LOCOMOTION OF HERMIT CRABS (*COENOBITA COMPRESSUS*) ON BEACH AND TREADMILL

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SUMMARY

Coenobita compressus (H. Milne Edwards) walk forward on six legs using an alternating tripod gait similar to that of insects. The first walking leg provides the driving force for locomotion aided secondarily by the second walking leg, while the chelipeds act largely as supports. The left appendages are longer and heavier than the right, and they extend further laterally from the midline during their stride, thus compensating for the asymmetry of the crab which has a dextrally coiled shell and an abdomen displaced to the right. The abdomen is normally carried off the ground, but it is dragged when the shell is large.

Bilateral leg autotomy alters gait patterns; usually a diagonal quadrupedal gait was adopted. Walking was poor in crabs without chelae (L_1 and R_1) because of problems of balance. Crabs without their first walking legs (L_2 and R_2) were the most accomplished amputee walkers. Crabs lacking legs L_3 and R_3 showed the most gait diversity.

Velocity of travel is a function of crab size and the substrate walked upon. Large crabs travel faster than small ones on the beach by increasing their stride length rather than stepping frequency. Studies on a miniature treadmill showed individual crabs change velocity by changing both stepping frequency and stride length.

Snail shells of the genus *Nerita* are carried; they are the lightest shells on the beach. Shell mass for an individual may vary three-fold, but usually the masses of the shell and crab are similar. Crabs running with and without shells have the same step frequency and stride length.

INTRODUCTION

Hermit crabs are unique animals for locomotion studies. They are specialized to carry snail shells (e.g. Reese, 1969; Vance, 1972; Bertness, 1980). The addition of this load obviously reduces the crab's speed and manoeuvrability, and increases the energy used for transport, while it provides the advantage of protection from predators and environmental extremes. It is the purpose of this paper and the next to consider the pattern of locomotion and energetic consequences in hermit crabs on the beach and on a treadmill in the laboratory.

In this first paper we will examine the stepping pattern and velocity pattern of hermit crabs with and without snail shells. While other crabs (decapod crustaceans) typically use octapedal locomotion and walk sideways, hermit crabs walk forward using six legs and provide an interesting comparison with other crustaceans as well as insects. Hermit crabs have an asymmetrical body morphology, and in the species used in this study, *Coenobita compressus*, the abdomen is displaced to the animal's right in order to fit the dextrally coiled shell. The left walking appendages and cheliped are enlarged compared to those limbs on the right.

In this paper we also consider how the loss of limbs affects locomotion. As other authors have noted (e.g. Delcomyn, 1971), many arthropods have limbs that may be autotomized. The animals frequently regenerate such appendages, but in the meantime, they must adjust their locomotion to compensate for imbalances created by the loss of such limbs. The effect of autotomy on locomotion does not seem to have been addressed in hermit crabs in any detail.

The novelty of hermit crab locomotion serves to remind us of the extraordinary plasticity of locomotor mechanisms in general and the study of these particular animals may give us insight into the broader questions of locomotion.

MATERIALS AND METHODS

Coenobita compressus is a terrestrial hermit crab living in the rocks and grass above high tide in the tropics. Usually, by day it is quiescent and at night it descends to the beaches to scavenge organic debris along the moist sand. Our field observations on the hermit crabs were conducted along Boyscout Beach just off Naos Island, near Panama City, Panama, in March 1981. Crabs were also collected in this area and transferred to aquaria a few hundred metres away at the Marine Laboratory of the Smithsonian Tropical Research Institute. Crabs were maintained for only a few days on damp sand while the laboratory experiments were performed.

Behavioural observations

Locomotion was examined on the beaches and in the laboratory. In the field we noted velocities by timing freely-walking crabs over moist sand for one metre, two or three measurements being obtained per individual. In cases where footprints were clearly visible, we measured the average stride length for five steps with a caliper and calculated stepping frequency. The crabs were then captured and weighed with and without their mollusc shells.

Locomotion could be analysed only superficially in the field. Consequently, crabs were brought to the laboratory where they were placed on a long table covered with dry beach sand. If we remained motionless we had no difficulty closely observing the crabs as they walked. In addition, we could time their rates of movement and measure the distance between footprints on the sand. In all descriptions of walking we have used the following designations: L_1 and R_1 represent the left and right chelae, L_2 and R_2 indicate left and right first walking legs, and L_3 and R_3 are the left and right second walking legs.

To determine how an individual animal achieves changes in velocity from moment to moment, we ran 11 crabs with and without their shells on a miniature treadmill (Herreid, 1981). Their average body mass without shell was $3·6 \pm 1·3$ g (S.D.). Each crab was placed on the latex treadmill belt and run at four velocities in sequence: 0·6, 1·0, 1·3 and 1·8 km h^{-1}. Each run lasted about 2 min before the velocity was increased to the next level. Not all crabs were able to run at each velocity. In order to determine the average stepping frequency, 50-step cycles were timed on three separate occasions during the 2-min run. The average of the three measurements is represented by a single point in Fig. 5. Stride length is a calculated value (step frequency/velocity = stride length).

