Chapter 10: Energetics and locomotion

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Biology of the land crabs

1. Introduction

The purpose of this chapter is to describe the general way that land crabs consume and use energy. Although techniques are available to measure food intake and its caloric content, and to determine the aerobic and anaerobic metabolism of organisms during activity and rest, a complete energetic evaluation of any animal, much less one for land crabs, has yet to be made. Thus, we are in possession of a few fragments of data — enough to embolden us to speculate but not enough to restrict our imagination.

This chapter presents an overview of the feeding process, digestion, assimilation, metabolism and the energetic cost of a variety of behaviors that crabs perform. Considerable information is available on locomotion, which is easily quantified and permits us to determine the metabolic range for each species. Other behavior patterns have scarcely been considered from an energetic point of view. This paucity of data will become evident in the following pages where we highlight the information that is required before we can work out an energy budget for any species.

2. Feeding

Crustaceans eat an enormous variety of food. Nutrition and feeding are reviewed by Marshall and Orr (1960) and Grahame (1983). Semi-terrestrial and terrestrial crustaceans include filter-feeders, scavengers, vegetarians, and predators (also see Chapter 3). Few studies have
identified the specific food items taken by a given species, and no caloric studies have been made.

A. Filter-feeding

A large number of crabs living in the intertidal flats consume detritus. For instance, the fiddler crab *Uca signatus* lives in burrows and feeds nearby as the tide recedes. The crab picks up mud with its spoon-shaped chelae and rapidly shovels it into its mouth. Some sorting of organic material from mud occurs by the mouthparts because small mud balls are spit out as fast as new sand is shoveled in. The process is repeated every few seconds, and the burrows are surrounded by rows of little balls. Similar feeding techniques are employed by tropical crabs *Dotilla*, *Scopimera*, *Ibyoplax*, *Metaplan*, and *Paraclei stostoma* (Marshall and Orr, 1960).

The feeding of *Uca pugilator* has been well studied (Altevogt, 1957a; Miller, 1961; Robertson and Newell, 1982). Sand is scooped up by the chelae and passed into the buccal cavity where it is sorted. Heavy inorganic particles fall to the bottom of the cavity and are pushed out of the mouth between the third maxillipeds. The buccal cavity may be flooded with water from the gill chamber, and light organic particles float to the top. On draining, the fine particles are left on the setae of the mouthparts. Food material adhering to sand grains is removed by the setae on the second maxillipeds, which are used to scrape the sand grains across the bristles on the first maxillipeds.

B. Scavengers and vegetarians

Land crabs are largely scavengers. For instance, in Panama the hermit crab *Coenobita compressus* rests above the tide line in trees, and under rocks and drift wood during the day and visits the beach at low tide to search for food. It eats fruit, dead animals, and even human feces on the shore (Herreid and Full, 1986a).

Crabs such as *Cardisoma guanhumi* are normally herbivores. This species' burrows are typically in mangroves or in areas with heavy vegetation. There the crabs harvest the grass as well as fruit and leaves falling from the trees, dragging them to their burrows to feed. Significant competition for food exists because crabs clear the vegetation around their burrows and move immediately to retrieve berries or leaves that fall to the ground. *C. guanhumi* eat a surprising variety of food. Herreid (1963), studying large colonies of crabs in a plant experimental station in Florida, noted them eating 35 families of plants. In addition, they ate filamentous algae, and carrion consisting of crabs, fish, and birds.

Bliss et al. (1978) and D. L. Wolcott and T. G. Wolcott (1984) reported that land crabs, *Gecarcinus lateralis*, in Bermuda are largely
herbivorous, but they are also opportunistic carnivores; they are cannibals, scavenge carrion and mammalian feces, and prey on small frogs and insects. Wolcott and Wolcott (1984) argue that nitrogen is a scarce and limiting resource for these land crabs, a problem partially offset by cannibalism (see Chapter 3). Soybean supplements with high nitrogen content markedly reduce the cannibalism of adults on conspecific juveniles.

C. Predators

Predation is common among the large marine decapods and stomatopods. Lobsters and crabs prey on fish, mollusks, worms, and echinoderms as well as other crustaceans. On land, only a few crabs depend on predation to any extent, although it may be a minor component in the diet of many scavengers. Ghost crabs, Ocypode, are perhaps the most effective crab predators on land. They are the fastest-running crabs and can easily run down a small Uca that strays too far from its burrow. However, even Ocypode depend largely on scavenging.

From our comments, one may safely conclude that virtually all land crabs are quite active in seeking food and that their diets are extremely diversified.

D. Caloric intake

There is little direct information on the caloric intake of land crabs. Basic data on oxygen consumption can be used to estimate energy demand, of course. However, there is no information on the efficiency of assimilation, where the caloric content of the following categories are known: Assimilation = Consumption - (Feces + Excreta). Excreta include all losses such as nitrogenous waste, mucus, and shed cuticle (Crisp, 1971). Excreta are often ignored or considered trivial in such calculations. Therefore, authors typically express assimilation as a ratio or efficiency by dividing assimilation by the consumption value. Techniques for its measurement are reviewed by Grahame (1983), who gives some values for aquatic decapods. Spider crabs, Libinia emarginata, eating algae, fish, and mussel have an efficiency of 95–99% (Aldrich, 1974). Juvenile lobsters, Homarus americanus, eating brine shrimp have an assimilation efficiency of 81% (Logan and Epifanio, 1978). It seems reasonable to expect equally high assimilation in terrestrial species, especially in view of the fact that crabs do possess cellulase and chitinase enzymes to break down plant fibers and exoskeletal material (see Gibson and Barker, 1979, for review).

The caloric content (kcal) of a gram of dry food is surprisingly constant: terrestrial plants, 4.5; algae, 4.9; insects, 5.4; invertebrates except insects, 3.0; vertebrates, 5.6 (see Odum, 1983). However, the
water content is so variable that great differences in caloric content exist when wet mass is considered. Nevertheless, most living organisms are two-thirds water and minerals; therefore, a value of 2 kcal·g\(^{-1}\) wet mass is the approximate caloric content. Thus, using resting \(\text{O}_2\) consumption values from *Ocypode quadrata* (Full, 1984), a ghost crab weighing 2 g would require about 0.048 kcal calories per day. Since the average gram of wet food would have about 2 kcal, the resting crab would only have to eat a fraction of a gram (.02 g) each day to survive. Alternatively, consider a 300 g land crab, *C. guanhumi*, using \(\text{O}_2\) consumption data from Herreid, Lee, and Shah (1979). This crab would require 0.865 kcal per day, which could be met by eating only 0.5 g of leaves. This is the equivalent of one small leaf per day. It is no wonder that crab population densities under tropical fig trees may reach 18,500 per hectare (Herreid and Gifford, 1963).

3. Digestive system

Detailed description of the digestive system in crustaceans is available in the recent multivolume work edited by Bliss (1982–5). The internal anatomy is summarized by McLaughlin (1983a); functional aspects of nutrition and digestion are covered by Dall and Moriarty (1983); metabolism and transport of carbohydrates and lipids are reviewed by Chang and O'Connor (1983); control of the mouthparts and gut is described by Wales (1982); and the adaptive aspects of feeding mechanisms are discussed by Grahame (1983).

The digestive system of crustaceans is a simple tube consisting of (1) a mouth with the associated mouthparts; (2) a foregut that consists of a short esophagus and (3) a two-compartment stomach; (4) a midgut; (5) the hepatopancreas and (6) other diverticula that extend from the gastrointestinal tract; and (7) a hindgut that ends at the anus (Fig. 10.1). The digestive system in land crabs appears similar to other crustaceans, but little attention has been given to the group specifically. Since the most careful and detailed work has been done on the mud crab, *Scylla serrata* (Barker and Gibson, 1978), we must of necessity use this species as our descriptive model even though it is not a land crab.

Food is picked up by the chelipeds and passed to the mouthparts. Ingestion consists of an interaction of the third maxillipeds and mandibles before being passed through the mouth into the esophagus and on to the stomach, where mechanical and chemical digestion is initiated. Food leaving the stomach passes either into the midgut or hepatopancreas where chemical digestion continues and absorption occurs. Undigested materials leave the midgut and pass into the hindgut and out the anus.
A. Esophagus

The esophagus and stomach comprise the foregut of the crab. The esophagus of an adult mud crab (carapace width 23 cm) is short, about 15 mm, and leads to the first chamber of the stomach.

The lumen of the esophagus is covered by a permeable chitinous cuticle that is shed and replaced during molting. The cuticle is penetrated by ducts that run from the epithelium into the lumen. These ducts connect with tegumental glands of the esophageal wall. The
glands produce mucus, which acts as a lubricant for food sliding along the gut. The esophageal epithelium lying under the chitin consists of columnar cells. Connective tissues packed with tegumental gland cells and hemolymph spaces underlie the epithelium. Surrounding this layer is a band of striated circular muscles encircled by a layer of longitudinal muscles irregularly arranged in bundles. Oblique radial muscle strands lead from both the longitudinal and circular layers and terminate at the junction of the epithelium and chitin. Such muscles produce peristaltic waves moving the food along the esophagus. A trilobed valve separates the esophagus and stomach; it is formed from invaginations of the walls of the esophagus, and it prevents a back flow of stomach contents during digestion.

B. Stomach

The stomach of decapod crustaceans has two chambers, the cardiac and pyloric stomachs, separated by a cardiopyloric valve. The stomach produces no digestive enzymes of its own, but does have an active role in chemical as well as mechanical digestion because of digestive juices that are introduced from the hepatopancreas. Small quantities of organic molecules (e.g., 12% of sugars) may be absorbed by the foregut (Dall and Moriarty, 1983).

The first and larger stomach chamber, the cardiac stomach, contains a specialized grinding region called the gastric mill. The gastric mill is least developed in species such as shrimps, where the mouthparts perform an efficient job of mastication or the diet consists of tiny particles. In contrast, in crustaceans such as lobsters, crayfish, and crabs where large pieces of food are quickly eaten, the gastric mill reaches its greatest development (Barnes, 1980). Even within this group there are enormous variations, ranging from crayfish having a few simple chitinous projections that serve as grinding teeth to the spectacular architecture of a ghost crab (*O. quadrata*), where the cardiac stomach has several elegant cutting plates (Fig. 10.2). The latter have dozens of fine teeth that are part of a marvelously complex movable jaw within the gut. To compare the gastric mills of the crayfish and ghost crab is like comparing the primitive architecture of Stonehenge with the elaborate design of the Taj Mahal.

