *Tribolium* (above), resistance acclimation often proceeds faster than capacity acclimation, and species from variable environments often acclimate faster than those from stable environments (Precht 1973b). Interestingly, acclimation, which is often considered a delayed reaction, can be much faster than "physiological regulation." For example, osmoregulation is generally not considered acclimation, yet, steelhead trout required 80 to 160 h to osmotically adjust transfer from fresh to sea water (Houston 1959). This is an order of magnitude longer than the initiation of thermal acclimation in trout (Werner et al. 2006), and 100 times longer than some rapid cold-or heat-hardening (see below). Finally, early workers realized that acclimation is not a change that continues indefinitely, i.e., at some point, additional conditioning produces no additional change in physiology (Fig. 4) (Atwal 1960a, Sømme 1968), and, in some cases, additional conditioning appears to reduce acclimation (Baldwin and Riordan 1956) (Fig. 5).

Permanency of Change

Historically, acclimation was considered a delayed and medium- to long-lasting, but reversible, adaptive change in physiology in response to

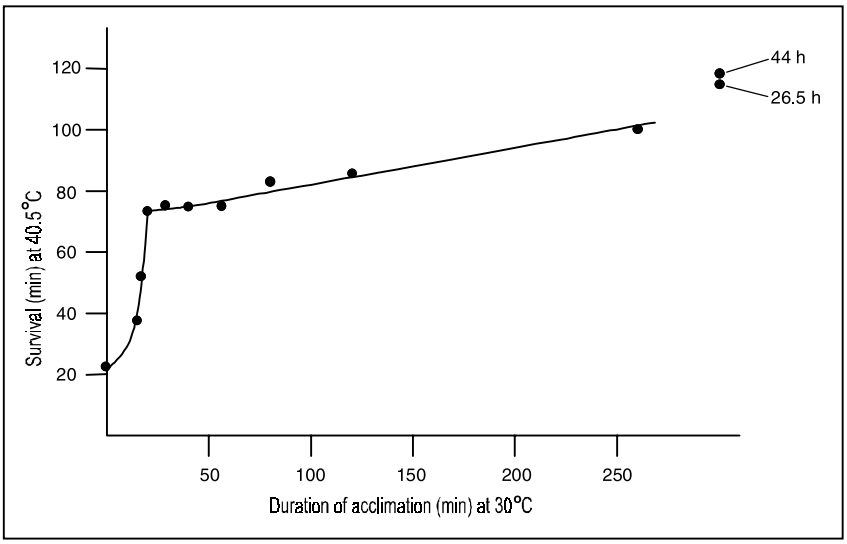

Fig. 4 Relationship between duration of acclimation period (time spent at 30°C) and degree of tolerance acclimation (survival at 40.5°C) for *Artemia* brine shrimp. Most acclimation occurs within the first 20 min. After Grainger (1958).

external conditions. As such, permanency of acclimation fell between highly flexible, acute, immediate, and labile regulation and irreversible developmental switches (Huey and Berrrigan 1996). However, acclimation grades into acute regulation on one hand and developmental switches on the other, in regard to speed, reversibility, and underlying physiological mechanisms (Prosser 1958b). Similarly, there are no clear criteria separating rapid-acting hardening and heat-shock from traditional, slower-acting acclimation (Precht 1973b), but see Bowler (2005).

Many acclimating traits, such as some metabolic traits, activity rates, and even morphological traits are rapidly reversible (Levins 1969, Precht 1973a). For example, although most temperature-, humidity-, and light-induced changes in grasshopper body color are permanent (Rowell 1971), *Kosciuscola* grasshoppers can rapidly (~1 h), change their color back-and-forth in response to temperature (Key and Day 1954a,b). In *Ephestia* moth pupae, acclimation is quickly reversible. Half-day-old pupae acclimate to cold in only 2-3 h, but can reverse cold acclimation after only 2 h under warm conditions (Atwal 1960a). Other acclimations and acclimatizations are permanent, such as when lowered oxygen level induces greater tracheation in *Rhodnius* and *Tenebrio* (Wigglesworth 1954, Locke 1958) or lowered salinity induces larger anal papillae in aquatic Diptera larvae (Fig. 1f) (Pagast 1936, Wigglesworth 1938, Harnisch 1951, Haas and Strenzke 1957).

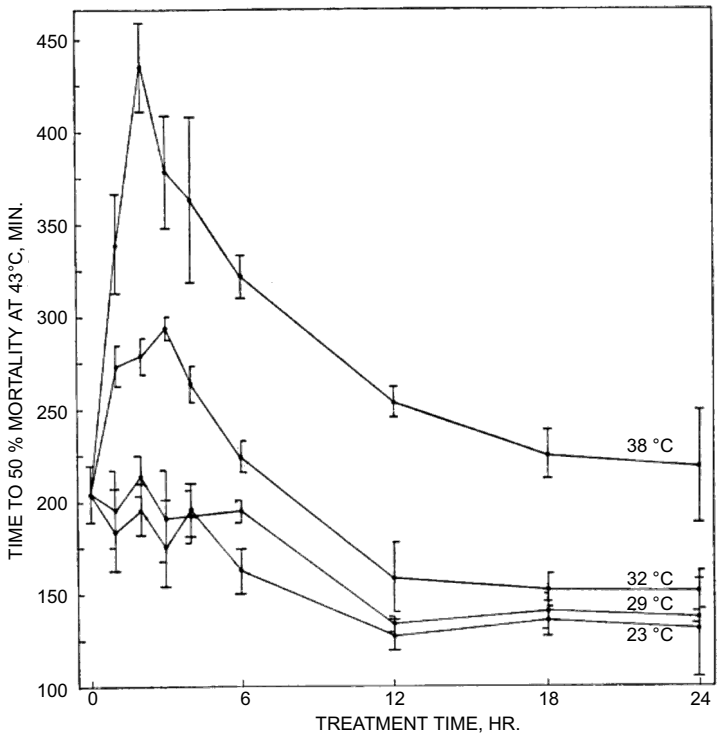

Fig. 5 Influence of acclimation temperature and length of acclimation on tolerance to high temperature (43°C) in the chalcidoid wasp, *Dahlbominus fuscipennis*. Higher acclimation temperatures induce greater acclimation. Maximal tolerance occurs after only 2 to 3 h of acclimation. Tolerance declines with increasing acclimation time, possibly because general heat resistance declines with adult development. From Baldwin and Riordan (1956), courtesy Canadian Journal of Zoology & NRC Research Press.

In *Drosophila suboscura*, high-temperature acclimation is semi-permanent. Rearing larvae at high temperatures increases high-thermal tolerance in adults, suggesting that larval acclimation is carried through the pupal stage (Maynard Smith 1957). A long-acting trans-generational acclimation is seen in some locusts, where nymphal density determines phase state of adult females, which then determines the type of egg diapause, and color and phase state of subsequent hatchling (Matthe, 1950, Uvarov 1966, Simpson and Sword, this Volume). Also, it must be remembered that acclimation is a continuing dynamic process. During acclimation, physiological parameters often under- or overshoot before settling at a new constant value (Precht et al. 1973, Prosser 1973). Because in nature conditions constantly change, acclimatizing individuals may never reach steady state.