To determine the effect that leg autotomy may have on hermit crab locomotion, we performed bilateral amputations of pairs of appendages. Three conditions were examined: removal of (1) chelipeds, or (2) first walking legs, or (3) second walking legs. In each case, crabs were first gently removed from their snail shells and both appendages were amputated by pinching off limbs at the junction of the coxa and merus, the normal site of autotomy. The crabs were allowed several days for recovery. Some crabs, especially those with cheliped removal, were traumatized by the experience and either died or would not perform on the treadmill. Only animals that appeared healthy were used in the reported experiments.

RESULTS

Behaviour and locomotion

The hermit crabs, *Coenobita compressus*, were observed frequently along the beach over 2 months. They were very active at night in the intertidal zone patrolling the moist sand in search of food. In certain areas, it was common to find several dozen hermit crabs per metre especially if decaying food (fish, bananas, human faeces) was on the beach. By dawn most crabs left the sand and retreated to the rock rubble above high tide, wedging themselves in cool moist cracks, crawling up tree roots and secreting themselves in the leaf litter. They remained quiescent during the hot daylight hours only to descend to the beach once again at dusk when the tide was out. Thus *C. compressus* is an animal that is extremely active, commonly covering distances of several hundred metres and exerting considerable effort as it climbs over rocks and vegetation.

General pattern of locomotion

Hermit crabs (Order Anomura) unlike the Brachyura usually move forward rather than sideways. Movement in *C. compressus* is principally produced by the second and third pairs of thoracic appendages. These walking legs are positioned laterally and appear to provide thrust with both a pulling motion during the early part of the leg cycle as they reach forward, contact the sand and flex, and a pushing motion in the latter phase of the leg cycle when the legs extend to the rear of the crab. The limbs initially contact the ground with the tip of the crescent-shaped dactylus which rolls forward towards the propodus, forming a comma-like indentation on the sand.

The chelipeds, the first appendages, participate in locomotion: they are primarily used for support rather than thrust. The chelae move directly anterior and posterior under the crab during locomotion, in contrast to the arching lateral swings of the walking legs. Each chela contacts the ground principally with the movable finger (dactylus) of the claw as the chela rolls forward along its edge from tip to base. The fourth and fifth pairs of appendages are markedly reduced in size and specialized for carrying snail shells; they do not participate in locomotion and are not visible unless the crab is removed from the shell.

C. compressus uses a basic alternating tripod gait. Limbs L_1, L_3 and R_2 alternate with R_1, R_3 and L_2. Fig. 1 shows a typical footprint pattern of C. compressus and it illustrates the normal tripod gait. The broad footprints of limbs 2 and 3 are produced by the 'knuckle walking' of the crab. The dactyls are bent backwards as they make contact across a broad surface. The chelipeds (L_1 and R_1) frequently lead the two walking legs of their respective triads. For example, R_1 lifts off of the ground and touches down slightly in advance of legs L_2 and R_3; similarly, L_1 leads R_2 and L_3. The chelae are often not lifted completely free from the substrate during retraction; consequently, they will leave a gouged-out groove in the centre of the crab track as they are dragged along the sand. Sometimes the shell is not lifted completely free of the sand either, especially in the large crabs, in which case it leaves a large groove in the middle of the track obliterating the inner part of the footprints.

In the footprint pattern of C. compressus the second appendages (L_2 and R_2) tend to fall outside or lateral to the third (L_3 and R_3), and the chelipeds are positioned along the centre of the track. This pattern is not invariable; commonly, the third limbs are extended outwards so that they fall in line with or even outside L_2 and R_2.

The left appendages are frequently extended further away from the centre of the track than the right appendages. The reason for such a pattern seems to be the asymmetry of the hermit crab. The crab's abdomen and the centre of gravity of the mollusc shell are displaced to the right of the crab's midline. In order to maintain balance, the crab has compensated behaviourally and morphologically. The behavioural change is the alignment of the legs. The left legs are extended and the right retracted. The morphological adjustments include the fact that the left appendages are enlarged compared to the right, counter-balancing the massive abdomen. This point is seen in the following measurements of four crabs with animal masses varying between 7·4 and 11·7 g. The right chela was only 53 % of the mass of the left; R_2 was 95 % of the mass of L_2; and R_3 was 80 % of the mass of L_3. The increased mass of the left appendages is due to both an increased width and length of the individual leg segments, as demonstrated by measurements with calipers. The asymmetry is used in locomotion, extending the left legs slightly more to the left of the midline than the right appendages. Also, it is used when the crab retreats back into the shell. The left appendages are folded over the right at the mouth of the shell forming a 'false operculum'.

Shifts in the centre of gravity are not dramatically evident in large crabs during locomotion. However, in small crabs the shell and abdomen yaw right and left with each step of the third appendages. As R_3 extends behind the crab, the shell posterior

yaws to the left; as L_3 extends in its power thrust, the shell yaws to the right. Such rocking motions may increase the cost of locomotion.