An extensive muscular system controls the movement of the cardiac stomach (Wales, 1982; McLaughlin, 1983a). These muscles exist as part of the stomach wall, and they extend from the stomach to the body wall. The muscles, teeth, and sclerites act to grind the stomach contents. This action is complemented by enzymes from the hepatopancreas that have been passed forward into the stomach. Together, mechanical and chemical digestion reduces the contents of the cardiac stomach to a fine chyme. In species such as *O. quadrata*, setae line both
Fig. 10.2. Photographs of the ghost crab digestive system. The upper picture shows the interior of a crab with the dorsal carapace removed. The light-colored hepatopancreas (H) is readily visible as is the cardiac stomach (CS), which has its dorsal wall removed to show the interior sclerites. The middle picture gives a more detailed view of the crab's viscera, and the lower picture shows the major sclerite architecture of the cardiac stomach. The "T"-shaped structure slides forward and backward articulating with the lower section at the three ends of the "T." Food passes beneath the "T" (posteriorly) toward its base and is chewed up by the underlying teeth, which are barely visible in the channel below leading to the pyloric stomach. Scale bars = 1 cm.
the walls and internal flaps and act to separate large food fragments from small (C. Herreid, unpub.). Only the latter pass into the pyloric stomach where digestion continues. The circulation of the stomach contents is surprisingly complex in thalassinid Crustacea (Powell, 1974), and perhaps this is the general pattern in crustaceans (Dall and Moriarity, 1989).

The pyloric stomach lying ventral to the cardiac stomach has complex folded walls with setae that act as a filtering mechanism (Barker and Gibson, 1978). The folds form distinct channels in the stomach, which direct food toward the two ducts of the hepatopancreas and midgut. Each channel passes through a gland filter laden with fine setae. Only the smallest particles pass through the filter into the ducts of the hepatopancreas; the larger particles are funneled to the midgut. The walls of the pyloric stomach have plates embedded within them and a system of muscles that regulates the size of the channels and assists in squeezing material through the filters and driving it into the midgut or hepatopancreas. The musculature, tooth arrangement, and neuronal control of the gastric mill and the pyloric press are reviewed by Wales (1982) and Wiens (1982). Histologically, the stomach is similar to the esophagus except that tegumental glands are absent.

C. Hepatopancreas

The hepatopancreas has been called midgut gland, gastric gland, digestive gland, pancreas, liver, digestive organ, midintestinal gland, and ceca anteriores. It is responsible for virtually all of the free digestive enzymes of the gut and for about 85% of the assimilation. Gibson and Barker (1979) have reviewed the literature and conclude that the term “hepatopancreas” is appropriate; we concur with this decision because the term is distinctive and descriptive of the organ’s function without suggesting the organ is identical with the vertebrate liver or pancreas. The following summary is based largely on their review.

The hepatopancreas of crustaceans reaches its greatest elaboration in the decapods, where it makes up 2–6% of the body mass (Brockerhoff and Hoyle, 1967; Stewart et al., 1967; Table 10.1). The organ consists of a large compact cluster of tubules lying on either side of the digestive tract where it fills much of the cephalothorax. In pagurid hermit crabs, the hepatopancreas is located in the abdomen and is developed asymmetrically.

Each half of the hepatopancreas is composed of two or three lobes ensheathed in a connective tissue membrane provided with a delicate network of circular and longitudinal muscle cells. Each side of the hepatopancreas opens from the gut via a primary duct near the pyloric stomach–midgut junction (Gibson and Barker, 1979). The primary duct branches into secondary ductules that enter the lobe masses
Table 10.1. Estimation of glycogen stores in Uca pugilator

<table>
<thead>
<tr>
<th>Organ</th>
<th>Organ mass (mg·g⁻¹)</th>
<th>Glycogen concentration (mg·g⁻¹)</th>
<th>Total glycogen (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hemolymph</td>
<td>250</td>
<td>20</td>
<td>5.0</td>
</tr>
<tr>
<td>Skeletal muscle</td>
<td>230</td>
<td>32</td>
<td>7.4</td>
</tr>
<tr>
<td>Hepatopancreas</td>
<td>40</td>
<td>16</td>
<td>0.6</td>
</tr>
<tr>
<td>Epidermis</td>
<td>16</td>
<td>16</td>
<td>0.2</td>
</tr>
<tr>
<td>Gill</td>
<td>16</td>
<td>26</td>
<td>0.4</td>
</tr>
<tr>
<td>Cardiac muscle</td>
<td>4</td>
<td>77</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Note: The organ masses are derived from our dissections of 5 Uca (mean body mass, 2.5 g). Hemolymph volume is assumed to be 25%. Glycogen levels are from Keller and Andrew (1973).

where they subdivide extensively to form dozens of blind-ending tubules. The tubules are variable in color, often yellow, brown, or greenish.

Muscle cells ensheathe each tubule of the hepatopancreas. Thick, striated, mononuclear circular muscle cells have been identified along with thin, nonstriated, longitudinal muscle cells that seem to connect adjacent circular muscles. Contraction of the muscles surrounding the tubules eject digestive enzymes into the gut and draw nutrients into the hepatopancreas (Loizzi, 1971). The nervous system coordinating this activity is not well understood.

The tubules of the hepatopancreas are lined with a layer of epithelial cells, one cell layer thick, except for the blind or distal end where several layers exist. Four types of epithelial cells have been identified as E- (embryonic or undifferentiated), F- (fibrillar), R- (resorptive or absorptive), and B- (secretory) cells (Gibson and Barker, 1979). E-cells are found only at the distal end of the tubules where they undergo mitotic division. These cells seem to specialize into either F- or R-cells as they migrate along the tubule toward the proximal end.

The F-cells have extensively developed rough endoplasmic reticulum, numerous Golgi bodies, and abundant vacuoles and vesicles. These character suggest F-cells synthesize digestive enzymes. Indeed, as Gibson and Barker (1979) argue, F-cells appear to mature into secretory B-cells, the largest hepatopancreatic cells.

The B-cells contain a single enormous secretory vacuole comprising up to 90% of the cell volume (Barker and Gibson, 1977). B-cells possess a brush border with microvilli at their apex projecting into the tubule lumen. B-Cells are the secreting cells releasing digestive enzymes. Early in digestion as an immediate response to feeding (0.5–1h), they are sloughed off the tubule wall intact in a holocrine secre-
1h), they are sloughed off the tubule wall intact in a holocrine secretion. The loose B-cell disintegrates and releases its vacuolar contents. Later after feeding, two other discharges of enzymes have been noted in crabs such as *Scylla serrata*, at three and eight hours after a meal (Barker and Gibson, 1978). These secretion pulses are merocrine or apocrine in nature; B-cells lining the hepatopancreas tubules discharge the digestive enzymes from the vacuole into the lumen. These B-cells and their vacuoles are reconstituted cyclically (Fig. 10.3, Loizzi, 1971; Gibson and Barker, 1979).

Gibson and Barker (1979) and Dall and Moriarty (1983) provide extensive reviews of the specific digestive enzymes that have been discovered in the decapod hepatopancreas. There is an impressive arsenal of enzymes to degrade carbohydrates, lipids, and proteins, along with the more unusual cellulase and chitinase enzymes found in some Crustacea (e.g., Yokoe and Yasumasu, 1964; Muzzarelli, 1977). Only small amounts of gastric juice are produced at any one time (van Weel, 1970). The pH of this fluid usually ranges from 5 to 7. Emulsifying agents (released from R-cells) analogous to bile are an important part of the gastric juice, where they function to reduce
particle size in fats and thus enhance hydrolysis (Gibson and Barker, 1979).

The R-cells are the most abundant cell, occurring throughout the length of the hepatopancreas tubules, except at the distal end where the embryonic cells have not differentiated. R-cells contain large numbers of vacuoles and have a brush border of microvilli; they resemble the absorptive cells of the vertebrate intestine. Glycogen granules and lipid droplets are evident. The evidence indicates that the R-cells are the major absorptive and storage cells of the hepatopancreas. In addition, their brush border probably is the site of digestive activities such as the final hydrolysis of lipids (Fig. 10.3).

Within two to five hours after a meal, minute vacuoles appear in the R-cells; these may represent the absorption of short-chain peptides or lipids (Barker and Gibson, 1977). Seven to nine hours after a meal, weak exopeptidase and lipase activity has been noted in Homarus R-cell cytoplasm. This appears to represent an intracellular phase of digestion for proteins and lipids. This conclusion appears to hold for the crab S. serrata (Baker and Gibson, 1978) as well.

The hepatopancreas is well supplied with hemolymph in the few crustaceans studied. Typically, hepatic arteries pass into the hepatopancreas lobes where they subdivide among the ducts and tubules forming channels variously termed capillaries, hemolymph sinuses, or hemolymph spaces (Gibson and Barker, 1979). Presumably, nutrients pass back and forth between hepatopancreas and hemolymph.

D. Midgut

The midgut has only a minor role in the absorption of nutrients, accounting for perhaps 5–10% of the organic nutrients absorbed during digestion. Unlike the foregut and hindgut, it lacks a chitinous lining (Barker and Gibson, 1978). The midgut varies in length, being quite short in crayfish and many crabs and relatively long in the lobster Homarus and snapping shrimp Alpheus, where all but the part of the intestine lying in the last abdominal segment is midgut. Diverticula (in addition to the hepatopancreas) are common extensions of the midgut; they appear to have a minor role in digestion and assimilation as well as water balance (Dall and Moriarty, 1983).

In S. serrata, the midgut comprises 40–50% of the postgastric intestinal tract and is 2–3 mm in external diameter (Barker and Gibson, 1978). There is a 1 mm posterior diverticulum, which arises from the dorsal wall of the midgut; it is about 100 mm long but is coiled on itself to form a solid disklike mass 10–20 mm in diameter. There is an anterior diverticulum as well, which bifurcates immediately after emerging from the dorsal anterior midgut wall. Each branch is about 1 mm in diameter and 20–30 mm in length, and these extend forward
to lie adjacent to the stomach wall where their distal ends lie in a loose tangle (Barker and Gibson, 1978). The origin and histology of the anterior and posterior diverticula are considered by Smith (1978).

In the midgut, enzyme activity (only acid phosphatases and esterases) occurs in the epithelium cytoplasm bordering the lumen; the diverticula show similar phosphatase activity in their epithelial cytoplasm. As with the hepatopancreas, nutrient uptake has occurred two to five hours after a meal, after which intracellular digestion continues. There is evidence that animals with long midguts (e.g., Homarus) use passive absorption whereas crabs (e.g., Scylla) with short midguts may require active transport to ensure adequate absorption.