Factors that Influence Acclimation

By the middle of the last century, scientists had identified numerous co-factors and variables that influenced the speed, strength, and permanency of acclimation. These included body size, sex, age, circadian phase and activity levels, molting and reproductive stage, hormones, diapause-, estivation-, and desiccation-state, and co-occurring environmental factors such as temperature, salinity, oxygen level, relative humidity, density and crowding, nutrition, time of day, photoperiod, light intensity, and season (Bodenheimer 1931, Gunn 1931, 1934, Lühmann and Drees 1952, Baldwin 1954, Dehnel and Segal 1956, Okay 1956, Edwards 1958, Kinne 1958, Prosser 1958a, Atwal 1960a, Dehnel 1960, Todd and Dehnel 1960, Hunter-Jones 1962, de Wilde 1962, Danilevskii 1965, McWhinnie and O'Connor 1967, Rowell 1970, Tauber and Tauber 1976, Takeda and Masaki 1979). For example, nymphal *Periplaneta americana* cockroaches show a greater acclimation response than do adults to temperature, and small adults acclimate better than large adults (Dehnel and Segal 1956). *Homarus americanus* lobsters can acclimate to temperature, salinity, *or* oxygen level, but acclimation to any two of these factors strongly alters tolerance to the third (McLeese 1956). Likewise, photoperiod strongly influences thermal-acclimation of metabolism in sunfish (Roberts 1964), and photoperiod and temperature interact in triggering diapause in many insects (Fig. 6) (Danilevskii 1965).

Experimental variables, such as speed or intensity of environmental change and time spent under the acclimating environment greatly influence acclimation (Figs. 4 and 5) (Nicholson 1934, Kennedy 1939, Bullock 1955, Precht et al. 1955, Baldwin and Riordan 1956, Grainger 1958, Atwal 1960a). For example, in *Ephestia* moth pupae, a 4-h cold-shock greatly improves subsequent cold-tolerance, but a 16-h cold-shock does not (Atwal 1960a). One confounding problem is that general physiology changes with development and age, and that high acclimation temperature accelerates such changes (Bowler 1967, Davison 1969, 1971). For example, because they are immobile, pupae may have evolved high thermal tolerances (Burnette 1957, Hollingsworth and Bowler 1966). Such tolerance may rapidly decline after eclosion (e.g., Fig. 5). Also, acclimating to a constant temperature or oxygen level may produce a different effect than acclimating to a cycling variable with the same mean as the constant variable (Rogers 1929, Salt 1956, Richards and Suanraksa 1962, Matthews 1976). Greater acclimation may be seen in nature than in the lab, possibly because multiple synergistic factors may operate in nature (Salt 1956). Likewise, the degree of acclimation

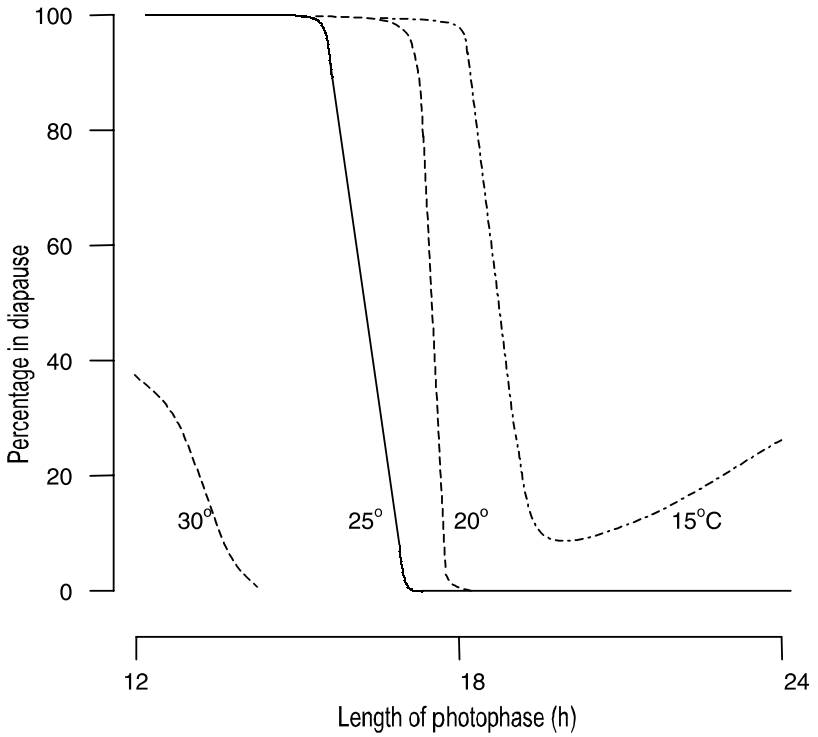

Fig. 6 Interaction of temperature and photoperiod on diapause induction in the noctuid moth, *Acronycta rumicis*. In this example, diapause is not temperature-compensated. Instead, the insect appears to adaptively adjust diapause induction, based on information from two elicitors. The response threshold to short photophase is raised at high temperatures (i.e., shorter photoperiods are required at high temperatures, to induce diapause), allowing the insect to remain active when temperatures remain favorable. After Danilevskii (1965).

recorded by a researcher varies with both the level of the environmental factor during acclimation and during subsequent measurement. Acclimation often occurs at one temperature, oxygen, or light level, but not at another (Prosser 1958a, Rowell 1971). Colhoun (1960) noted rapid (3 h) cold-acclimation when *Blattella* roaches were transferred from 25 to 15 °C, but slow acclimation (> 24 h) from 35 to 25 °C. Despite having to delay their publication because of "*. . . injuries sustained by one of us during an air raid*," Gunn and Hopf (1942) emphasized that speed and direction of changing test conditions influenced the expression of acclimation. Perhaps Gunn and Hopf came to study rapid acclimation as a result of a pressing need to rapidly complete their experiments.

Overall, organisms tend to acclimate better and exhibit better compensatory acclimation at viable vs. extreme environmental values (Kinne 1958, Buffington 1969). For example, cold-acclimation is often induced by cool temperatures, but not extreme cold temperatures (Mellanby 1940a). Thresholds for elicitation vary greatly among traits. In some cases, only a brief exposure to the elicitor stimulates rapid and strong acclimation (Meats 1973). A 2-hr-long high-temperature shock increases heat-tolerance in *Dahlbominus* wasps, but this response declines as the length of the heat-shock increases, even at relatively low heat-shock temperatures of 29 and 32°C (Baldwin 1954, Baldwin and Riordan 1956), probably due to developmental changes in base line tolerance (Davison 1971) (Fig. 5). *Ephestia* flour moth pupae require only a 4-h exposure to cool temperatures to increase survival at 15 °C (Atwal 1960a). In contrast, thermal acclimation in *Drosophila subobscura* is transitory unless the insects are conditioned at the high temperature for a long period (Maynard Smith 1957). Hence, to fully understand acclimation, it is essential to acclimate organisms to, and subsequently measure them, at a wide range of any variable (Precht et al. 1955, Prosser 1958b).

Acclimation researchers should be aware of confounding factors. For example, temperature-induced change in activity rates (escape response, torpor) and thermal pathologies may alter O_2 use, which may be mistaken for metabolic acclimation (Anderson and Muchmor 1971). Likewise, unrecognized physiological damage that may occur under extreme conditions may underlie the inability of some animals to acclimate to extreme vs. moderate conditions (e.g., Edwards 1958, Atwal 1960a). Acclimation to high temperature may really represent increased resistance to desiccation at high temperatures, and not temperature-resistance, per se (Maynard Smith 1957). Finally acclimation triggered by environmental factors must be separated from developmental physiological changes; under warm (as opposed to cold) treatments, insects continue to age, which might confound interpretation of acclimation data (Bowler 1967, Davison 1971).