Shell and body mass of hermit crabs

To appreciate the magnitude of the shell mass and its effect on the energetic cost of locomotion, we weighed 100 hermit crabs together with their snail shells and obtained masses ranging from 0·8 to 35·4 g. The crabs did not represent a random sample of the population but were chosen to represent the range of shell sizes used by the species. Most shells were of the most common snail, *Nerita*, in the intertidal area. By gently prying the crabs from their shells, the separate masses of the crabs and their mollusc shells were determined. The results are depicted in Fig. 2. There is a
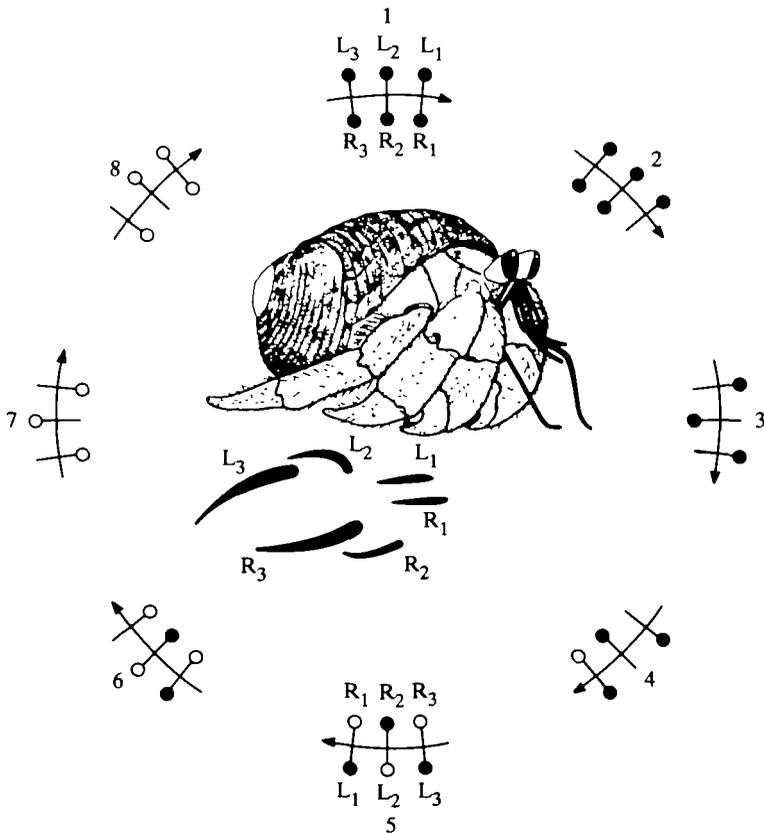

Fig. 1. Stepping pattern and footprint of *Coenobita compressus*. The stepping cycle passes through eight phases beginning with phase 1. The arrow represents the body axis and the direction of movement. The transverse lines on the arrow represent the six appendages used in walking. L and R designate the left and right limbs, respectively. L_1 and R_1 are chelae. The circles on the ends of the limbs indicate that the feet are in contact with the substrate. Thus, in phase 2, R_1 has lifted while the other limbs remain on the ground. Open circles indicate which limbs have been lifted and replaced on the ground. The footprint as it would appear on the sand is shown below the crab.
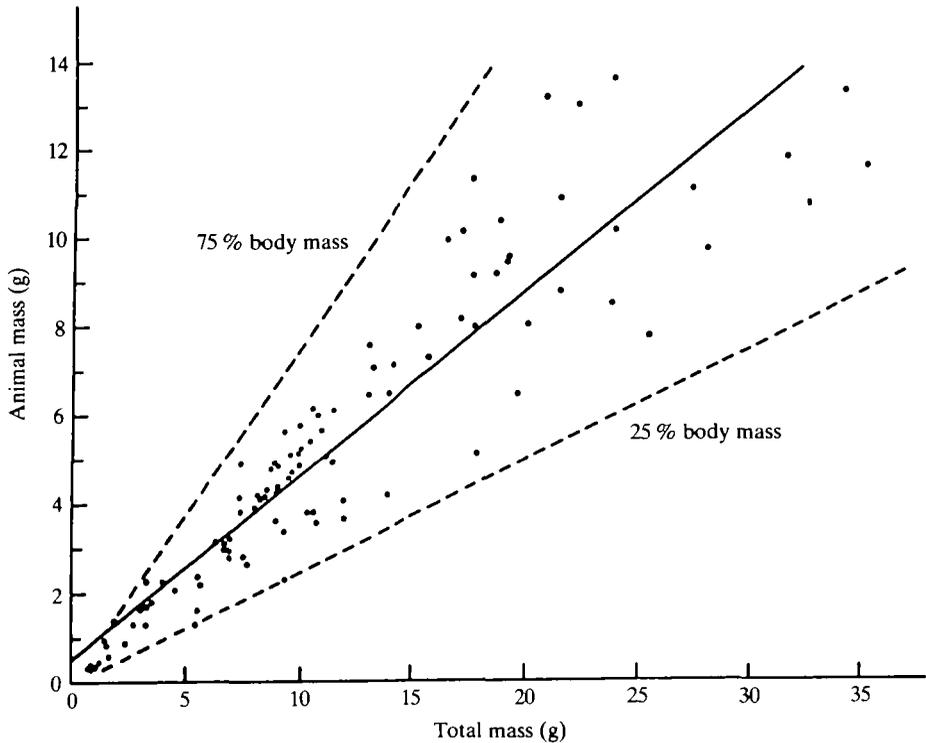
Fig. 2. Hermit crab mass without snail shell compared to the total mass (crab plus shell). Each point represents a single animal. The solid line is the least-squares regression line. The dashed lines indicate where the crab is 25 % and 75 % of the total mass.