E. Hindgut

The hindgut of the crab Scylla extends throughout the abdomen, which is flexed beneath the cephalothorax. The hindgut represents 50–60% of the postgastric tract and terminates at the anus, an orifice in the last abdominal segment, the telson. The hindgut is always filled with feces (Barker and Gibson, 1978). The hindgut is infolded with longitudinal ridges, which are covered with a cuticular layer. Underneath lies an epithelium. Located just outside the epithelium are connective tissues containing circular and longitudinal muscles. Tegumental glands, which probably secrete mucus for lubrication of the waste matter, are abundant in the glandular swelling of the anterior hindgut at the junction of the midgut.

To summarize the digestive process: Food is first passed into the mouth by the chelipeds. The mouthparts may cut up the food into smaller bits or help filter it from sand or mud before swallowing. Food is passed via the esophagus into the stomach where it is mechanically chewed and chemically attacked by enzymes added from the hepatopancreas. Small organic particles are drawn into the tubules of the hepatopancreas; larger particles pass into the midgut. In both sites organic molecules are absorbed by epithelial cells that continue digestion intracellularly. The products of digestion and assimilation pass from the epithelial cells into the hemolymph where they are the raw materials for the general metabolism of the body. Undigested matter proceeds from the midgut into the hindgut where water is absorbed and fecal pellets are formed for later expulsion out of the anus.

4. Metabolism

Reviews of crustacean metabolism include Munday and Poat (1970), Vonk (1960), Hohmke and Sheer (1970), and most recently Chang and O'Conner (1983) on carbohydrate metabolism; O'Connor and Gilbert (1968), Gilbert and O'Connor (1970), and Chang and O'Con-
nor (1983) on lipid metabolism; and Schoffeniels and Gilles (1970) and Claybrook (1983) on protein metabolism. From these surveys it is evident that data on the metabolism of land crabs are particularly sparse and fragmentary. Different species have been studied by different techniques under an array of different conditions. Furthermore, even a given species or individual can show extreme variability in metabolic function due to a myriad of processes (e.g., molting stage, reproductive cycle, activity) and environmental factors (e.g., temperature, salinity, food availability) that undergo complex oscillations. As a result, generalizations are of limited value. Here, our intention is to provide a brief overview of crustacean metabolism that will lend structure to future investigations on land crabs.

A brachyuran crab contains about 20 kJ·g⁻¹ or 4.8 kcal·g⁻¹ in total energy, expressed on an ash-free, dry-mass basis (DuPreez and McLachlan, 1983). The energy can be roughly divided into three pools: 21% carbohydrate, 6% lipid, and 73% protein. Obviously, only a fraction of each pool can serve as an energy source for the animal. This section focuses on (1) the form and location of energy sources, (2) the general route by which they are transported to deliver energy, and (3) the control mechanisms involved. A final energy source, the high-energy phosphate pool, will be mentioned in conclusion.

A. Carbohydrates

i. Location. Most of the carbohydrate in crustaceans is stored as the nitrogenous polysaccharide, chitin. In fact, chitin constitutes 64–74% of all of the organic material in the brachyuran exoskeleton (Drach and LaFon, 1942). However, this source does not appear to be readily available to the carbohydrate pool. Carbohydrate can also be complexed with protein-forming mucopolysaccharides present in the epidermis and hepatopancreas. Glycogen and glucose form a third part of the carbohydrate pool; these forms act as the animal's primary fuel source. Glucose appears to be the major carbohydrate constituent in the hemolymph. Other carbohydrates, such as the oligosaccharides, maltose, maltotriose, and trehalose, have been found mostly in low concentration (Schwoch, 1972; Telford, 1968). Glucose concentrations in the hemolymph of Carcinus maenas can vary from 1 to 100 mg·100 ml⁻¹ hemolymph (Williams and Lutz, 1975). This variation does not appear to be exceptional among crustaceans. A host of parameters have been shown to influence hemolymph sugar levels, including (1) stage of molting, (2) stress, (3) activity, (4) stage of reproduction, (5) starvation, (6) time of sampling after feeding, (7) temperature acclimation, and (8) level of hyperglycemic hormone (Chang and O'Connor, 1983). These diverse effects suggest that the
hemolymph functions as a transient storage place for glucose removed from cells or tissues (Fig. 10.4).

Of particular interest is the finding that hemolymph itself may store glucose in the form of glycogen. Hemolymph cells called hemocytes may contain large amounts of glycogen and possibly chitin. In fact, they have been argued to be the main repository for glycogen in *C. maenas* (Johnston, Elder, and Davies, 1973). Hemocytes may function as “freely circulating hepatic cells” breaking down and storing carbohydrate as they travel through the circulation. The total contribution of this carbohydrate store could be significant, since crabs have large hemolymph volumes (Table 10.1). Johnston et al. (1973) reported that hemolymph glycogen could be nearly six times the amount found in the hepatopancreas.

Many studies deal with glycogen storage in muscle and hepatopancreas because these organs are often considered the major reservoirs (Parvathy, 1971). Yet, glycogen concentration in the epidermis can exceed that found in either organ (Hohnke and Scheer, 1970). Histological examination of the blue crab, *Callinectes sapidus*, showed that spongy connective-tissue cells (which maintain the position and shape of organs and tissues) were filled with glycogen (Johnson, 1980).
These separate investigations reveal those tissues capable of storing carbohydrate, but a summary of the fuel reserves has not been prepared. Table 10.1 presents such an analysis for *Uca pugilator* based on values from the literature and data from dissection (C. Herreid and D. Sperrazza, unpub.).

Skeletal muscle and the hemolymph function as the major storage sites for glycogen in *U. pugilator*. Other tissues appear to be of minor importance. The gut and hepatopancreas have a supply of energy via digestion and assimilation. Tissues such as gills, heart, and epidermis have only modest fuel reserves and probably withdraw their metabolites from the hemolymph on an ad hoc basis. Skeletal muscle, however, not only has a significant reserve for itself but may act to release carbohydrates into the hemolymph pool when demand arises (Fig. 10.4).

*ii. Transport.* Carbohydrates removed from storage appear to have at least four major fates: (1) chitin synthesis, (2) mucopolysaccharide production, (3) ribose and nicotinamide adenine dinucleotide phosphate (NADPH) synthesis, or (4) glycolysis leading to the end products L-lactate or carbon dioxide and water.

A new cuticle must be secreted each time an animal molts. Since most of the entire exoskeleton is chitin, its synthesis could represent a substantial drain on a crustacean’s organic reserves. De novo synthesis of chitin requires glucose units, which must be aminated, and high-energy phosphate (ATP and UTP) used for its subsequent polymerization. However, since aminated glucose units derived from the breakdown of the old cuticle can serve as a starting point for synthesis (Stevenson, 1985), probably considerable energy is saved by this recycling method.

Two other important routes of carbohydrate utilization are the pentose–phosphate and glucuronic pathways. The pentose–phosphate pathway shunts glucose away from glycolysis and results in the production of NADPH and ribose. NADPH appears to be a required cofactor for lipid synthesis, and ribose acts as a substrate for nucleic acid metabolism. The glucuronic pathway also diverts carbon from glycolysis. Its end products are acid mucopolysaccharides, carbohydrate moieties bound to a polypeptide or protein. Mucopolysaccharides have been found in the digestive tract and hepatopancreas where they function in food lubrication. In addition, they appear to be a component of the cuticle in *Hemigrapsus nudus* (Meenakshi and Scheer, 1959). Unfortunately, no data are available on the amount of carbohydrate diverted into these pathways.

Glycolysis is the major starting point for glucose (or glycogen) breakdown in crustaceans (Hohnke and Scheer, 1970). This pathway is
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critical, since glycolysis is the only pathway that can operate under anoxic conditions. Crustacean skeletal muscle, in particular, has been reported to be a highly glycolytic tissue (Hochachka, 1976). Despite the many end products described for mussels, L-lactate appears to be the major anaerobic end product in crustaceans, much the same as in vertebrates (Long, 1976; McMahon, 1981; Zebe, 1982; Full, Herreid, and Assad, 1985). Under conditions of hypoxia or exercise, glycolysis produces a considerable amount of energy as well as lactic acid. *U. pugilator* has been shown to survive 26 hours of anoxia by depleting glycogen stores and tolerating a 20-fold increase in lactic acid (Teal and Carey, 1967). Moreover, 60–70% of the ATP required for locomotion in the fiddler crab may be supplied by accelerated glycolysis (Full and Herreid, 1984).

Glucose can also be completely oxidized to carbon dioxide and water. A functioning tricarboxylic acid cycle and oxidative phosphorylation chain has been demonstrated in mitochondria, and this pathway appears to be the major catabolic route for carbohydrates (Huggins and Munday, 1968). It is important to note, however, that the energy content of oxidized carbohydrate on a per gram basis is about half that of fat.

iii. Control. Carbohydrates must be stored, transported, and utilized at the appropriate time, so that diverse demands, such as growth, activity, or molting, can be met (Fig. 10.3). Given this situation, it is not surprising to find hormonal feedback mechanisms operating to provide the necessary control.

Hyperglycemic hormone (HGH) is probably the best understood crustacean hormone involved in metabolism and can serve as an example of carbohydrate control. Eyestalk removal has been shown to produce hypoglycemia, and injections of eyestalk extract have resulted in elevated hemolymph sugar levels (Keller and Andrew, 1973). HGH is apparently released from the eyestalks and travels in the hemolymph to the site of action. Target tissues include muscle, integument, hepatopancreas, gill, and gonads (Parvathy, 1971; Keller and Andrew, 1973). Various enzymes are then affected causing a mobilization of glucose. For example, glycogen phosphorylase, which catalyzes the breakdown of glycogen to glucose-1-phosphate is activated. By contrast, HGH has also been shown to inhibit the enzyme glycogen synthetase, which would normally favor the formation of glycogen.

HGH is probably not the only hormone involved in the regulation of carbohydrate metabolism. A hypoglycemic factor has been reported by Rangneker, Sabnis, and Nirmal, (1961). Also, Sanders (1983) has found insulin-like peptides in the lobster hemolymph and hepato-
pancreas that promote glycojenesis in the muscle. However, these peptides do not seem to have a glucoacemic role, and their function remains unclear. Recently, Herreid and Mooney (1984) have found that exercise induces hemolymph-borne factors altering the color of land crabs. The color change may be only a secondary effect of a hormonal reaction to exercise, the primary effect being the stimulation of carbohydrate or fat mobilization. Indeed, the neurotransmitter 5-HT is known to trigger the release of hyperglycemic hormone; it also causes pigment dispersion in red chromatophores (e.g., Keller and Beyer, 1968; Rao and Fingerman, 1983).