Modeling Acclimation

Early workers produced numerous descriptive and graphical models of acclimation (Agrell 1947, Precht 1951, 1958, 1973b, Smith 1951, Zerbst et al. 1966, Brett 1971, Prosser 1973), and these remain instructive, today. Both Precht (1951, 1958) and Prosser (1958b) emphasized how acclimation could alter rate curves by displacing them up, down, left, or right (translation), or

via rotation (clockwise or counterclockwise), or by altering their length or shape (Precht 1951, Bullock 1955) (Fig. 7). Changes in length or shape, and rotation of rate curves altered Q_{10} (Fig. 7). Precht (1949) proposed five types of acclimation responses (Fig. 8). Although he stressed thermal acclimation, his model is appropriate for acclimation to other factors as well. In Fig. 8, each line represents one possible way that an individual might acclimate a rate (such as metabolic rate) to three different levels of a particular environmental factor such as temperature. Line 2 represents an organism with perfect compensation (i.e., the organism acclimates such that it maintains a similar rate in all environments. Line 4 shows no acclimation. It also represents the acute rates that would occur immediately following transfer to a new environment, *before* acclimation occurred. Because, in this case, the acute rates do not change after a long period at the new environment, there is no acclimation. Line 1 represents excess compensation, Line 3 represents incomplete or partial acclimation, and Line 5 represents inverse acclimation. One might not expect inverse acclimation, but it occurs (Gunn and Hopf 1942, Garside and Tait 1958, Sømme 1968, Davison 1971). For example, some crab and crayfish muscles show Type 5 acclimation to temperature (Bowler 1963, Vernberg and Vernberg 1967a,b, Jungreis and Hooper 1968), and *Tribolium* reared in cold temperatures for a month survive better at hot temperatures than those reared at hot temperatures (Edwards 1958). However, as Prect and Prosser pointed out, each pattern of acclimation, including inverse acclimation, may (or may not) be adaptive under the appropriate environmental and physiological conditions. For example, inverse acclimation of a specific enzyme might aid general homeostasis if it moderated the effects of harmful rate changes in other enzymes (Precht et al. 1973).

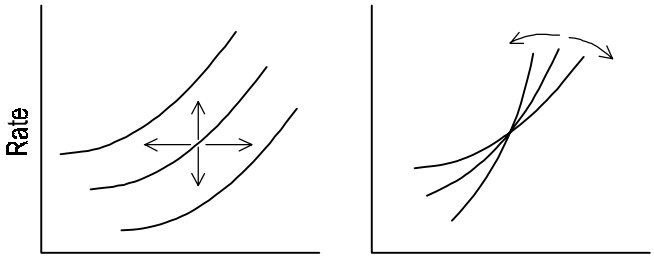

Fig. 7 Possible theoretical changes in biological rates during acclimation as per Precht (1951) and Prosser (1958b). Left graph shows translation. Right graph shows rotation, which alters Q_{10}.

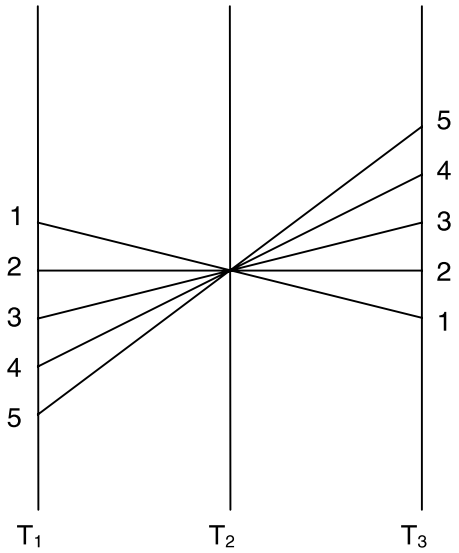

Fig. 8 Five patterns (lines 1-5) of acclimation response for animals acclimated to, and tested at, three different temperatures, as per Precht (1949) and Prosser (1973). Vertical axis represents physiological response (rate, tolerance, titer of metabolic product, etc.) after acclimation. T_1, T_2, and T_3 represent low, medium, and high acclimation and test temperatures, respectively. Line 2 represents perfect compensation, whereby the physiological response does not change when the individual is successively acclimated to and tested at three different temperatures. See text for further explanation.

Adaptive Value of Acclimatization

Early workers touted the adaptive value of acclimatization (Davenport and Castle 1985), which seemed obvious in nature, when non-acclimatized individuals died and acclimatized ones lived. Adaptive evolution was also implied by the fact that acclimatization was often integrated and anticipatory, whereby organisms altered their physiology in complex ways *before* harmful conditions occurred. Adaptive arguments were especially strong for those insects that responded to token elicitors that were not themselves harmful, but which served as proxies for those that were, such as when photoperiod triggered beneficial acclimation to harmful temperatures (Hoar and Robertson 1959). It was hypothesized that because some harmful environmental factors could change too fast for animals to prepare, organisms had evolved to respond to proxy elicitors that predicted future dangers. Hence, acclimatization was seen as a type of phenotypic plasticity that permitted individuals to adaptively alter their physiology in response

to environmental cues that signal changing conditions. In some cases, acclimatization allowed organisms to extend tolerances or limits (Baldwin 1954, Mellanby 1954, Salt 1959). In other cases it permitted compensation such that an individual maintained the same physiological rate or function (such as metabolism, heartbeat, ventilation, activity, etc.) in the face of changing environmental conditions (Parhon 1909, Sayle 1928, Lühmann and Drees 1952) (Figs. 2 and 9). Trans-generational acclimatization allowed parents to adaptively alter their offspring's physiology, based on the parent's knowledge of the current environment, which predicted the offspring's environment (Levins 1968). However, acclimation could also be responsive, such as when chironomid midges increase hemoglobin *after* being moved to a low-O_2 environment (Fox 1955).

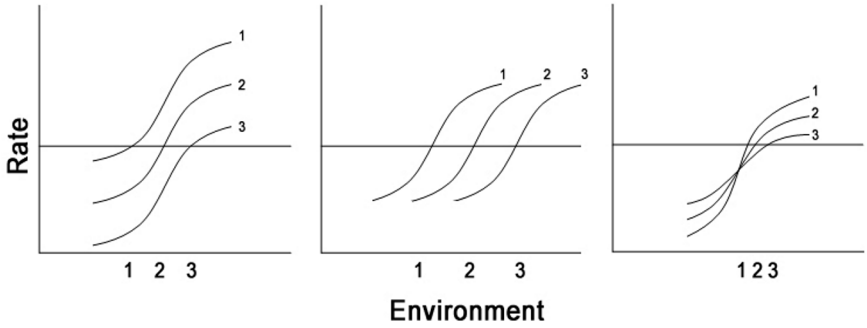

Fig. 9 Three ways that change in rates during acclimation can result in compensation. Curves 1, 2 and 3 show acute biological rates following acclimation to three different environments (1, 2 and 3), when tested at various levels (horizontal axis) of a given factor (temperature, osmolarity, O_2 concentrration, etc.). Points 1, 2, and 3 on horizontal axis represent when testing conditions equal acclimation conditions. Note that in each case, rate is identical (i.e., perfect compensation) at each of the three acclimation levels.

Acclimatization may be beneficial in that it permits organisms to continuously adjust their physiology, throughout their lives (Fig. 10). This presumably allows organisms to become more competitive and to inhabit broader ecological niches and wider seasonal and geographical ranges (Bullock 1955). Prosser (1958b) suggested that many physiological races actually represent acclimatization, and not genetically distinct populations.