direct relationship between animal mass (M) and total mass (animal + shell): the larger the animal, the larger the total mass (T). The regression line showing the relationship between these two variables is $M = 0.52 + 0.41T$; the correlation coefficient is $r = 0.92$.

Fig. 2 shows the high degree of variation in shell and body mass among animals with the same total mass. Indeed, the percentage of body mass varied from 25 to 75 % of the total, with an average being about 47 %. Thus, it was possible to find two crabs of the same body mass, one carrying a shell three times heavier than the other.

Velocity, stride length and step frequency

The velocity on the beach directly depends upon the size of the crab; doubling the linear dimensions of the crab (or doubling the cube root of its mass) approximately doubled the velocity (V) at which the crab freely travelled (Fig. 3). The regression equation is $V = 0.02 + 14M$; $r = 0.77$. Also represented on this figure are data collected in the laboratory for crabs walking over dry sand ($V = 0.01 + 0.07M$; $r = 0.85$). Two points are evident: (1) the velocity in the laboratory increases with body size in the same general way as data collected in the field; (2) the speed of travel on the dry sand in the laboratory is lower than that seen on moist sand in the field.
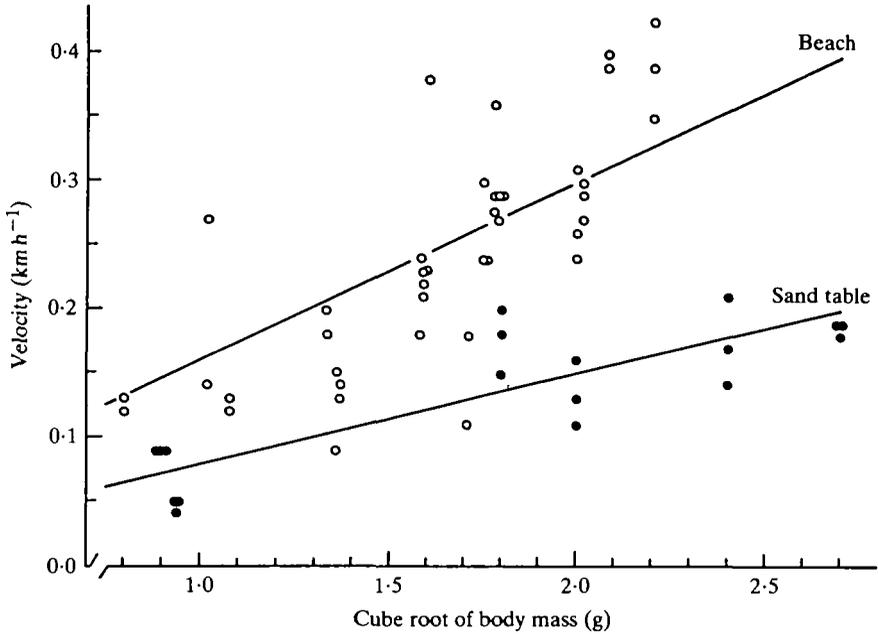
Fig. 3. Velocity of hermit crabs walking on the moist beach and dry sand (sand table) as a function of body size. Cube root of body mass is used as an estimate of linear dimensions. Each point is for a separate crab. The lines are least-squares regression lines.
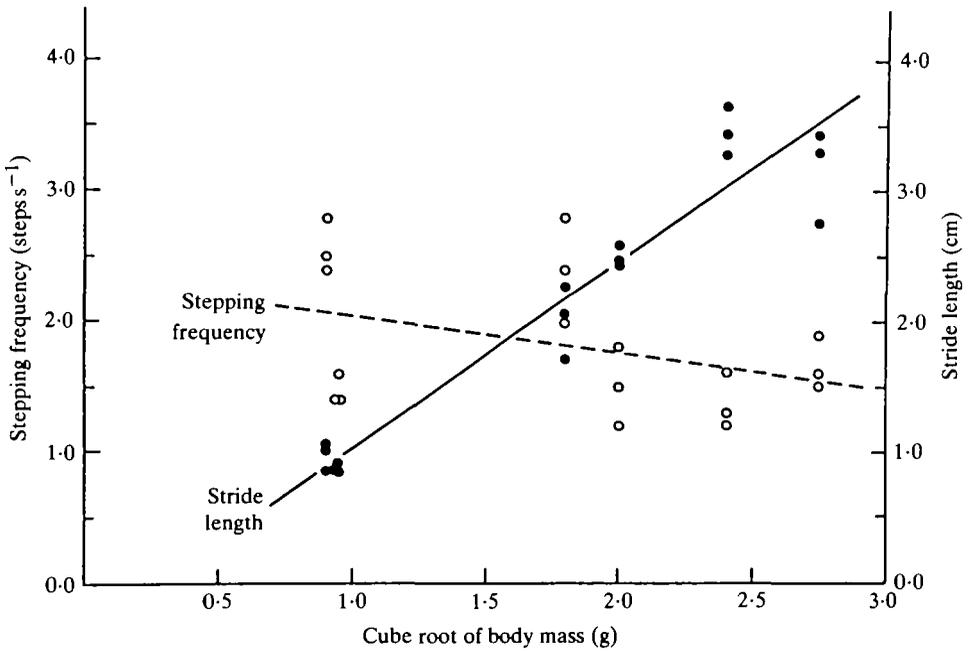