**B. Lipids**

1. **Location.** Lipids have been suggested to be the predominant organic storage reserve in crustaceans (O'Connor and Gilbert, 1968). Total body lipid can exceed levels of glycogen by 10-fold (Vonk, 1960). Moreover, the energy content of fat on a per gram basis is twice that of carbohydrate. However, values of the respiratory quotient (ratio of CO₂ production to O₂ consumption) for the land crabs *C. guanhumi* and *C. lateralis* during rest are about 0.85, which suggests the burning of a mixed carbohydrate, lipid, and protein diet (Herreid, Lee, and Shah, 1979, 1983). Supporting the lipid hypothesis are data from *Cardisoma carnifex* (Wood and Randall, 1981) showing a resting respiratory quotient of 0.6. Yet in all three cases, respiratory quotient increased over 1.0 during exercise. This probably does not suggest a shift to carbohydrate catabolism so much as an increase in CO₂ release from hemolymph bicarbonate (see Chapter 8). The primary source of fuel remains in doubt.

The hepatopancreas is the major storage site for lipid. Although data for land crabs are not available, in *Cancer pagurus* lipid constitutes 30% of the organ's dry mass (Vonk, 1960). Some of the highest hepatopancreatic lipid levels have been found in the terrestrial anomurans *Birgus latro* and *Coenobita* spp. (Gibson and Barker, 1979). Caloric values of the hepatopancreas, alone, in these species ranged from 2 to 48 kJ. Analysis of the fat content of the hepatopancreas has shown that neutral fats (fatty acids, triglycerides, and sterols) account for 50–60% of the fat, while phospholipid content can range from 12% to 50% (Gibson and Barker, 1979).

2. **Transport.** Large variations in lipid concentration occur, possibly as a result of starvation. For example, crayfish have been reported to rely primarily on lipid stores during the first two weeks of starvation (Speck and Ulrich, 1969). Such variations tend to greatly confound quantitative interpretations of lipid utilization.

Lipid mobilization and transport occur during molting and ga-
metogenesis (Chang and O’Connor, 1983). In late premolt and in postmolt, crabs draw on lipid reserves in the hepatopancreas. The rate of lipid synthesis is decreased, and lipid is secreted into the hemolymph. This lipid can then serve as an energy source for the growth and regeneration of tissues following molting. Hepatopancreatic lipid is also mobilized at the onset of egg maturation. Neutral lipids are transported to the ovary for use by the developing egg (Gibson and Barker, 1979).

One surprising finding is that phospholipids act as the principal circulating lipid in the hemolymph of a number of species (Gilbert and O’Connor, 1970). This is in contrast to that observed in mammals and insects where free fatty acids and diglycerides, respectively, are the transport lipid. In other crustacean species, such as U. pugilator and C. maenas, hemolymph lipid was shown to exist as a complex lipoprotein moiety (Chang and O’Connor, 1983).

Lipids arriving at the tissues can be converted to triglycerides and stored or used as an energy source. Oxidation is thought to occur by way of beta-oxidation, but the complete crustacean pathway has yet to be described (Chang and O’Connor, 1983). The tricarboxylic acid cycle and respiratory chain appear similar to those described in mammals (Munday and Poat, 1970). Mitochondrial phosphate:oxygen ratios determined in C. sapidus and C. maenas are consistent with three functioning sites of phosphorylation in the electron-transport chain (Chen and Lehninger, 1973).

iii. Control. Hormones have been implicated in the control of lipid metabolism in crustaceans and in land crabs, in particular. Neutral lipids and phospholipids in the hepatopancreas have been shown to increase one day after eyestalk removal in G. lateralis (O’Connor and Gilbert, 1968). This effect appears to be independent of the level of molting hormone, which is also affected by eyestalk removal. Injected eyestalk extract from this land crab resulted in a reduction of the rate of lipid synthesis. Moreover, incubation of G. lateralis hepatopancreas with and without eyestalk extract produced similar results.

C. Proteins

i. Location. Proteins and amino acids must not be ignored as a potential energy reserve (Claybrook, 1983). These compounds easily constitute the bulk of crustacean tissues. Muscles appear to be the richest source of protein in crustaceans. In Cancer magister over 70% of the muscle dry mass (16% wet mass) is protein (Allen, 1971). Free amino acid levels in the tissues of decapods have been found to be several times higher than in vertebrate tissue; muscle levels range from 80 to 385
μmol·g⁻¹ muscle mass (Claybrook, 1983). In contrast, hemolymph levels are comparable to those found in the blood plasma of vertebrates: 2–6 μmol·ml⁻¹. In the green shore crab Carcinus maenas, about 50% of the hemolymph free amino acids are located within hemocytes (Evans, 1972). The difference in tissue and hemolymph free amino acid levels probably reflects the cells' role in volume regulation, using free amino acids in osmotic balance (see Chapter 7).

ii. Transport. It is not certain whether protein is the energy source of last resort or whether amino acids serve as a ready substrate for oxidation, as proline does in insects. Protein has been demonstrated to serve as a metabolic fuel during periods of starvation. Speck and Urich (1969) calculated that over 70% of the required energy between two and six weeks of starvation was provided by protein. Radiolabeled amino acids are oxidized by tissues both in vivo and in vitro (see Claybrook, 1983). Removal of the amino group appears to be accomplished by transamination for a number of the amino acids. However, the pathways of catabolism have not been well defined in Crustacea generally. The pathways are assumed to be conservative and similar to those of mammals. Because the pathways are not yet understood, control cannot be discussed adequately.

D. High-energy phosphates

Carbohydrate, fat, and protein provide the fuel required for prolonged chemical and mechanical work. Many energy demands, however, are of short duration. Muscular contractions during an activity such as escape can be brief, and energy may come directly from the high-energy phosphates stored in the tissue. These stores include ATP and arginine phosphate, the invertebrate version of creatine phosphate. Large stores of ATP have not been found in crustaceans. In the lobster Homarus vulgaris, ATP levels are approximately 7 μmol·g⁻¹, and ADP and AMP levels are considerably lower (Beis and Newsholme, 1975). In general, the adenine nucleotide concentrations are comparable to those of other invertebrates and vertebrates. Low levels of ATP are not surprising, since adenine nucleotides are involved in regulating their own production. On the other hand, arginine phosphate levels in the lobster tail muscle were three to six times the levels found in insects and twice those of creatine phosphate measured in mammals (Beis and Newsholme, 1975). Enzymatic breakdown of arginine phosphate by arginine kinase appeared to be extremely rapid. Since so few data are available, it is difficult to evaluate the significance of this short-term energy source. Yet, high levels of arginine phosphate in leg muscle may very well be critical for burst locomotion on land.
5. Animal energetics

Oxygen consumption (\(\dot{V}O_2\)) has served as the universal measurement of metabolism for most organisms, and crustaceans are no exception. Anaerobic contributions have been largely neglected. \(V_O_2\) depends on a variety of parameters: body size, temperature, partial pressure of \(O_2\) in the environment, molting cycle, activity, etc. These topics have been reviewed for crustaceans, generally, by Wolvekamp and Waterman (1960), Herreid (1980), and McMahon and Wilkens (1983), and are considered for land crabs in particular in Chapter 8. Our major focus in this section will be to evaluate the normal limits of metabolism in land crabs and to give an estimate of how they use their energy, so we will briefly touch on some of these topics here.

A. Resting metabolism

Many crabs and other crustaceans spend large periods of time, perhaps the majority of their lives, in apparent rest in crevices and burrows. Periods of inactivity may last for hours, as in the case of \(U. pugilator\) retreating into their burrows during high tide, or extend to weeks and months, as in the case of \(C. guanhumi\) in southern Florida, which plug their burrows with mud in the winter (C. Herreid, unpub.). We can only speculate on the metabolic state of these animals under natural conditions based on laboratory data.

Prosser (1973) reports standard metabolic rates for crustaceans ranging from 1 to 8 \(\mu\text{mol-}O_2\text{-g}^{-1}\text{-h}^{-1}\). But as McMahon and Wilkens (1983) emphasize, values considerably lower than these are readily measured when animals are allowed to acclimate to experimental conditions resembling their natural habitat. Also, \(V_O_2\) lactic acid levels, and acid-base balance continue to change for 24–48 hours after crustaceans are first introduced into metabolic chambers. Consequently, minimal \(V_O_2\) rates (those values needed for bare maintenance) may vary considerably from the values published as "resting" rates. This clearly has significance when comparing resting and active metabolic rates, i.e., metabolic factorial scope.

B. Body size

Oxygen consumption is directly related to body mass. Thus, \(\dot{V}O_2 = aW^b\), where \(\dot{V}O_2\) is mass-specific \(O_2\) consumption (i.e., \(O_2\) consumption per gram body mass) and \(W\) is the mass of the animal in grams. When this exponential equation is written in logarithmic form (\(\log \dot{V}O_2 = \log a + b \log W\)), the coefficients \(a\) and \(b\) represent the intercept on the y-axis and the slope of the function, respectively. Slope values range between 0.67 and 1.0 for crustaceans, with 0.85 apparently representing a reasonable average for interspecific com-
comparisons (see Wolfekamp and Waterman, 1960). These values indicate that the food requirement and mass-specific \( VO_2 \) are considerably higher in small individuals than large. This metabolic principle appears practically universally throughout the animal kingdom in invertebrates and vertebrates and among poikilotherms and homeotherms alike, although the coefficients vary (Zeuthen, 1953). Mammalogists fondly refer to their "mouse to elephant curve" (e.g., Benedict, 1938; Kleiber, 1961), but an analogous situation prevails for carcinologists: We have our "fairy shrimp to spider crab curve" (e.g., Scholander et al., 1953).

In spite of the fundamental nature of this metabolic principle, and the speculations as to its cause (e.g., Wolfekamp and Waterman, 1960), we are largely unable to explain its origin. However, some ecological consequences are clear. An ecosystem can support a larger biomass of animals, \( ceteris paribus \), if it is packaged into a few large individuals (with a low metabolic rate per gram) than it can a large number of small individuals (with a high metabolic rate per gram). The maintenance costs for the latter are much higher. Also, as we will see, the mass specific energy cost for activity is greater for small individuals.

C. Temperature

Temperature influences \( VO_2 \) in a predictable fashion in crustaceans. In general, with a 10\(^\circ\)C increase of temperature, metabolic rates rise two to three times (i.e., \( Q_{10} = 2-3 \)). Most land crabs are limited to a modest temperature range, with thermal limits perhaps between 15 and 40\(^\circ\)C, although short-term exposure to higher temperatures is possible. \( C. guanhumi \) in southern Florida has a normal operating temperature much narrower than this range (C. Herreid, unpub.).