However, acclimatization may carry physiological costs (Hoffmann 1995) and does not always easily lead to an adaptional explanation (Tantawy and Mallah 1961, Huey and Berrigan 1996, Huey et al. 1999. Gilbert et al. 2001). This is especially true in cases of reverse acclimation (see

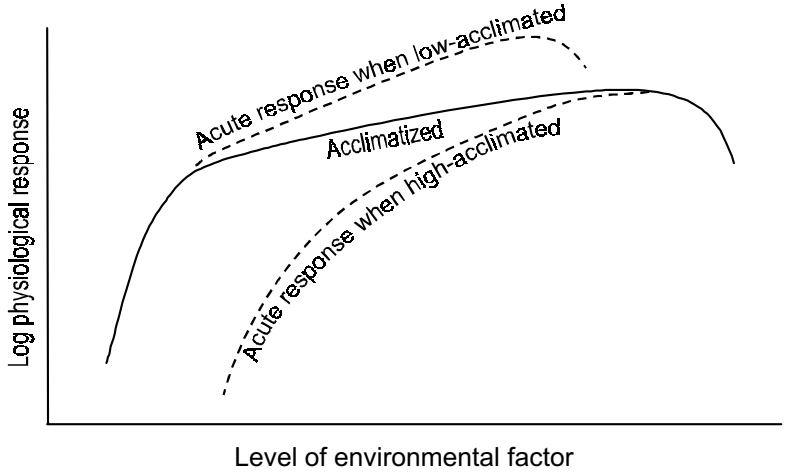

Fig. 10 Hypothetical effects of acclimation on acute physiological response. Solid line shows acute physiological response for an individual acclimatized to each tested level of a given factor (temperature, salinity, O_2 concentration, etc.). Dotted lines show acute physiological response at various factor levels for individuals acclimated to a low level of a given environmental factor (top curve) vs. a high level (bottom curve). Note that, in this example, acclimatization improves both tolerance and compensation. After Bullock (1955).

above). In some cases, "acclimation" makes insects more susceptible to a stressful environmental factor, such as when acclimation to 38°C made *Tribolium* beetles less tolerant to 40°C than beetles acclimated at 18°C (Edwards 1958). However, pretreatments at extreme conditions may produce lingering damage, masking or disrupting acclimation, or making individuals less viable, and high temperatures may speed aging and developmental changes in physiology (Davison 1971). Although Laudien (1973) cautioned that lab-derived conclusions about adaptive value should be tested in the field, the laboratory physiologists who studied acclimation generally did not do so, nor did they consider lifetime fitness consequences of specific acclimations.

The benefits of tolerance adaptation can be illustrated by a tolerance polygon, which shows the tolerance of individuals acclimated to all possible levels of a particular environmental factor. Tolerance polygons derived from empirical data often show that acclimated organisms can tolerate a wider range of conditions and thus extend their ecological niche. Figure 3 shows a hypothetical tolerance polygon, illustrating complexities when considering different traits. In this hypothetical example, different traits have dramatically different tolerance thresholds, different traits

acclimate differently, individual traits acclimate differently to high vs. low levels of a given environmental factor during acclimation, and tolerance to low extremes show a different pattern than tolerance to high extremes. Actual tolerance polygons derived from real animals (Fig. 11) show the great diversity of responses present in nature, and reaffirm that, in biology, anything is possible, and that not all acclimation may be beneficial.

Early researchers assumed genetic control for the ability to acclimate, and that populations had undergone selection for both an ability to acclimatize, and degree of response (Key 1954, Prosser 1955, Rowell 1971). Breeding, hybridization, and selection experiments on high-temperature acclimation (Maynard Smith 1956, Bowler and Hollingsworth 1965), diapause induction (Danilevskii 1965), environmentally induced color morphs (Fuzeau-Braesch 1960, Nel 1968), and locust phase characteristics (Gunn and Hunter-Jones 1952) supported these beliefs. After 21 generations of selection for high salt tolerance, *D. melanogaster* pupae not only had larger anal papillae (used in osmoregulation) and greater survival in salty media, but had evolved greater plasticity for papillae size than non-selected flies, demonstrating that plasticity can be selected (Waddington 1959).

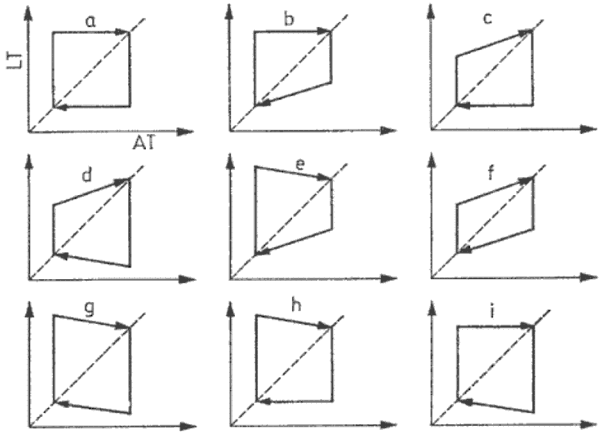

Fig. 11 Tolerance polygons for interaction of acclimation temperature (AT) vs lethal temperature (LT), showing possible acclimation patterns among different species. a) No acclimation. b) Cold acclimation only. c) Heat acclimation only. d) Heat acclimation, but paradoxical (reverse) cold acclimation. e) Cold acclimation, but paradoxical heat acclimation. f) Both cold and heat acclimation. g) Paradoxical or reverse acclimation to both cold and heat. h) No cold acclimation, but paradoxical heat acclimation. i) No heat acclimation, but paradoxical cold acclimation. Precht (1973) gives actual species examples for each type. Reprinted from Precht (1973), Fig. 2, p. 429. With kind permission of Springer Science and Business Media.

Geographic and habitat differences in acclimation abilities further supported genetic-adaptational hypotheses (Heart 1952, Precht et al. 1955, Prosser 1955). Indeed, related species inhabiting highly variable environments often (but not always) showed better compensatory acclimation capability than those inhabiting less-variable environments (Payne 1926, Marzusch 1952, Hunter 1968, Levins 1969, Anderson and Mutchmor 1971). For example, temperate fiddler crabs exhibited greater thermal acclimation than tropical ones (Vernberg and Vernberg 1966, Vernberg 1969). Furthermore, species that remain active over a wide range of environmental conditions (temperature, salinity, oxygen) are generally better acclimators than those that relocate, hibernate, estivate, or enter dormancy in response to variable conditions (Prosser 1973).

For an organism to function, all biochemical and physiological processes must be coordinated and balanced. But, in some cases, acclimation of one function interferes with another (Clark 1967, Hoffmann and Stockmeier 1975). As such, the difficulty of integrating acclimation (plasticity) among innumerable physiological systems and functions was hypothesized to be the factor that ultimately limited adaptation in organisms (i.e., why all individuals cannot perfectly acclimatize to all environmental conditions, and why populations and species must specialize or are restricted to specific environments). At extreme environmental conditions, it becomes harder for organisms to maintain steady rates (to compensate). Hence, compensatory acclimation generally only occurs over a certain medium range (Fig. 10) (Platzer 1967). For example, metabolic rates remain relatively steady for *Culex* mosquitoes acclimated between 15 and 25°C, but deviate beyond that range (Buffington 1969). Acclimation may speed speciation, when sympatric races acclimate differently or possess different environmental sensitivities (thresholds to elicitors). Genetic divergence may increase in locals where hybrids produce inappropriate acclimation responses to the local environment. As previously mentioned, many species and many traits show no acclimation (Nabours 1929, Dryer 1932, Keister and Buck 1961), and in fact, only a few species have been shown to undergo simultaneous capacity and tolerance acclimation (Precht 1958, Lagerspetz 2006). Answering why some species, functions, and traits acclimate and others do not, and understanding the consequences of such differences presents major challenges to evolutionary biology.