Fig. 4. Stepping frequency and stride length of hermit crabs as a function of body size. Cube root of body mass is used as an estimate of linear dimensions. Each point is for a separate crab. The points are fitted with least-squares regression lines.

This suggests that the energetic requirements for travel over dry sand are increased due to slippage of the substrate.

Fig. 4 represents data taken on stride length (L) and stepping frequency (F) in the laboratory on the sand table. As the size of the animal increases, the stride length increases ($L = -0.04 + 1.43\,M$; $r = 0.96$) whereas a slight decline in the stepping frequency occurs ($F = 2.38 - 0.30\,M$ and $r = -0.39$). A similar pattern is seen for the more limited data collected in the field. Thus the increased velocity that occurs with increased size during voluntary locomotion seems to be the exclusive effect of an increase in stride length; step frequency remains the same or decreases slightly with growth in size.

Fig. 5 indicates that individual hermit crabs on a treadmill increased velocity (V) by increasing both stride length (L) and step frequency (F): $F = 0.69 + 6.4\,V$ ($r = 0.80$) and $L = 1.2 + 8.9\,V$ ($r = 0.8$). The removal of the shell did not seem to affect this pattern: $F = 0.74 + 6.3\,V$ ($r = 0.96$) and $L = 1.2 + 7.6\,V$ ($r = 0.96$). On the other hand, in the field and on the sand table, hermit crabs without shells were much more tentative in their locomotion than crabs with shells. The former moved more slowly, took shorter steps and stopped more frequently than the latter. 'Nude' hermits often walked backwards, with head and chelipeds facing the observer. This type of locomotion was seen only occasionally in hermit crabs with shells in the field.

Amputation studies

Cheliped (L_1 and R_1) removal

Walking was poor in crabs without chelipeds. Although the chelae do not normally seem to give much thrust, they are important supports. The pattern of locomotion is
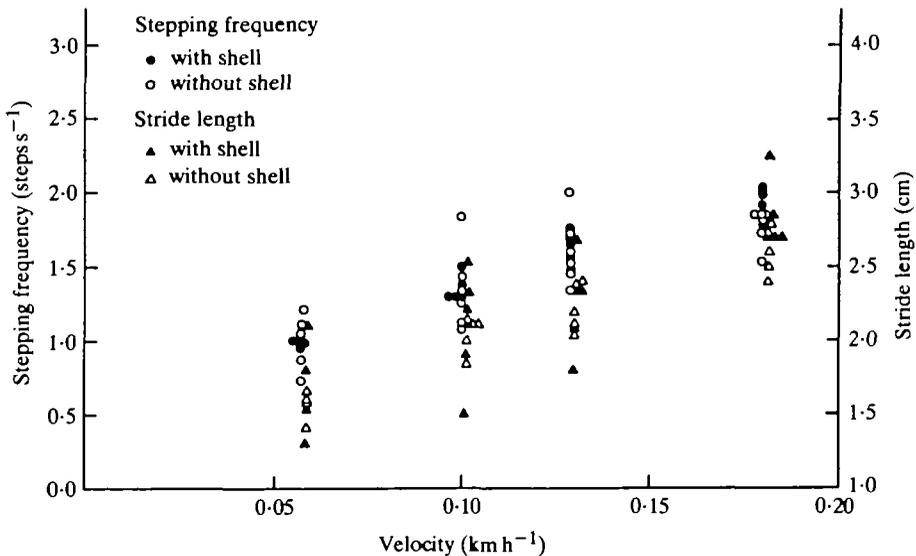

Fig. 5. Stepping frequency (circles) and stride length (triangles) of hermit crabs as a function of velocities on a treadmill. Measurements were taken on the same crabs carrying a snail shell (solid symbols) or walking 'nude' (open symbols) without a load (snail shell).

shown in Fig. 6 along with a simplified version of normal locomotion for comparison. L_2 and R_3 thrust the crab forward as legs R_2 and L_3 are lifted and moved ahead. This is followed by a phase where all four intact legs are on the ground. Then R_2 and L_3 thrust the crab forward as legs L_2 and R_3 are lifted. Again this is followed by a phase where all four legs are on the ground. Thus, just as in normal walking, legs R_2 and L_3 move together and L_2 and R_3 are in synchrony.