Land crabs use behavioral and physiological methods for regulating temperature. They use their burrows for protection from the more major changes in temperature. In addition, evaporative cooling from their gills and through their shell becomes important at high temperatures (see also Chapter 7). \( Cardisoma \), during migration on hot summer days in Florida, dashes from shady spot to shady spot, maintaining body temperature \( 1-2 \)\(^\circ\)C below air temperature (C. Herreid, unpub.). Similar temperature depression has been seen for fiddler crabs and ghost crabs (cf. Cloudsley-Thompson, 1970). Moreover, \( C. guanhumi \) will urinate over the extensive bristle patch just under its eyes every few minutes when body temperatures approach the lethal temperature of 39\(^\circ\)C (C. Herreid, unpub.). The increased evaporation slows the rise in body temperature. This method of temperature regulation under heat stress is reminiscent of storks or vultures urinating on their legs.
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Given a $Q_{\text{10}}$ of 2–3 and a temperature range of 20°C, temperature may cause a variation in resting VO$_2$ by as much as 10-fold. Realistically, a five-fold variation due to temperature might be normal. Obviously, this means that in cool conditions a crab’s food reserve could last perhaps five times longer than when the crab is warm. Given that starvation depresses metabolism, as does a lack of disturbance, the food reserves could easily maintain a resting crab 10 times longer in a cold, undisturbed condition than in a warm disturbed state.

D. Air versus water as the respiratory medium

Water contains relatively small amounts of oxygen (generally less than 10 ml O$_2$·l$^{-1}$ compared to 210 ml O$_2$·l$^{-1}$ of air) and is dense and viscous compared to air. Consequently, one might expect a significantly higher proportion of the metabolic energy to be devoted to breathing in water than in air. Unfortunately, no data exist for crustaceans on this point directly. Some species, such as the land crab C. guanhumi, are capable of survival in both water and air, and there is no significant change in VO$_2$ in the different media (Herreid and O’Mahoney, 1978; O’Mahoney and Full, 1984). Consistent with our expectations, the ventilation rate is three times higher in water than in air. Since no major change occurs in VO$_2$, we must assume that (1) the total cost of ventilation is quite small in both media and thus any differences are difficult to detect or that (2) crabs breathing water compensate for the increased work load by decreasing metabolism in other ways.

The most recent direct measurements of energy involved in crustacean ventilation occur in the shore crab C. maenas (Wilkens, Wilkes, and Evans, 1984). The O$_2$ requirement of ventilation in water was measured by comparing VO$_2$ before and after removal of the scaphognathites. The cost of ventilation for resting crabs was 30% of the total VO$_2$. Indirect estimates of the cost of aquatic ventilation have been made for Callinectes sapidus (0.02% of the total O$_2$ consumption), Cancer pagurus (17–76%) and Orconectes virilis (1%), and Cancer magister (6%) (Batterson and Cameron, 1978; McDonald et al., 1980; Burnett and Bridges, 1981; Burggren and McMahon, 1983). The relative cost of ventilation in air-breathing species of crabs should be lower, but no direct measurements or calculations have been made.

It would be particularly interesting to determine the energetic cost of ventilation in the Australian land crabs of the genus Holthuisana, which have radically different patterns of ventilation in air and water (Greenaway, Taylor, Bonaventura, 1983; Greenaway, Bonaventura, Taylor, 1983; see Chapter 8).
E. Molting, growth, and regeneration

Molting is such an integral part of a crab's existence (see Chapter 6) that it is difficult to separate its energetic cost from other metabolic expenditures. Changes occur in the integument for 70% or more of the time between successive molts, and during the remaining 30% of the intermolt period the crab is storing energy reserves for the new exoskeleton in the hepatopancreas (Passano, 1960a). As Passano (1960a) states, "The normal physiology of the crab is thus continuously and intimately concerned with the successive stages of the intermolt cycle. Hibernation, ovarian maturation, and the carrying of developing eggs by females are the only interruptions in this series of periodically recurring molts." Complicating the problem of energetic measurement is that drastic changes in the activity level of crabs are correlated with the molt cycle. During intermolt (i.e., stage C crabs; see Passano, 1960a) both aquatic and land crabs are fully active, whereas they become inactive at the time of ecdisis (exuviation) when the exoskeleton is shed.

No studies seem to have been made of oxygen consumption in land crabs during molting. However, in the blue crab, C. sapidus, molting is apparently associated with relatively minor changes in \( V_O_2 \) (Mangum et al., 1985). For example during premolt (stage D1-D4 crabs), which occupies about 25% of the duration of the life cycle (Passano, 1960a), blue crabs actually show a slight decline in \( V_O_2 \), which is associated with a reduction in activity. No data are given for ecdisis. However, \( V_O_2 \) immediately following ecdisis (stage A) is only doubled compared to intermolt (stage C). \( V_O_2 \) declines rapidly to intermolt levels by the time late stage B is attained, when feeding begins and activity returns to normal levels. Thus, \( V_O_2 \) is elevated for only a brief time in the molt cycle (less than 5%). Moreover, even at its highest level, the aerobic rate is modest.

Hemolymph lactate remained low except prior to molt (stage D4) whereupon lactate concentrations doubled to 0.53 mM·L\(^{-1}\). Immediately after molt (stage A), hemolymph lactate jumped to 2.26 mM·L\(^{-1}\) or over six times intermolt conditions, suggesting a significant anaerobic contribution is present. However, this was short-lived and by the B2 stage, hemolymph lactate had fallen to 0.23 mM·L\(^{-1}\). Thus, even though molting and its preparation and aftereffects are profound events in the life of the crab energetically, they do not appear to match the maxima seen during sustained swimming. Booth (1982) noted hemolymph lactate levels for swimming Callinectes reached 9.8 mM·L\(^{-1}\) with aerobic factorial scopes of 2.6. However, these swimming values are of short duration compared to those elevated values occurring over several days of molting. Finally, we should note that the crab
progressively decreases feeding and locomotion until it is immobile at the time of ecdysis (stage E) and then becomes gradually more active until stage B₂ is reached (Passano, 1960a). Thus, energy normally used in digestion and locomotion may be diverted for activities involved with molt.

Limb loss and regeneration is a common phenomenon in Crustacea (Bliss, 1960). The energetics of regeneration are difficult to evaluate and have hardly been considered. One problem is that limb autotomy stimulates precocious molting with limb regeneration typically confined to the premolting stage. As a result, the energetic cost of regeneration is difficult to separate from the general effects of growth and molt itself.

The cost of limb regeneration is clearly distributed over a relatively long period. In Alaskan king crabs (*Paralithodes camtschatica*), a regenerated limb does not reach normal size until after four to seven molts (Skinner, 1985). In the land crab *G. lateralis*, a single lost limb is replaced by a regenerated limb that is only two-thirds the size of the normal limb. If more than six limbs are autotomized, the regenerated limbs are reduced to half normal size (Skinner and Graham, 1972). Crabs are probably restricted in the amount of tissue they can synthesize, perhaps to 12–15% of their metabolically active body mass. Therefore, intensive regeneration reduces the size of the animal itself as well as the regenerating limbs (see Skinner, 1985, for review). It appears that the metabolic resources are mainly redistributed rather than scaled up in a major way; energy normally used for general growth and activity is diverted to regeneration. From these considerations we would not anticipate a major elevation in overall metabolism and O₂ consumption during regeneration.

6. Locomotion

Crabs can have extensive daily and seasonal movement patterns (see Chapter 3). For example, intertidal movements of *Uca*, *Ocypode*, and *Coenobita* may exceed 100 m (Herrnkind, 1983). Ghost crabs, which are the fastest running crustaceans (up to 3.4 m·sec⁻¹), move as much as 300 m during daily activity periods (Wolcott, 1978; Roe, 1980). Seasonal reproductive migrations of *C. guanhumi* (Gifford, 1962a) and *G. lateralis* (Bliss, 1979) may cover several kilometers. The energetic costs of such behaviors have received little attention until recently, when it was discovered that crabs walk well on treadmills. This opened an avenue for studying the metabolism of crabs in motion. Because the intensity of work could be quantified and rigorously controlled, it was possible to explore the limits and range of physical exertion while aerobic metabolism was measured continuously.
Since 1979, when *C. guanhumi* was tested with a respiratory mask while walking at various speeds (Herreid, Lee, and Shah, 1979), metabolic data during locomotion have been accumulated on about a dozen species of land crabs. The use of a mask, applicable in only special circumstances, has yielded ventilation data but tends to encumber the crab. Hence, in most later studies, freely moving crabs have been tested on a treadmill enclosed in airtight chamber while \( V_O_2 \) is measured with an automatic \( O_2 \) analyzer (Herreid, 1981). Studying voluntary locomotion, Wheatly et al. (1985) have carried out studies of crabs walking in a low-friction system while metabolism was monitored. Recently, Blickhan and Full (1987) have run ghost crabs across miniature force plates and presented the first analysis of the mechanical energy changes during terrestrial locomotion in an arthropod. Combining metabolic and mechanical data allows estimates of the efficiency of locomotion. Before considering such data, it is helpful to have a general description of the walking and running styles of land crabs.

A. Locomotion patterns in land crabs

Two major groups of crabs walk extensively on land: the brachyurans such as *Uca*, which walk with eight legs, and the anomuran hermit crabs such as *Coenobita*, which walk with six limbs. Both taxa have different styles of walking, and both patterns clearly were established before these groups left the aquatic environment, since their aquatic cousins possess similar patterns.

The brachyurans typically walk sideways, although they do walk forward, backward, and diagonally on occasion (Lochhead, 1960). When walking sideways, the four legs trailing the crab provide the principal thrust, as they push the crab. The chelipeds do not normally participate in locomotion, being held close to the body off the ground, except in slow walking where they may contact the earth intermittently. Walking sideways avoids one of the major problems facing an animal with multiple limbs: The legs cannot overlap or interfere with one another because they swing sideways.

Leg movement can be described by numbering the pairs of legs, anteriorly to posteriorly. The chelifeds on the right and left sides of the body are designated \( R_1 \), and \( L_1 \), respectively. The first walking legs are \( R_2 \) and \( L_2 \), etc. When brachyurans such as *U. pugnax* walk, their neighboring legs alternate with one another. They also alternate with their partner on the contralateral side. Limbs \( L_3 \), \( L_4 \), \( R_3 \), and \( R_4 \) tend to step in unison, and \( L_5 \), \( L_6 \), \( R_5 \), and \( R_6 \) are coupled (Barnes, 1975). This pattern of locomotion results in an alternating tetrapod gait. At any one time the center of mass is always contained within a quadrangle of support and is obviously a very stable gait.
Gait changes have been observed in land crabs (Lochhead, 1960); the most striking is that seen in the ghost crab, *Ocypode ceratophthalma* uses fewer and fewer legs as the speed of locomotion increases (Burrows and Hoyle, 1973). At low speeds, all four pairs of walking legs are used. The crab can continue this movement indefinitely, although it may change leads, switching the trailing and leading sides, to avoid fatigue. As velocity increases, the crab raises R₄ and L₃ off the ground and uses only three pairs of walking legs. At the highest speeds, the third pair of walking legs (R₄ and L₄) is raised also, leaving only two pairs of legs for locomotion. The latter gait constitutes a true run, since the crab literally leaps off the ground. Virtually all of the power for this sprint comes from the two trailing legs; hence, the crab has been said to have a bipedal gait (Burrows and Hoyle, 1973).