Mechanisms Underlying Acclimation

Early studies on acclimation laid the framework for how current workers analyze acclimation mechanisms (Fox 1936, 1939). For example, Prosser

(1950, 1961), Bullock (1955), Precht (1955, 1964), Knox (1958), and Clarke (1966) discuss inductors, sensing elements, signal detection, effectors, controllers, information-control, servo-loops, adapting systems, and the possibility of enzymatic, cellular, and hormonal regulation of plastic responses. As such, these workers presaged the elicitors, receptors, and signal transduction pathways that are discussed in the current literature. Altered enzyme activity was an early focus, be it changes in conformation (Milkman 1967), concentration (Knox 1958, Rao 1967), or isozymes (Baldwin and Hochachka 1970). Hochachka (1967) proposed that acclimation initiated alternative pathways, and Gordon (1972) suggested that some animals compensate by changing one set of rate-determining reactions for another. Hence, organisms store in their genetic closets, different biochemical ensembles, to be employed under the appropriate environmental conditions. Prosser (1958b) even discusses the possibility of environmental factors inducing acclimation by acting directly on the DNA of individuals, and Ritossa (1962) and Tissieres et al. (1974) showed that heat shock induced both transcription and translation. Hence, by 1970, workers understood that acclimation was accomplished by regulation of hormones, enzymes, transcription, translation, and concentrations of specific compounds (Marzusch 1952, Carlson 1953, Precht 1953, Prosser 1958a, Siminovitch et al. 1967, Somero 1969, Weiser 1970).

Although pioneering physiologists lacked modern molecular methods, some still made impressive progress, elucidating partial physiological pathways for acclimation. Thus, Fox (1955) showed that acclimation to low O_2 level in chironomid midge larvae (blood worms) and *Daphnia* was effected by up-regulation of oxygen-transport pigments such as hemoglobin, and (in *Daphnia*) increased cytochrome. Thermal acclimation of metabolic rate in whole *Sarcophaga* or *Calliphora* (Diptera) was mirrored by that in isolated mitochondria (Spencer-Davis and Tribe 1969, Danks and Tribe 1979). Likewise, researchers quickly determined that winter acclimation in insects was often accomplished by simultaneously decreasing water and increasing polar, polyhydric solutes such as glycerol, sorbitol, and mannitol. The organic solutes inhibit ice nucleation, and both processes lower freezing point by increasing osmolarity (Salt 1961, Prosser 1973). Hence, increasing hemolymph glycerol concentration to 5 M (25% of fresh mass) allowed some *Bracon* wasp larvae to supercool to –47 ^{o}C (Salt 1958, 1959, 1964). Similarly, winter acclimation in tent caterpillar (*Malacosoma*) eggs raised glycerol concentration to 35% (dry wt), giving them the ability to supercool to –41^{o}C. Pre-acclimation eggs could supercool to only –21^{o}C

(Hanec 1966). Other insects acclimated to winter by becoming freeze tolerant (Salt 1962, Sømme 1964), with some surviving freezing as low as −80°C (Miller 1982).

By the 1950's, researchers already had a fair understanding of how environment induced color change in insects, whereby known wavelengths of light, perceived via the eyes or individual epidermal cells of the integument, induced production of specific pigments, sometimes under endocrine control (Knight 1924, Schlottke 1926, Kaestner 1931, Ergene 1954, Key 1954a,b, Rowell 1971). Similarly, scientists discovered that animals often acclimate to temperature by altering the saturation of membrane lipids (homeoviscous adaptation). Saturated lipids are less fluid, which stabilizes membranes and lipoproteins at high temperatures. Temperature and humidity can elicit this response (Fraenkel and Hopf 1940, Precht et al. 1955, Holmstrup et al. 2002), but so does feeding on saturated lipids (House et al. 1958). Note that all three examples use the same mechanisms (altered lipids) to produce the same consequences (increased thermal tolerance or compensation), but initiate via different factors (temperature, humidity, or diet). This illustrates the difficulty in defining acclimation: despite the similarities in all three examples, change in lipid saturation via diet would be considered a passive process, and not acclimation.

Early workers realized that acclimation to different factors required different underlying mechanisms, that different traits acclimated differently (Fig. 3) (Precht 1951, 1958, Precht et al. 1955), and that different mechanisms operated during exposure to high vs. low states of a given environmental factor (Fig. 3) (Brett 1946, Prosser 1950). Rearing insects at high temperatures often increased thermal-death points, but had relatively small effects on cold torpor temperatures, and vice versa (Edwards, 1957, 1958), suggesting independence of the mechanisms effecting high- vs. low-temperature acclimation (Mellanby 1954, Precht 1958). In contrast, Salt (1961) opined that cold-acclimation could be considered as the loss of heat-acclimation and vice versa.

Initial researchers also articulated the need to maintain overall internal physiological balance – Precht (1958) used the phrase, "*harmony of cell metabolism*." Hence, for acclimatization to be beneficial and adaptive, the thousands of individual biochemical reactions and physiological rates and functions, which in total comprise a viable organism, all must work in harmony and synchrony *after* a phenotypic change (phenotypic integration). Separate traits must acclimate in lock-step.

Current Studies of Acclimation

Acclimation continues as an exciting and active research area. In this section, I briefly highlight some current trends. Good treatments of various topics relating to acclimation include: Huey and Berrigan 1996, Johnston and Bennett 1996, Kingsolver and Huey 1998, Bale 2002, Hoffmann et al. 2003, Wang et al. 2003, Chown and Nicholson 2004, Morris and Vosloo 2004, Bowler 2005, Danks 2005, Sinclair and Roberts 2005, Gimenz 2006, Harrison et al. 2006, Lagerspetz 2006, Lagerspetz and Vainio 2006.

The greatest change in acclimation research has been the advent of modern molecular biology and bioinformatics, which has dramatically transformed physiological research (Cossins et al. 2006, Gracey 2007, Kültz et al. 2007, Quackenbush 2007, Wittkopp 2007, Shiu and Borevitz 2008), providing powerful tools for understanding how phenotypes are made, maintained, and altered (but see Feder and Walser 2005, Barrett et al. 2007). For the first time, transcriptome, proteome and metabolome open-screens facilitate system-wide assessment of acclimation responses (Malmendal et al. 2006), aiding understanding of mechanisms and regulation at the molecular level, allowing identification of candidate genes, and, importantly, generating new hypotheses (Liang et al. 2004, Storey 2004, Kayukawa et al. 2005, Cossins et al. 2006, Malmendal et al. 2006, Sonoda et al. 2006, Mathias et al. 2007). Mutant and transgenic lines aid this process (Raushenbach et al. 2004, Nielsen et al. 2005). We now know that regulation of gene expression underlies much acclimation, and that the environment can influence phenotype by *directly* turning on or off specific genes (Buckley et al. 2006, Henry et al. 2006, Nielsen et al. 2006, Sonoda et al. 2007). For example, a 1-h heat shock altered expression in 1222 *D. melanogaster* genes (Sorensen et al. 2005). The environment can also directly stimulate hormones (Gade 2004, Schooley et al. 2005), and hormones can turn on or off genes (Clever 1961, Thissieres et al. 1974, Raikhel et al. 2005).

Debate continues as to the definition of acclimation (Bowler 2005, Loeschcke and Sørensen 2005, Sinclair and Roberts 2005, Lagerspetz 2006) and how adaptive acclimation differs from passive responses (Pigliucci 1996, Wilson and Franklin, 2002a,b). In adaptive acclimation, the capacity for, and mechanism to produce, the physiological change are presumed to have undergone natural selection. The response is considered active, specific, coordinated, and beneficial. That is, the organism has evolved to respond adaptively to environmental elicitors via specific sensors, signal transduction pathways, effector systems, and integration, all controlled by

the coordinated activities of numerous regulatory genes and feedback loops. In contrast, passive responses are assumed to include unavoidable, direct, inevitabilities, biophysical effects, pathologies, physiological damages, and environment-induced physiological or developmental constraints. Such responses may or may not be detrimental. These categorizations, however, are problematic, because it is not only difficult to document their defining qualities, but at some point, passive and active physiological responses grade into one another. In addition, natural selection chooses among phenotypes, not genes. Thus, as previously mentioned, whether an environmentally induced change in phenotype is passive or gene-regulated, beneficial or detrimental, it still is a change in phenotype, and thus places that individual into a different selective regime. Recurrence of those particular environmental conditions, leading to recurrence of the new phenotype, allows the environment to select for genes that produce a beneficial plastic response (given genetic variability and heritability for plasticity) (West-Eberhard 2003). In this sense, an unavoidable, passive physiological pathology may be the first stage of adaptive acclimatization evolution. Thus, environmental susceptibilities and highly evolved, gene-regulated acclimatization responses may represent two points on a continuum.