Balance is a major problem in crabs lacking chelae. Crabs that maintained their body close to the ground, swinging their limbs in long, arching, lateral power and recovery strokes, and dragged their abdomen along the ground had no real problem with balance. On the other hand, crabs that attempted to walk more normally, abdomen off the ground, moving their legs in closer to the body and walking with limbs more extended, pitched forward when the limbs L_2, R_3 or R_2, L_3 pushed the crab forward. The crab would tip backwards immediately afterwards and before the next forward thrust. As might be expected, this gait is not fast and is irregular. This is the case for most amputations.

First walking leg (L_2 and R_2) removal

Crabs with their first walking legs (L_2 and R_2) amputated were the most accomplished walkers in our ablation tests. This necessitated a change in walking pattern: in contrast to normal walking, L_1 and R_3 were in phase rather than out of phase with each other; the same is true for R_1 and L_3. The resulting diagonal quadrupedal gait pattern is shown in Fig. 6. There were no problems in balance, since the legs amputated were the middle ones, leaving the widest base of support intact.

Second walking leg (L_3 and R_3) removal

Hermit crabs without L_3 and R_3 showed the most diversity in their locomotion patterns. The most common gait used is the 'diagonal quadrupedal gait' shown in Fig. 6. As we saw in the cheliped amputations, this is a modified normal gait: L_1 and R_2 are coupled together and so are R_1 and L_2 just as in the normal tripod pattern. However, there is a balance problem because of the heavy abdomen with the absence of the rear walking appendages. As can be seen in Fig. 6, the crab solved this problem by touching the abdomen to the ground as a support when R_1 and L_2 were lifted. The abdomen was then lifted when all legs are on the ground. Interestingly, when L_1 and R_2 were lifted, the abdomen was not touched down, at least in the animals we observed.

A second gait was used by several animals without L_3 and R_3. This 'rowing gait' is shown in Fig. 6 and again the abdomen plays an important support role. To begin with, all legs and the abdomen are in contact with the ground. Then the walking legs (L_2 and R_2) are picked up together and moved forward to a new position. As they touch down, they lift the front end of the body up along with the chelae, and the crab tilts back, resting much of its weight on the abdomen. Walking legs L_2 and R_2 thrust the crab forwards, the crab tilts forward and the abdomen is dragged. Then the crab stops momentarily as it shifts its weight to the L_2, R_2 and abdomen. The chelae are lifted up and moved forwards and the cycle repeats.
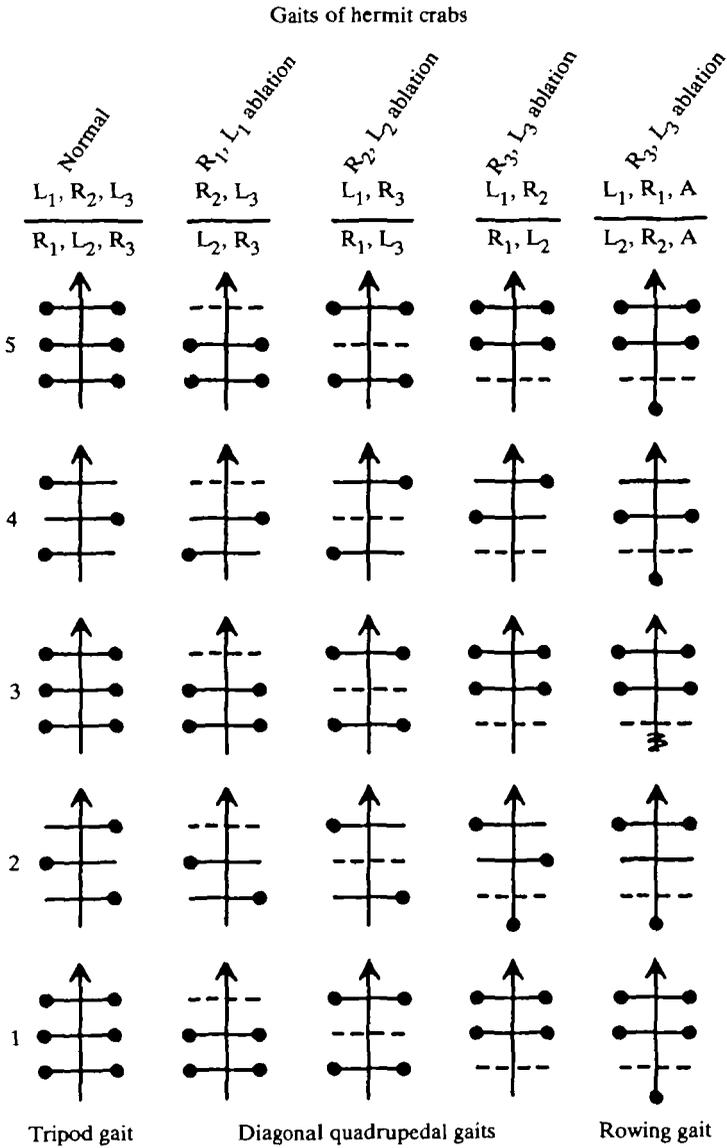
Gaits of hermit crabs