The method of walking used by hermit crabs involves only two pairs of walking legs. The posterior two pairs of appendages not involved in locomotion have been modified to hold a protective snail shell. In contrast, to the brachyurans, hermit crabs normally walk forward, although they can move in other directions. Like insects, the land crab *C. compressa* uses six-legged locomotion (Herreid and Full, 1986a). It uses its chelipeds as support levers, while the two pairs of walking legs are used for thrust. Also like insects, this hermit crab uses an alternating tripod gait. Limbs L₁, L₂, and R₂ alternate with R₁, R₃, and L₃. This is the most stable six-legged gait, since the center of mass always lies within a triangle of support. Moreover, because the crab shell is often dragged, an extra point of support is also gained.

As with all pedestrian animals, energy for locomotion is used in several ways: to move the center of mass up and down with each step, and to accelerate and decelerate the limbs as they provide thrust and support for movement. As will be seen in the following section, land crabs function energetically very much like land vertebrates during locomotion.

**B. Metabolic energy patterns during locomotion**

The basic procedure in energetic studies during locomotion has been to collect oxygen-consumption data on crabs during a rest period on a stationary treadmill, then to turn the treadmill on for 10–20 min at a particular speed. The bout of exercise is usually followed by a period of recovery. Typically, once modest exercise begins, V̇O₂ rapidly rises to a relatively constant rate, which has been called the steady-state (V̇O₂ss) and remains there until the exercise is over. The time it takes to arrive at 50% of the V̇O₂ss (t₁/₂ on-response) is a convenient measure of the rapid adjustment of the crab to endurance running. Similarly, it is possible to measure the half-time to recovery (t₁/₂ off-response) after the treadmill is turned off.
Another method of evaluating the oxygen-consumption pattern involves the calculation of an \( O_2 \) deficit and \( O_2 \) debt, terms borrowed from vertebrate physiologists (Stainsby and Barclay, 1970). Oxygen deficit represents the lag in an animal's \( \dot{V}O_2 \) response to steady-state exercise. Thus, \( O_2 \) deficit represents the difference between two values: the actual rise in \( \dot{V}O_2 \) that occurs as the animal begins to run at a constant speed and the theoretical abrupt rise in \( \dot{V}O_2 \) that should occur if the steady-state \( \dot{V}O_2 \) were reached the instant that exercise began.

Oxygen consumption does not immediately fall to resting levels when exercise ceases. The delay in the \( \dot{V}O_2 \) recovery is called \( O_2 \) debt or extra postexercise oxygen consumption (EPOC), and is operationally defined as the area under the recovery \( \dot{V}O_2 \) curve, above resting \( \dot{V}O_2 \). These terms and concepts are graphically illustrated in Stainsby and Barclay (1970) and Herreid (1981).

\[ \text{i. } O_2 \text{ consumption during locomotion.} \]

Crabs give a range of responses in \( \dot{V}O_2 \) during locomotion. Three basic patterns have been identified so far.

1. **Aerobic pattern.** Some species such as the Panamanian ghost crab, *Ocyopode guadalchauddii*, have good endurance and are highly aerobic (Full and Herreid, 1983). For example, the \( t_{1/2} \) on-response for submaximal running of *O. guadalchauddii* is brief, less than 2 min. The \( t_{1/2} \) off-response is only slightly longer with complete recovery usually within 15 min. Consequently, the \( O_2 \) deficit and \( O_2 \) debt are small. The aerobic factorial scope values are high, reaching a maximum of 12 times the resting rate. Data for *O. quadrata* (shown in Fig. 10.5) and for the hermit crab *C. compressus* (Herreid and Full, 1986b) indicate that similar aerobic patterns exist in these species. The fast on- and off-response in these crustaceans is similar to that in mammals and insects (e.g., Cerretelli et al, 1977a; Herreid and Full, 1984a).

2. **Mixed aerobic and anaerobic pattern.** Anaerobic metabolism plays a prominent role in some crustaceans. Semiterrestrial and terrestrial crabs such as *U. pugilator*, *G. lateralis*, *C. guanhumi*, and *C. carinifex* show a mixed aerobic and anaerobic response to exercise (Herreid, Lee, and Shah, 1979; Wood and Randall, 1981a, b; Herreid, O'Mahoney, and Full, 1983; Full and Herreid, 1984). These animals have poor endurance, typically managing only 10–15 min on a treadmill at modest speeds. Even at low speeds, they may not reach steady-state \( \dot{V}O_2 \) before they fatigue (Fig. 10.6). Their factorial scope values are low; maximum \( O_2 \) consumption is about three to five times rest. Recovery from exercise is prolonged, often well over an hour in duration. Also, measurements of whole-body lactate in *U. pugilator* show that such crabs have a significant dependence on anaerobic metabolism (Full...
and Herreid, 1984). In the fiddler crab *U. pugilator*, whole-body lactate increases in a linear fashion with the speed of locomotion even at the lowest velocity, 0.06 km·h⁻¹. We estimate that even at this speed, anaerobic metabolism (and phosphagen and O₂ stores) accounted for 40% of the total ATP generated. During medium- and fast-velocity experiments (0.11 and 0.16 km·h⁻¹), anaerobic contributions via lactate fermentation rose to 60% and 70% of the total ATP produced.

The mixed metabolic response of exercising land crabs resembles that of exercising mammals running at velocities where O₂ consumption approaches maximum rates; near this point only small increases in VO₂ can occur, and the rate of lactate production in the blood increases linearly with velocity (Margaria et al., 1963; Seeherman et al., 1981). The mixed response is also similar to that found for humans who are untrained and thus have a poor aerobic response to exercise (Cerretelli et al., 1979).

3. *Non-aerobic patterns.* The wharf crab *Sesarma cinereum*, which lives in intertidal areas, shows an unusual metabolic response to running. Endurance tests reveal that *Sesarma* fatigues sooner than *U. pugilator* and much sooner than *O. quadrata* (Full et al., 1985). Even though *Sesarma* has a resting VO₂ comparable to *U. pugilator*, running does
not stimulate \( \dot{V}O_2 \) to increase more than 1.6 times the resting rate. This suggests that anaerobic metabolism may play a major role. Surprisingly, whole-body lactate measurements show *Sesarma* to have much lower levels than *U. pugilator*. Thus, the typical aerobic and anaerobic indicators of crustacean metabolism point to a much lower energy demand for the wharf crab running at the same speeds as *U. pugilator*. Preliminary testing for other possible end products of anaerobic metabolism does not show unusual levels of alanine, succinate, D-lactate, octopine, or strombine (Full and Herreid, 1985). Thus, no evidence exists for unusual rates of anaerobic metabolism to compensate for the low aerobic contribution to exercise. This crab's apparent low energy demand could be due to unusual levels of \( O_2 \) stored in the hemolymph or to high levels of arginine phosphate in the muscle. This does not seem likely because the crab can walk at least an hour; these energy sources would have to be unrealistically high to produce this result. Moreover, when *Sesarma* was exercised in pure nitrogen gas, it did not show unusual endurance, but it did improve when exposed to a pure oxygen atmosphere, thus emphasizing that the species is not unusual in anaerobic abilities. How this crab accomplishes its locomotion without raising \( \dot{V}O_2 \) except to a minor degree is unknown.
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In summary, at least three different metabolic responses to exercise have been identified. These are exemplified by *Ocypode*, *Uca*, and *Sesarma* in Figure 10.7. The remarkable feature of this comparison is that the individuals illustrated here are the same size (2–3 g) and are running on a treadmill at similar speeds.

How can such differences be explained? Clearly, anaerobic metabolism, high-energy phosphate reserves, and \( \text{O}_2 \) stored in the hemolymph may account for some of the variation. But we must entertain the possibility that the crabs have very different energetic efficiencies during locomotion. Moreover, other differences probably exist. First, differences in \( \text{O}_2 \) conductance and utilization seem likely, but have not yet been identified. It is likely that circulation systems vary, with differences in hemolymph \( \text{O}_2 \)-carrying capacity and \( \text{O}_2 \) dissociation being important (see Chapter 8). Certainly, the gill surface area is not dramatically different among the species (Full et al., 1985), and the leg muscle mitochondrial density, distribution, and size are similar (C. Privitera and C. Herreid, unpub.).

Second, there are significant differences in endurance (Fig. 10.8). The highly aerobic species such as ghost crabs, with high maximal rates of \( \text{V} \text{O}_2 \) and low lactate concentration, can sustain walking for well over an hour at modest speeds. It is not surprising that these
species are very active foragers in the wild, routinely traveling several hundred meters each day (see Chapter 3). Crabs such as *Uca*, with mixed aerobic and anaerobic patterns, show less stamina. They are less consistent walkers on the treadmill at high speed, have a low maximum VO\textsubscript{max}, and require anaerobic metabolism. *Sesarma*, possessing the poorest aerobic capacity, can sustain only very slow rates of locomotion. Whatever the limitations, it appears that crabs that can consume oxygen at high rates can sustain more intense activity, whereas those with more limited aerobic capacities move at slow speeds or only intermittently.

ii. O\textsubscript{2} consumption versus velocity. In vertebrates (mammals, birds, and reptiles), the VO\textsubscript{2} for steady-state running tends to rise with an increase in velocity until a maximum (VO\textsubscript{max}) is reached (e.g., Taylor et al. 1970; Taylor, 1973, 1977). This pattern holds true for aerobic insects, which use progressively more O\textsubscript{2} the faster they run (Herreid and Full, 1984a). A linear rise in VO\textsubscript{2} with velocity also occurs in the aerobic land crabs such as *Ocypode* (Full and Herreid, 1983; Full, 1987). Figure 10.9 shows the pattern for *O. quadrata*. Even in those less aerobic species that never show a steady-state VO\textsubscript{2} during exercise (e.g., *C. guanhumi, G. lateralis, U. pugilator*), the sum of the O\textsubscript{2} used

![Endurance Time vs. Velocity](image)
Fig. 10.9. Steady-state oxygen consumption for 5 ghost crabs (*Ocyopode quadrata*) as a function of velocity. Maximal $O_2$ consumption is plotted for comparison on the right. (From Full, 1984.)

during both exercise and recovery is directly related to the velocity of travel (Herreid, Lee, and Shah, 1979; Full and Herreid, 1983).