Definitions of acclimation and related phenomena will become less importation in the future. As modern molecular physiology clarifies the pathways and mechanisms underlying physiological change, the traditional categories (homeostasis, heat shock, hardening, acclimation, developmental switches, etc.) will be distinguished or replaced by mechanistic categories. Hence, homeostasis, acclimation, and developmental switches (in different species) that utilize the same genes, mechanisms, and pathways, will be grouped together.

A lively discussion centers around the question of the adaptiveness of acclimation (Huey and Berrigan 1996, Huey et al. 1999, Hoffmann and Hewa-Kapuge 2000, Thompson et al. 2001, Woods and Harrison 2001, 2002, Loeschcke and Hoffmann 2002, Wilson and Franklin 2002a,b, Deere and Chown 2006, Lagerspetz 2006). This has spurred articulation of methods to test adaptive hypotheses (Huey and Berrigan 1996, Kingsolver and Huey 1998, Garland and Kelly 2006), and research on the costs and benefits of acclimation (Kingsolver 1995, 1996, Krebs and Holbrook 2001, Loeschcke and Hoffmann 2002, Hoffmann et al. 2003, Stillwell and Fox, 2005), especially in the field (McMillan et al. 2005, Kristenson et al. 2007, Loeschcke and Hoffmann 2007). Realization that the single, rapid, large-step

environmental changes applied in the lab do not accurately represent nature (Wang et al. 2006) has stimulated a call for more ecological relevance in testing (Bale 1987, Feder 1997, Feder et al. 1997, Kelty and Lee 2001, Sinclair 2001).

Although we know that a single environmental factor can induce manifold changes in gene expression, and numerous subsequent biochemical and physiological cascades, we need to sort out which of these myriad phenotypic changes represent adaptive physiological adjustments, and which are developmental pathologies and other non-beneficial pleiotropic and physiological by-products (Fischer et al. 2003). Likewise, we need to take a more holistic view when assessing costs, benefits, and tradeoffs of acclimation (Angilletta et al. 2003, Seebacher and Wilson 2006, Loeschcke and Hoffmann 2007), including considering long-term effects (Layne and Peffer 2006). Acclimatization might provide any number of unrecognized benefits such as enhanced mating or fighting ability (Lagerspetz 2000, Seebacher and Wilson 2006). In contrast, acclimatization might greatly improve a specific physiological function, but still lower overall fitness when it reduces competitiveness, disease resistance, longevity, etc. (Zwaan et al. 1992, Zamudio et al. 1995, Wilson et al. 2007). A stress factor may elicit an adaptive beneficial acclimation response, and simultaneously induce physiological damage (Woods and Harrison 2001, 2002, Wilson and Franklin 2002a). The two opposite effects are difficult to disentangle.

Some have called into question the existence of, or at least the correct measurement of, acclimation. For example, Clark (1993) suggests that seasonal acclimation of metabolic rate has no useful biological meaning. This is because temperature influences nearly all physical properties of organisms (lipid fluidity, diffusion rates, water density, viscosity, solubility, pH, ionization, etc.), and we do not know how these combined factors affect metabolic rate. Also, growth, activity, and reproduction often slow in winter, because of seasonal changes in resource availability, and these changes greatly influence metabolism. Hence, observed changes in metabolic rate may or may not have anything to do with direct thermal adaptation per se. Other authors have pointed out similar problems with Q_{10} (Johnson et al. 1974). Acclimation researchers have yet to adequately reply to these criticisms. Sinclair and Roberts (2005) point out that interpreting acclimation studies is difficult given the great diversity of treatments applied (seconds to months), and responses measured. Also, supercooling points may not be a reliable metric for estimating cold hardiness or survival (Wang and Kang 2005).

Despite the above arguments, documentation of acclimation continues at a furious pace, with weekly reports of new species or traits showing one-or-another form of acclimation (Hawes et al. 2007, Jensen et al. 2007, Slabber et al. 2007, Sonoda et al. 2007), and some showing no acclimation (Pitts and Wall, 2006, Terblanche and Chown 2007). For example, many additional insects have been found to acclimate lipids to environmental temperature (Kostal et al. 2003, Overgaard et al. 2006, Tomcala et al. 2006), such as *Melanoplus sanguinipes* grasshoppers, which synthesize higher-melting-point *n*-alkanes when reared at high temperatures (Gibbs and Mousseau 1994). Drought, short cold-shock, and photoperiod, induce altered lipids in Collembola (Holmstrup et al. 2002), *Sarcophaga* flies (Michaud and Denlinger 2006), and *Pyrrhocoris* bugs (Hodkova et al. 2002), respectively. In Collembola, drought acclimation improves cold-tolerance (Bayley et al. 2001, Holmstrup et al. 2002). Both polyols and heat shock proteins can be induced by cold *or* heat shock, and both apparently aid in thermal tolerance (Wolfe et al. 1998, Salvucci et al. 2000). Caterpillars and some other insects may acclimate to dry conditions by altering cuticular transpiration and rectal water absorption (Martin and Van't Hof 1988, Reynolds and Bellward 1989, Woods and Bernays 2000, Woods and Harrison 2001). Rapid cold hardening can be induced by both high temperatures (Goto and Kimura 1998, Sinclair and Chown 2006) and anoxia (Coulson and Bale 1991). In tsetse flies, thermal acclimation strongly affects rates of water loss (Terblanche et al. 2006). Thermoperiod influences cold hardening in locust eggs (Wang et al. 2006) and beet armyworms (Kim and Song 2000). Additional arthropods have been shown to acclimate to hypoxia by increasing tracheal diameter or branching (Loudon 1989, Jarecki et al. 1999, Henry and Harrison 2004, Harrison et al. 2006), or to salinity (Henry et al. 2006, Mendonca et al. 2007). Salinity acclimation alters salt uptake in freshwater shrimp, *Gammarus zaddachi*. *Culex tarsalis* mosquito larvae acclimate to salty water by increasing concentrations of two organic osmolytes; trehalose increases 2-fold, and hemolymph proline 50-fold (Patrick and Bradley 2000). Other mosquito larvae acclimate to pH (Clark et al. 2004). Caterpillars respond to thermal stress by lightening body color (Nice and Fordyce 2006). Cold acclimation allows *Periplaneta japonica* roaches to walk on ice (Tanaka 2002). In Colorado potato beetles, chilling or temporary freezing, followed by transfer to 24°C alters behaviors, causing the beetles to burrow into the soil and remain there for 3-4 weeks, a response possibly mediated via JH (Hiiesaar et al. 2001). We now know that insects can acclimate to dietary toxins by up-regulating P450 and other enzymes (Mazumdar-Leighton and Broadway 2001, Agrawal et al. 2002, Berenbaum

2002, Cianfrogna et al. 2002, Li et al. 2002, 2004), and to pollutants by producing heat-shock proteins (Lee et al. 2006). Insects can acclimate to tough and fibrous food by altering head, mandible, and muscle morphology (Thompson 1992). Insects can "acclimate" to novel foods (Agrawal et al. 2002), and time to oviposit (Scott 1996, Batemann et al. 2005), and even ability to reproduce can be said to acclimate (Scott et al. 1997). There is also growing interest in transgenerational acclimation (Huey et al. 1995, Crill et al. 1996, Watson and Hoffmann 1996, Magiafoglou and Hoffmann 2003, Guan and Wang 2006a,b, Rako and Hoffmann 2006, Simpson and Sword, this Volume).