Fig. 6. Stepping patterns of normal and amputated crabs. Each arrow represents the body axis of the crab and shows the direction of movement. The transverse lines on the arrow represent the six appendages used in walking. Dashed lines represent limbs which were amputated. The circles on the ends of the limbs indicate which feet are in contact with the substrate. A circle on the trailing end of the arrow indicates that the abdomen is in contact with the ground. In phase 3 of the 'rowing gait', the irregular end of the arrow indicates the abdomen is dragged across the ground. The letters L and R show left and right limbs, respectively. L_1 and R_1 are chelae; L_2 and R_2 are first walking legs; L_3 and R_3 are second walking legs. Gait patterns are shown in formulae for each animal at the top. Those legs coupled together are written on the same line. Thus in normal crabs, L_1, R_2, L_3 move in synchrony and alternate with R_1, L_2, R_3.

Finally, a third gait was used by one animal on the treadmill for several minutes. It is not represented in Fig. 6, and we call it the 'sideways push–pull gait'. Briefly, the crab is arranged diagonally in the treadmill, right side forward. R_1 is lifted and moved laterally towards the front of the treadmill. This is followed by L_1 and R_2. Finally L_2 moved laterally. Each of these phases is interrupted by a phase when all four legs are on the ground. The major thrust seems to come from L_2 (as it pushes off) and the subsequent pull of R_1. Again, this gait seems to be a simple modification of the normal tripod pattern: L_1 and R_2 are coupled together as usual, and even though R_1 and L_2 are uncoupled, one follows the other in sequence.

DISCUSSION

The six-legged locomotion of the hermit crab, *Coenobita compressus*, resembles the typical insect pattern. The hermit crab moves forward like other crustaceans, such as the lobster and crayfish, rather than sideways, and it has an alternating tripod gait: legs L_1, L_3 and R_2 alternate with R_1, R_3 and L_2. The primary thrust for locomotion seems to be provided by the middle pair of legs (L_2 and R_2), whereas the rear legs (L_3 and R_3) and especially the front limbs (chelae) are used more for support.

Six-legged locomotion in arthropods has evolved several times from ancestors with multiple numbers of limbs (Manton, 1972). Early in this transition there probably was an elongation of legs to increase the speed of locomotion (Hoyle, 1976). This has necessitated a reduction in the number of limbs in order to reduce the interference with one another in their fields of motion. Six-legged animals have reduced this number to the minimum and still have the mechanical advantage of stability. In spite of the many possible gaits using six limbs, the alternating tripod gait is almost always chosen because the centre of gravity is always within the triangular base of support. Consequently, the animal can turn or stop rapidly without losing balance (e.g. Wilson, 1966; Delcomyn, 1981).

Hermit crabs have evolved from ancestral decapods with 10 limbs, eight walking appendages and two chelae. During evolution the last two walking legs have become very reduced and specialized to hold the snail shell. Thus they have come to the hexapodal mode of locomotion by a very different evolutionary route from that travelled by the insects. They seem to have independently evolved the alternating tripod gait for its obvious advantages of stability. Moreover, we noted that the sequence of footfalls on each side runs from posterior to anterior, i.e. once the crab is in motion, we saw the repeating R_3, R_2, R_1 and L_3, L_2, L_1 sequence. This posterior–anterior pattern is frequently encountered among arthropods and may be derived from annelid-like ancestors.

Limb loss in arthropods is a common occurrence; it may occur during moulting, fighting, escape from getting caught in narrow crevices, or from predators. Investigators have been impressed with the rapid adjustment that arthropods make in their pattern of locomotion once the leg number has been altered. We noted such an

adjustment in the hermit crabs when the first walking legs (R_2, L_2) were amputated from both sides. If the crab had maintained its normal walking mode R_3, L_2, R_1/R_2, L_1, L_3, the crab with only four limbs left would have undoubtedly lost its balance since two limbs on the same side would be lifted simultaneously. Instead, the crab shifted to a diagonal quadrupedal gait R_3, L_1/R_1, L_3, alternately lifting two diagonal limbs together. This is the most stable pattern for quadrupeds walking fast and it is typical for mammals and for insects with their mesothoracic legs removed (e.g. Hughes & Mill, 1974). Such rapid change in walking after amputation has been considered evidence that proprioceptive input plays an important role in altering the neural central programme generator for locomotion.

Another indication of the adaptability of the locomotor system in hermit crabs is seen in the several cases where a rowing gait was employed (Fig. 6). Some crabs with their second walking leg (R_3, L_3) removed used the abdomen as a support; R_1 and L_1 were coupled together in their movements as were R_2 and L_2.