Oxygen consumption versus velocity shows a curvilinear rise in some animals. Humans walking on a treadmill show this pattern, although $V_O_2$ during running is linear (Margaria et al., 1963). The curvilinear response also occurs in ponies forced to walk or trot at higher or lower velocities than normal (Hoyt and Taylor, 1981). Such patterns may not be evident in treadmill experiments because animals change gaits. It has been argued that gait changes serve to maintain the most economical travel at a given velocity. Gait changes have been observed in some land crabs (e.g., *Ocyopode*; Hafemann and Hubbard, 1969), and they may play a similar role.

iii. Y-intercept problem. When the $V_O_2$ is plotted as a function of velocity, for many species the regression line passing through the data points may be extrapolated back to zero velocity. This y-intercept is the anticipated $V_O_2$ value of the animal at rest. In most species tested, the y-intercept is considerably higher than the actual measured resting $O_2$ consumption (e.g., Taylor et al., 1970). Data for land crabs also show this trend (Herreid, Lee, and Shah, 1979; Full and Herreid, 1983; O'Mahoney, Herreid, and Full, 1983; Fig. 10.9).

Herreid (1981) has reviewed the many possible reasons for the
Fig. 10.10. Possible reasons for an elevated y-intercept when \( \dot{V}O_2 \) is plotted against velocity. A. Case in which \( \dot{V}O_2 \) would show a curvilinear pattern if measured at slow speeds. Thus, the intercept is an artifact. B. The y-intercept is deflected upward if the animals show extraneous movement at slow speeds. C. Upward deflection results from anaerobic metabolism at high speeds. D. The y-intercept might be elevated if there were a constant postural cost of locomotion.

Y-intercept. Perhaps the most likely explanations for the phenomenon in the crabs studied, as illustrated in Fig. 10.10, are the following:

1. At slow speeds, \( \dot{V}O_2 \) may decrease curvilinearly to resting levels. The elevated y-intercept may be an artifact since very few measurements are made at very slow speeds.

2. Crabs walking at very slow speeds on the treadmill may use more \( O_2 \) than predicted because they are apt to wander and have extraneous movements. Consequently, treadmill velocity underestimates their exercise output at slow speeds.

3. Crabs walking at fast speeds may increase their dependency on anaerobic metabolism. Therefore, the \( \dot{V}O_2 \) at high speeds would not be an accurate measure of the energy used during locomotion; i.e., the measured \( \dot{V}O_2 \) is less than expected. If either scenario (2) or (3) occurs, it would have the effect of deflecting the \( \dot{V}O_2 \) versus velocity regression line to elevate the y-intercept (Fig. 10.10).
4. Schmidt-Nielsen (1972) has suggested that the elevation of the y-intercept represents the “postural cost of locomotion.” Presumably, this means there is a cost associated with lifting the body into a position for locomotion and maintaining it there. If this is the case, it suggests the entire $V_O_2$ vs. velocity curve may be displaced upward. At present, except for the hermit crabs discussed later, there are insufficient data on any animal to clearly resolve this problem.

C. Mechanical energy patterns during locomotion

The mechanical energy required for locomotion can be estimated by using a force plate (Cavagna, 1975; Cavagna, Heglund, and Taylor, 1977). As the animal runs or walks over the plates, both horizontal and vertical forces are recorded. Integration of the forces yields the horizontal and vertical velocity changes of the center of mass. Kinetic energy (horizontal and vertical) can then be calculated using these velocities. A second integration of the vertical velocity gives the vertical position changes. By knowing the degree of oscillation in the center of mass, changes in gravitational potential energy can be determined.

i. Mechanical energy changes of the center of mass during locomotion.

Changes in mechanical energy during locomotion in land crabs appear to follow at least two different patterns (Blickhan and Full, 1987). During sideways walking in the ghost crab O. quadrata, the body moves up and down and the legs are moved in an irregular, alternating tetrapod gait: Adjacent legs on one side of the body move out of phase with one another, as do contralateral legs on opposite sides of the body.

Horizontal kinetic and gravitational potential energy fluctuate out of phase (Fig. 10.11A). As the crab’s center of mass rises and falls, energy is alternately transferred from kinetic to potential energy, much like a swinging pendulum or an egg rolling end over end. In this way considerable energy is conserved. In a walking crab, as much as 55% of the energy is recovered during a stride (Blickhan and Full, 1987). This mechanism for conserving energy during walking appears to be very general, as it has been thoroughly described for bipedal and quadrupedal vertebrates (Cavagna et al., 1977; Heglund et al., 1982a).

At high running speeds, photographs show that the ghost crab literally leaps through the air, becoming bipedal and using a running gait (Burrows and Hoyle, 1973). Force plate measurements show the periods of zero vertical force where all eight legs are off the ground (Blicken and Full, 1987). The records also show that at high speed, horizontal, kinetic, and gravitational potential energy are in phase, so little energy exchange is possible (Fig. 10.11B).
Fig. 10.11. Energy changes of the center of mass of a ghost crab walking and running across force plates. A. Data for a 53 g crab (0.52 N) walking during one stride at 0.25 m·sec⁻¹. B. Data for a 61 g crab (0.60 N) running at 0.66 m·sec⁻¹. The upper and middle traces represent the changes in vertical and horizontal kinetic energy. The middle trace shows the fluctuations in gravitational potential energy. The lower trace represents the changes in total mechanical energy of the center of mass. (From Blickhan and Full, 1987.)

The energy fluctuations during running in the crab are very similar to the patterns observed for trotting, hopping, and galloping vertebrates (Heglund, Cameron, and Taylor, 1983). In fact, the frequency at which the ghost crab cycles its legs during fast running is almost identical to that predicted for a galloping mammal of a similar mass, as is the speed at which it switches from a slow to a fast run (Fig. 10.12; Heglund, Taylor, and McMahon, 1974). This could mean that the body of a crab, as well as that of a mammal, functions as a tuned, mechanical spring system (Taylor, 1985).

ii. Mechanical energy changes versus speed. Total mechanical energy is extremely difficult to determine. A major portion of the mechanical power expended for locomotion is required to lift and accelerate the center of mass $E_{CM}$, especially for small, slow-moving animals (Heglund et al., 1982b). Additional energy is necessary to accelerate the limbs and the body relative to the center of mass, while energy exchange and elastic storage decrease the energy demanded from muscles. For the ghost crab mechanical energy was estimated from $E_{CM}$.
Fig. 10.12. Stride frequency as a function of speed for a 55 g ghost crab. *Shaded regions* represent gait transitions (Blickhan and Full, 1987). The *diamonds* indicate the predicted trot-gallop transition for a mammal of the same mass (Heglund et al., 1974).

During walking and running (Blickhan and Full, 1987), $\dot{E}_{CM}$ increased linearly with speed and was directly proportional to body mass.

**D. Efficiency of locomotion**

How efficient is terrestrial locomotion in land crabs? Since both metabolic and mechanical energy measurements are available, we can estimate efficiency as follows:

\[
\text{Efficiency} = \frac{\text{Mechanical energy output}}{\text{Metabolic energy input}} \times 100.
\]

For the ghost crab, $\dot{E}_{CM}$ is taken to be the best estimate of the total mechanical energy output, and $V_{O_{2s}}$ represents the total metabolic input. $\dot{E}_{CM}$ for the ghost crab is not significantly different from that required by a vertebrate of the same mass (Fig. 10.13). As in vertebrates, the mechanical power used for locomotion appears to increase in direct proportion to body mass (Heglund et al., 1982b). This suggests that the mechanical energy required for locomotion is relatively independent of the animal’s morphological pattern.

In terms of metabolic energy, endothermic vertebrates demand high rates even at rest. If resting metabolism is removed, the rate of power required during locomotion becomes more similar to that of an ectotherm. Over the range of speeds (0.32–0.50 km·h⁻¹), where both metabolic and mechanical measurements have been obtained, the efficiency of ghost crab locomotion is approximately 5–10% (Blickhan and Full, 1987). These values are remarkably similar to the 2–5% values predicted for a bird or mammal of the same mass (Heglund et al., 1982b). Although more data are certainly needed, the major
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![Graph showing power requirements for different modes of transport](image)

Fig. 10.13. Metabolic ($\dot{E}_{\text{metab}}$) and mechanical ($\dot{E}_{\text{mech}}$) power required for a ghost crab (25°C) and a mammal of the same mass (~30g). $\dot{E}_{\text{metab}}$ for the mammal was predicted from Taylor et al. (1982). $\dot{E}_{\text{mech}}$ for the ghost crab is from Full (1987). The slopes, representing the minimum cost of transport, are not significantly different from that of the mammal. Horizontal bars represent the range of sustainable speeds (> 20 min) for each animal.

The difference between the crab and the mammal may not involve the economy or efficiency of locomotion, but rather the endurance at high speeds. Mammals can sustain high rates of locomotion for long periods, but the crab is limited to slow walking with occasional brief sprints.

E. Economy of locomotion

The energetic cost of steady-state locomotion can be calculated by dividing the animal's $O_2$ consumption by its velocity. In aerobic species this yields a relationship indicating that $O_2$ consumption per distance traveled is highest at slow speeds; it progressively declines with velocity, gradually approaching a minimum cost of transport ($C_m$). The $C_m$ value is the slope of the regression line for $V_{O_2}$ versus velocity (Taylor et al., 1970). Considering only the economy of travel, one might predict that animals traveling long distances should move at relatively fast speeds to conserve energy. Little attention has been given to this point. Certainly, in *C. compressus* traveling over the beach this appears to be the case (see section 6.9). (This hermit crab study is also of interest because it suggests that the type of terrain may alter the energetics of transport; crabs walking on dry sand travel more slowly than those on moist, packed sand.) The total energetic cost of locomotion is greater for large animals than for small (Taylor et al., 1970; Tucker, 1970). However, the relationship is not simple; a doubling of the mass does not necessitate a doubling of the energy output. Less energy is required. Often this relationship is shown by plotting the minimum cost of transport (i.e., ml O$_2$·g$^{-1}$·km$^{-1}$) against body mass; it is argued that animals to the crossbills to be inv...
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![Graph showing cost of transport versus body mass](image)

Fig. 10.14. Minimum cost of transport versus body mass on a log scale. Data are from Taylor et al. (1982) for birds and mammals; Bakker (1972) for lizards; Herreid and Full (1984a) for cockroaches; Herreid (1981) for arachnids, some land crabs, and centipedes; and Jensen and Holm-Jensen (1980) for ants. Uncircled x = Orconectes quadrata from Full (1987). The circled x = Uca pugnax from Full and Herreid (1984) calculated by the sum of aerobic and anaerobic metabolism.

mass; it is immediately obvious that small animals use relatively large amounts of energy for travel. Land crabs are no exception (Fig. 10.14). What is the explanation for this pattern? Taylor et al. (1980) have argued that small animals must expend more energy than large animals to generate a given force at the same speed. If the intrinsic velocity of muscle shortening is proportional to the rate of myofibrillar crossbridge cycling, then this rate should increase in direct proportion to the cost of generating force. Since the shortening velocity appears to be inversely related to mass (i.e., small animals have high intrinsic velocities), the cost of generating muscular force should increase for animals of small size.