Particularly important for entomologists who use CO_2 as a narcotizing agent, is that this molecule can induce numerous, profound, and long-term physiological changes in insects. CO_2 can alter metabolic pathways, changing titers and types of proteins, lipids, carbohydrates, and hormones (Nicolas and Sillans 1989). It also changes nerve function, behavior, development, growth, body size, and reproduction (Nicolas and Sillans 1989). Such effects were realized over 50 years ago. For example, a single exposure to high CO_2 alters temperature preferences and causes individual honey bees to switch from hive work to foraging (Ribbands 1950). It also influences JH titers (Buhler et al. 1983) and initiates vitellogenin production and oviposition in queen bees (Mackensen 1947, Engels et al. 1976). CO_2 induces permanent changes in body color in some insects (Rowell 1971). In *Helix* snails, it influences estivation (Michaelidis et al. 2007). However, at this time, it is not known if such responses represent pathologies or beneficial acclimation. Interestingly, some midges, ants, weevils, and tiger beetles switch to anaerobic respiration under hypoxia or high CO_2 levels (Hoback and Stanley 2001, Nielsen and Christian 2007). Nilson et al. (2006) believe that short CO_2 exposure does not significantly influence cold hardiness in *D. melanogaster*.

The study of stress proteins, including heat shock proteins (HSPs), has become a major research industry unto itself (Korsloot et al. 2004, Henderson and Pockley 2005, Yin et al. 2006, Asea and DeMaio 2007, Calderwood et al. 2007, Pappas et al. 2007, Wang et al. 2007). Stress proteins are induced by various environmental factors, including heat, cold, desiccation, crowding, heavy metals, organic toxins, toxic gases, UV, anoxia, salinity, parasites, disease, and mechanical injury (Kulz 1996, Nepple and Bachofen 1997, Feder and Hofmann 1999, Tammariello et al. 1999, Bayley et al. 2001, Sørensen and Loeschcke 2001, Rinehart et al. 2002, Hoffmann et al. 2003, Williams et al., this Volume). They are often mediated by cytoplasmic stress-induced heat-shock factors that bind to promoter regions of HSP genes,

initiating transcription. HSPs repair or protect enzymes from stress-damage, and play a vital role in increasing thermal or cold tolerance, and thus appear to function in acclimation. They can be induced within minutes of stress. During and following heat shock, normal protein synthesis can be largely replaced by production of heat-shock proteins (Chown and Nicolson 2004), demonstrating that environmental stress can redirect much of the cell's biochemistry. A critical goal is to determine if HSP-production is only reactive or if it can be anticipatory (i.e., can be induced by harmless levels of factors or harmless elicitors that predict changing environments).

Researchers continue to explore the many factors that influence acclimation, including exposure time (Jian et al. 2005, Mahroof 2005), rate of environmental change (Wang and Kang 2005, Overgaard et al. 2006, Powell and Bale 2006), fluctuating conditions (Colinet et al. 2006, Wang et al. 2006, Lalouette et al. 2007, Hawes et al. 2008), repetitive exposure (Woods et al. 2001, Hawes 2007), age and ontogeny (Miyazaki et al. 2006, Terblanche and Chown 2006, Jensen et al. 2007, Pappas et al. 2007), season (Lee et al. 2006, Ma et al. 2006), diapause state (Izumi et al. 2005, Kayukawa et al. 2005, Teixeira and Polavarapu 2005, Cho et al. 2007), and interactions among multiple, simultaneous environmental factors (Hernandez et al. 2006, Kandori et al. 2006, Tomcala et al. 2006).

Recent studies have uncovered new physiological mechanisms and pathways (Gorr 2004, Michaud and Denlinger 2004, Storey 2004, Marjanovic et al. 2005, Marden 2008), and consequences of acclimation (Gulevsky et al. 2006, Kim et al. 2006, Sonoda et al. 2006, Lalovette et al. 2007, Tsai and Lin 2007). For example, reports continue to suggest an important role for insect hormones in stress response and acclimation (Gruntenko et al. 2000a,b). Both cold and heat acclimation are much more complicated than previously thought (Bale 2002). Some Collembola dramatically lower supercooling points by actively dehydrating (Worland et al. 1998). Other insects may track daily temperature cycles by constantly resetting their thermal thresholds, (Kelty and Lee 2001, Powell et al. 2004). Locust hoppers become cold hardened after only 2 h of cold shock, greatly increasing their survival at –7 ^{o}C; however, they quickly lose this protective physiology if returned to 30^{o}C for 2 h (Wang and Kang 2003). Long-term acclimation is both differentiated from, and related to, rapid cold-hardening and rapid heat shock (Hoffmann et al. 2003, Sinclair and Chown 2003, Bowler 2005, Loeschcke and Sørensen 2005, Powell and Bale 2005, Sinclair and Roberts 2005). In *Drosophila*, thermal acclimation influences ethanol tolerance by changing membrane lipids (Montouth et al. 2006), in *Heliocoverpa* caterpillars it influences susceptibility to pathogens (Chandrashekar et al.

2005), and in *Cherax* crayfish, thermal acclimation improves fighting ability (Seebacher and Wilson 2006).

Researchers are just beginning to trace the temporal patterns of gene, proteome, and metabolome expression during and following acclimation (Hayward et al. 2005, Sorensen et al. 2005, Malmendal et al. 2006, Sonoda et al. 2007), but in the next few years, we will have compete pathways, including their temporal expression, for some acclimations. This will help answer whether acclimation is top-down (centrally controlled via hormones or the CNS), vs. bottom-up (i.e., produced via an aggregate of individual biochemical and cell responses) (Bowler 2005). Cuculescu et al. (1999) and Pearson et al. (1999) employed a clever method to test central vs. local control of acclimation (Fig. 12). By differentially heating different body regions, they showed that thermal acclimation in crabs was relatively independent of both CNS and endocrine control. Indeed, isolated cells can acclimate (Schmidt et al. 1984).

There is accelerated effort in trying to understand the hierarchal physiological relationships that produce acclimation (Garland and Kelly 2006, Gracey 2007, Wittkopp 2007) – how numerous lower-level transcriptional, translational, and enzymatic responses combine to shape complex traits, such as metabolic rate, growth rate, body size, etc., which

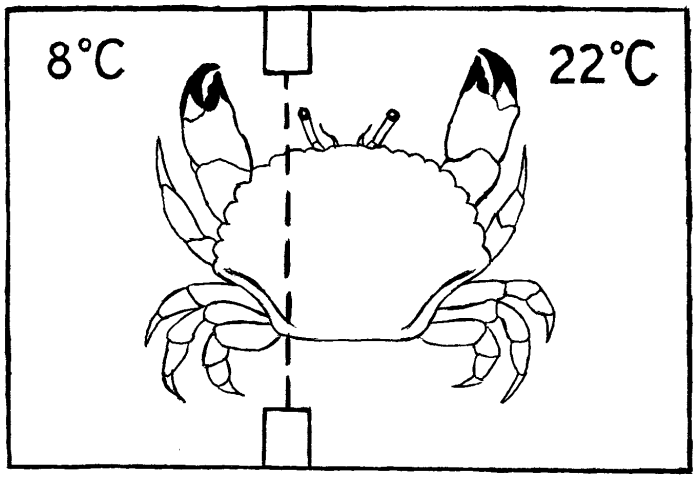

Fig. 12 Apparatus to produce heterothermal acclimation. Crab is suspended by a tight-fitting rubber diaphragm (dotted line) between two chambers of different temperature. Diaphragm is positioned such that the CNS and most of the endocrine system is on one side. Pearson et al. (1999) and Cuculescu et al. (1999) used this method to determine that thermal acclimation in crabs was under local, not central, control.

determine life history. This is important, because genes and gene × environmental interaction control the lower-level processes, yet, natural selection may occur primarily on complex traits (Swallow et al. 2005), partially because complex traits may be more closely related to fitness (Garland and Kelly 2007). Because complex traits are aggregates of dozens of underlying, basic traits, which are themselves controlled by hundreds, if not thousands of genes, selection on a single complex trait must influence many genes. Furthermore, natural selection may act on numerous complex traits simultaneously (Arnold 2003, Ghalambor et al. 2003, Sinervo and Calsbeek 2003). Thus there is a great need to understand hierarchical interactions, including pleiotrophy and epistasis (Swallow et al. 2005). How is integrative physiology maintained under change? Adaptive analyses of acclimation are difficult, when each level of biological organization has its own tradeoffs and constraints, and when there are incalculable, unrecognized interactions (Woods and Harrison 2001, Angilletta et al. 2003).