As might be predicted, not all amputations required a change in footfall sequence. In two of our amputation patterns no change in footfall pattern occurred. Bilateral ablation of either the chelae (R_1, L_1) or the second walking legs (R_3, L_3) necessitated no change from the basic pattern of walking (R_3, L_2, R_1/R_2, L_1, L_3). Note that in each case the crab could still keep its original stepping sequence and be reasonably stable. The two legs that would remain on the ground as supports during quadrupedal locomotion were always in diagonal positions on opposite sides of the body, thus giving the most stable support. Thus the removal of R_1, L_1 still leaves R_3, L_2/R_2, L_3 and removal of R_3, L_3 leaves L_2, R_1/R_2, L_1 cycling as before amputation. However, even in these conditions there are alterations in balance such that we can expect significant increases in energy expenditure during locomotion.

Adult hermit crabs are somewhat asymmetrical although their larvae are bilaterally symmetrical. The asymmetry appears during development and ultimately extends to their neuromuscular systems (Chapple, 1977). *Coenobita compressus* has its abdomen displaced to the right to match the curvature of the snail shells (e.g. *Nerita*) which it occupies. Our observations indicate that this hermit crab compensates for the asymmetry of the shell it carries by morphological and behavioural mechanisms. The left appendages are enlarged and elongated compared to the right. The left limbs are often extended more laterally, while the right are positioned under the body. Chapple (1973) has considered the problem of asymmetry in the hermit crab *Pagurus pollicarus*. The crab carries its shell at a relatively constant position above the substrate but this position is a direct function of the mass of the shell. The abdomen and the right, fifth pereiopod lift the shell with the abdomen giving about one-tenth of the total lift. At rest with the shell on the ground, its centre of gravity is shifted to the right, where the fifth pereiopod makes contact. When the crab lifts the shell, the centre of gravity is shifted towards the midline with the fifth pereiopod serving as a lateral strut and the major support. The abdomen's major role is the maintenance of position.

During locomotion the hermit crab keeps its shell in a relatively constant position according to Chapple's (1973) data. We have had similar experiences except that

small crabs clearly have major oscillations during walking and crabs with relatively large shells drag their shells. Chapple (1973) argued that the abdomen acts as a passive spring system, with the spring constant under moment-to-moment adjustment by abdominal musculature and especially the fourth pereiopod in the reflex regulation of shell position. One would predict on the basis of such considerations that a significant portion of energy might be utilized for the postural control of the shell (see Herreid & Full, 1986).

Snail shells are in short supply and hermit crabs compete for this limited resource (Abrams, 1978; Bertness, 1981a). The crabs often occupy shells that appear less than optimum in shape or size. We noted a three-fold variation in the shell size carried by two individuals of the same 'nude' body mass (Fig. 2). Since shell size partly determines the energy used in locomotion, it is to the crab's benefit to carry the smallest shell that is compatible with growth, development and protection. It is noteworthy that hermit crabs have compensated for this extra load in that they have a partly decalcified exoskeleton and thus reduce their own body mass. Also, they compensate by reducing the mass of the snail shell, by chemical or mechanical abrasion, thus enlarging the effective shell size (Abrams, 1978). Moreover, although this hermit crab has been found using at least 30 species of snail shells, they prefer those of the lightest genus, i.e. *Nerita*, even though this shell confers less protection and holds less water than many others (Abrams, 1978; Bertness, 1981a,b).

The velocity of locomotion as measured by the free-walking crabs on the beach and in the laboratory ranged from $0.1 \, \text{km h}^{-1}$ to $0.4 \, \text{km h}^{-1}$. Velocity is a function of the substrate; on moist, packed sand, crabs travel more rapidly than on loose, dry sand (Fig. 3). Velocity is also a function of body size (Figs 3, 4); large crabs travel more rapidly than small ones because of differences in stride length (Fig. 5). Doubling the length of the legs causes a doubling of the free-walking speed. Thus, a large crab in contrast to a small one typically takes less time to travel from point to point and potentially is exposed for shorter periods of time to predators and environmental extremes.

There is considerable variation in speed among crabs of the same size, and, of course, there is variation in speed of an individual. For example, our experiments with a treadmill showed that individual crabs of 2-g body mass travel over a range of speeds up to $0.2 \, \text{km h}^{-1}$, which is comparable to the fastest steady locomotion on a moist beach. Such velocities could be sustained for at least 20 min. Higher speeds for crabs of this size could neither be induced in the laboratory nor stimulated in animals in the field. Our attempts to startle crabs into sprints were unsuccessful since the animals simply stopped and retreated into the shell. Similar experiments with 2-g fiddler crabs (Full & Herreid, 1984), which rely upon speed and agility to escape predators, had quite different results. We noted *Uca pugilator* could also travel at $0.2 \, \text{km h}^{-1}$ but they could run twice as fast for about 3 min and sprint at much higher speeds for a few seconds. This behaviour is essential if fiddler crabs are to dash back to their burrow to escape predators. Thus, it seems that hermit crabs have specialized in slow endurance locomotion while carrying a heavy load and have traded off sprinting behaviour for the protection of a mobile home.

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