Because arthropods have a variable number of appendages, it is logical to ask if the number of legs influences the cost of terrestrial locomotion. Consider first the problem of autotomy when land crabs may lose a leg to a predator. Herreid and Full (1986b) have removed limbs from hermit crabs by bilateral amputation, forcing the animals to walk with four limbs rather than the normal six. Of five individuals tested, one showed no increased cost of travel, and the remaining four showed only modest elevation; but the greatest increase in VO2 was only 1.8 times the normal rate. At least in this experiment, only modest changes in energy consumption occurred when limb number
was reduced from six to four, although the speed and agility of the crab were certainly affected. Possibly, practice would improve performance. Limb autotomy probably has even less effect in species with eight walking legs, especially if it involves only one appendage. The question of leg number may be addressed by comparing the minimum cost of transport among widely different species. Figure 10.14 shows data for minimum cost of locomotion in animals with various numbers of legs ranging from 2 (birds), 4 (lizards and mammals), 6 (ants and cockroaches), 8 (crabs and arachnids), to dozens (centipede). All species tend to follow the same general trend, thus indicating that the number of legs does not appear to affect the cost of locomotion among species. Similarly, there is little correlation with different styles of locomotion or the taxonomic position of the animals. All animals of similar mass appear to have a similar fuel economy when traveling a given distance on land. This does not mean that their total \( \text{Vo}_{2} \) per gram is the same, since homeotherms have higher maintenance costs than poikilotherms, but their minimum costs of transport are similar. This suggests that we are dealing with a fundamental property of muscle energetics.

F. Locomotion on land versus in water

Swimming animals have a much lower minimum cost of transport than pedestrian animals on land (Schmidt-Nielsen, 1972). Aquatic species are buoyed by the water around them and use less energy for support against gravity than terrestrial species. Also, land pedestrians are very uneconomical because their legs tend to slow their progress each time they hit the ground after a recovery stroke. The body must be reaccelerated after each step. To appreciate the effect of this braking and reaccelerating action, consider the relative ease of pedaling a bicycle. Bicycle riders do not have to use their feet to support themselves against gravity. Cyclic accelerations and deaccelerations are minimized; thus their efficiency of locomotion is very high. Hargreaves (1981) has reviewed the meager evidence available for swimming crustaceans and proposes that a similar reduction in the cost of travel may exist in this case.

Many crustaceans walk along the bottom of the ocean. They are supported by the water and would be expected to use less energy than if walking on land. On the other hand, walking in water should result in greater drag than in air especially in view of the potential turbulence that would be produced from multiple limbs in motion. Lobsters are known to walk in long queues during migrations and in this way may reduce drag (Bill and Herrnkind, 1976).

Attempts have been made to measure \( \text{O}_{2} \) consumption while crabs were walking underwater. Houlihan, Mathers, and El Haj (1984) ex-
ercised *C. maenas* in a circular respirometer by prodding them gently. In typical experiments, crabs made 25 circuits of the chamber in 10 min, before they became fatigued. The PO₂ of the seawater was determined at 0-min, 5-min, and 10-min time periods in the run, so it was not possible to determine the O₂ kinetics. The poor endurance and the fact that whole-body lactates were significantly elevated even during the slow speed tests suggest that this crab has a mixed aerobic and anaerobic response to exercise. The authors found VO₂ increased with velocity in large crabs but not small individuals, which is puzzling. Another surprising finding was that the net minimum cost of transport (including aerobic and anaerobic contributions) for this species walking underwater is similar to that of terrestrial crabs. This finding might have several explanations, including the possibility that the drag in the experiments might be high. However, Houlihan et al. (1984) remark that water currents produced by the crab’s movement and the prodding stick seem negligible at low speeds. Yet, the hydrodynamic interactions of a crab in a shallow tank with alterations in speed and periodic reversals in direction are difficult to evaluate.

Houlihan and Innes (1984) compared walking in air and water in a circular respirometer using the amphibious intertidal crab, *Pachygrapsus marmoratus*. The exercise period lasted 6 min or less before fatigue occurred in either water or air. Oxygen kinetics could not be followed, but it was clear that O₂ debts were repaid in 20 min. VO₂ increased linearly with velocity in both *P. marmoratus* and another crab, *Carcinus mediterraneus* walking in water. Once again Houlihan and Innes (1984) note that the cost of transport for these species walking in water is similar to decapods walking on land, even though the crabs “weigh over 10 times less in water than in air [sic].” This problem awaits further study.

**G. Energetics of load carrying**

Some crabs carry significant loads at some time during their life. A crab may drag food material back to its burrow. Females may carry egg masses. Certain aquatic crustaceans become heavily encrusted with sponges, barnacles, and sea anemones. In each of these cases, we would expect extra energy to be expended to carry the additional mass, less so in the aquatic environment than on land because of the effects of buoyancy. The energetics of load carrying in crustaceans has been recently investigated in the terrestrial hermit crab, *C. compressus* from Panama (Herreid and Full, 1984b, 1986b; Wheatly et al., 1985). Hermit crabs of this species are particularly valuable subjects for investigation because they naturally live in gastropod shells of varying masses. Two crabs of the same size may carry snail shells differing in weight by a factor of 3 (Herreid and Full, 1986a). More-
over, they can be induced to switch shells or to walk on a treadmill without any snail shell at all. Terrestrial hermit crabs with and without snail shells both show a linear increase in $V_{O_2}$ with velocity; both lines are parallel, but the "nude" crabs use significantly less energy than those carrying a shell about the same mass as their body (Fig. 10.15). There is no difference in the resting $V_{O_2}$ in crabs with and without shells. Hence, it seems reasonable to conclude that the difference in the two curves represents the cost of carrying a snail shell. It is not the postural cost of locomotion, because crabs lacking shells do not show an elevated y-intercept.

The difference between the cost of transport of loaded and unloaded animals is the extra cost of transport, $C_E$. This value falls as velocity increases (Fig. 10.16). At slow velocities the extra cost of carrying a gram of shell is similar to carrying a gram of body mass. However, as velocities increase, $C_E$ drops until it is negligible at speeds where the minimum cost of transport occurs. Consequently, another advantage accrues to crabs traveling rapidly across the beach. Perhaps the most interesting finding for the terrestrial hermit crabs is that increasing the load does not cause a corresponding proportional increase in $V_{O_2}$. Instead, the $V_{O_2}$s loaded/unloaded ratio rises much less than the loaded/unloaded mass ratio. This is in contrast to data collected for several mammals (Taylor et al., 1980). Terrestrial hermit
crabs seem especially efficient at carrying loads, especially the heavier shells; there is essentially no increase in \( \text{VO}_2 \) as shell sizes increase from two to four times the body mass. The reason for this unusual phenomenon probably has to do with an increase in mechanical efficiency. With greater loads, crabs shift their leg position and tend to drag their shells.

7. Energy budgets

Ideally, one would like to be able to identify each behavior of an organism and measure its energetic cost. This would permit the development of daily and seasonal energy budgets. We are far from this ideal in land crabs. Nevertheless, a few comments can be made. Based on field observations, crabs spend most of their time “resting.” There are only brief periods when energy demand may rise severalfold because of behaviors such as an explosive escape response, pursuit of prey, or a fight. These activities are vital to the animal’s survival and are energetically expensive, perhaps elevating metabolism to 10 times that at rest. However, these activities are of such short duration and
so infrequent as to be of minor importance to the energy budget. Most common activities that are prolonged and frequent are probably energetically inexpensive. Crabs eat, explore, defecate, make courtship displays, and molt with what appears to be modest energy expenditures when we compare these activities to treadmill exercise. Simply stated, most energy is used for maintenance rather than for behavioral activities. Certainly, most daily activities do not even double the resting VO2 we observed in the laboratory. Realizing that the resting metabolism is probably much higher in the laboratory than in the undisturbed condition in the field, it seems that the daily energy budget probably is not much higher than the resting rate we measure, certainly no more than double the latter. This may hold true for most animal species. Consequently, the estimate of an energy budget may be fairly approximated using “resting metabolism.”

8. Conclusion

In retrospect, energetics in land crabs is reasonably well understood. Their feeding processes are relatively simple and have been observed closely in several species. More information would be useful but probably would not change our perspective. We are, however, grossly ignorant about the caloric intake and assimilation efficiency of crabs in the field. The digestive system of land crabs has not been studied in any detail at all. Even though it is desirable to correct this deficiency, enough crustaceans have been examined that it is unlikely that any major surprises are in store here. Land crabs are probably similar to their aquatic relatives.

Crustacean metabolism appears surprisingly similar to vertebrate metabolism. Moreover, land crabs do not appear unique in any way when compared with aquatic crabs. However, a great deal more attention needs to be focused on intermediary metabolism. For example, we do not even know what is the major metabolic fuel for crustaceans. The role of protein as an energy source and its role in osmotic balance are quite intriguing. The hormonal control of metabolism is undoubtedly complex, but it is poorly understood except for some data on carbohydrate metabolism.

As far as the principles of whole-animal energetics are concerned, crustaceans in general, and land crabs in particular, are reasonably well understood. An impressive array of “resting” rates have been obtained, but it would be useful to have more data on crabs in an undisturbed state in conditions approximating the natural environment.

In contrast to other facets of metabolism, land crabs are better studied during exercise than any other crustacean group. From the dozen species that have been investigated, both “marathoners” and
"sprinters" have been studied using treadmills and voluntary walking. Since the techniques are established, the next 10 years should see the number of exercise studies mount. Greater attention will be paid to morphological and physiological differences among species such as *Uca* and *Ocypode* that give rise to the different metabolic responses that have been measured between species. Also, the next decade should bring a clearer analysis of the mechanical energy used in locomotion in pedestrian arthropods.

Although work with treadmills demonstrates the metabolic scope for land crabs and allows a clear indication of the metabolic cost of locomotion, other behavior patterns have not been studied. If we are to evaluate the energy budgets of crabs in the future, we must have good studies of the energetics of feeding, courtship, agonistic displays, egg laying, growth, molting, regeneration, climbing, burrowing, etc. These are now lacking (also see Chapter 4). Oxygen-consumption measurements of these behaviors could be readily obtained in the laboratory. Their overall importance in the energy budget would be appreciated only if there were concomitant field studies where the frequency and duration of the behavior were measured. Collection of this information should be straightforward, and it would be a major advance in our investigations of the energetics of land crabs.

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