Numerous researchers are exploring the broader ecological consequences of acclimation – how acclimation influences abundance, distribution, and interspecific interactions (Slabber et al. 2007, Terblanche et al. 2007). Acclimation may allow individuals to enter new niches or expand geographic ranges. Plasticity can determine the strength and direction of ecological interactions, including both con- and allospecific interactions (Fordyce 2006). Acclimation has traditionally emphasized abiotic factors, but individuals may also acclimate to biotic factors, such as other organisms or organism-influenced factors. An exciting new idea concerns reciprocal plastic responses, where two individuals interact reciprocally to one another (Agrawal 2001, Fordyce 2006). We would expect to observe reciprocal acclimation among symbiotic organisms such as mutualists or parasitoids and hosts.

Overall, acclimation research is becoming increasingly integrated, combining genetic, molecular, endocrine, systems physiology, ecological, phyletic, biogeographical, and evolutionary studies, and each benefits from the other (Chown and Nicholson 2004, Loeschcke et al. 2004, Tian et al. 2004, Kellett et al. 2005, Angilletta et al. 2006, Almaas 2007). To a certain extent, acclimation has been subsumed into phenotypic plasticity and phenotypic plasticity into stress studies (Bijlsma and Loeschcke 2005). There is greater awareness of interaction effects and the connections, tradeoffs and constraints among different functional modules (Angilletta et al. 2003, Korsloot et al. 2004, Gimenez 2006, Rako and Hoffmann 2006, Quackenbush 2007). For example, behavioral plasticity in choice, can place animals into

different habitats (climatic, nutrition, etc.) which then influences their subsequent physiology (Price et al. 2003, Garland and Kelly 2006). Swallow et al. (2005) propose "self-induced adaptive plasticity" for cases where a plastic behavior results in a physiological plastic change, which subsequently feeds back to enhance the ability to perform that behavior. Examples would be when an animal switches habitat preferences, subjecting it to a different temperature, salinity, O_2 level, etc., or switches diet. The former might lead to beneficial acclimation to those stressful environmental factors, and the latter might (1) alter preference, which increases feeding, and (2) induce new digestive enzymes that increase tolerance to dietary toxins, resulting in greater fitness for those insects with greater behavioral plasticity (Agrawal et al. 2002). In the above cases, physiological acclimation cannot be separated from behavioral plasticity.

Because acclimation is now accepted as phenotypic plasticity, it is now included in modeling and theoretical studies of plasticity evolution (Gabriel 2005, Borenstein et al. 2006, Garland and Kelly 2006). A growing literature demonstrates the genetic basis of acclimation, its heritability, and its ability to be selected (Harshman et al. 1991, Cavicchi et al. 1995, Krebs and Loeschcke 1996, Loeschcke and Krebs 1996, Lerman et al. 2001, Scheiner 2002, Hoffmann et al. 2003, Wang and Kang 2005). Plasticity may preserve genetic diversity (Lagerspetz 2006) or drive evolution (Schlichting and Smith 2002, Price et al. 2003), and directional selection on a trait mean can increase plasticity (Waddington 1959, Garland and Kelly 2006).

Theoreticians and empiricists are examining the broad patterns that favor the evolution of acclimation vs. other types of homeostatic mechanisms. Clearly, rapid dramatic environmental changes require rapid homeostatic adjustments. Slow-changing marine and aquatic environments might favor the evolution of enzymatic acclimation whereas rapid-changing land environments might favor behavioral plasticity and acute physiological homeostasis. Land is more spatially variable, which allows individuals to rapidly move among habitats, therefore favoring behavioral responses, such as microhabitat shifts, thermoregulation, shelter building, migration, etc., over physiological responses. In contrast, many deep caves and marine environments are thermal- and osmo-stable, and, hence, there might be no need for acclimation (Willmer et al. 2005). Likewise, length of stress periods (Gabriel 2005, Garland and Kelly 2006), cue reliability and predictability of environmental changes (Deere and Chown 2006, Deere et al. 2006), latitude (Ishiguro et al. 2007), altitude (Sorensen et al. 2005), lifespan (Lee et al. 2006), and phylogenetic constraints (Deere and Chown 2006, Terblanche et al. 2007), should all influence evolution of acclimation.

Global warming appears to already be selecting for altered acclimatory responses (Bradshaw and Holzapfel 2006). There are multiple mechanistic pathways to achieve the same functional endpoint. Understanding why one species evolves one solution and another species a different solution is an important focus of current evolutionary physiology (Angilletta et al. 2003).

Scientists have come to realize that acclimation represents just one segment along a gradation of available options that individuals can employ to counter the negative effects of habitat variation. These options include behaviors, acute physiological adjustments, longer term acclimations, and developmental switches (Chown and Nicolson 2004). Parents can also influence offspring physiology via trans-generational effects. Finally, natural selection acts on altered phenotypes, favoring those with genomes that produce beneficial physiological responses to environmental variation. These various responses grade into one-another and interact, blurring divisions (Price et al. 2003). In sum, acclimation is just one of many adaptation strategies, all of which are, more-or-less, interconnected.

Acclimation, of course, has a practical, applied side. Understanding insect acclimation may allow us to predict species ranges (Chen and Kang 2004, Klok and Chown 2005, Régnière and Bentz 2007) and establishment of invasive species (Bale 2002, Slabber et al. 2007). It can also aid pest control (Bean et al. 2007, Jagdale and Grewal 2007, Jian et al. 2007, Kaliyan et al. 2007, Luczynski et al. 2007, Pereira et al. 2007, Terblanche et al. 2008), and ecological monitoring. We may be able to assess relative levels of environmental stress, such as pollutants, by measuring the degree of stress acclimation in insects (De Coen et al. 2006, Lee et al. 2006). Understanding of acclimation may help us predict species responses to changes in Earth's ecology, such as global warming (Bradshaw and Holzapfel 2006, 2008, Gienapp et al. 2008). In the future, we will select or design organisms for economically beneficial acclimation (Collier et al. 2006). Acclimation is also important in animal husbandry and dairy, poultry, and fisheries production (Collier et al. 2006). Finally, a general knowledge of acclimation helps us understand the fascinating topic of human acclimation (Beal 2001, Bae et al. 2006, Flück 2006, Geurts et al. 2006, Swynghedauw 2006, Asea and DeMaio 2007, Calderwood et al. 2007, Radakovic et al. 2007), including human stress and disease response, and pharmacology (Nedeau and Topol 2006).

Lastly, returning to the theme that current researchers can learn from past acclimation studies, I end with a caution from Mellanby (1940b). Although he addressed temperature, his warning is apropos for nearly all environmental factors: *At every temperature, some acclimatization is probably going on in a living tissue, and the extent of the acclimation depends partly on the*

length of the exposure. This appears to me to mean that at any particular temperature there may be no absolute rate for a biological process, and that all conditions previously experienced by the animal must be considered.

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