

ADAPTIVE CHANGES IN LOCUST KICKING AND JUMPING BEHAVIOUR DURING DEVELOPMENT

ALEX P. NORMAN*

Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK

Accepted 9 February 1995

Summary

The hind, or metathoracic, leg of a locust is specialised, enabling it to store energy that is used to extend the tibia rapidly during kicking and jumping; behaviours which share a common motor pattern. This study describes developmental changes in kicking and jumping behaviour and relates these changes to the development of the exoskeleton and jumping performance. In mature adults and intermoult larvae, the exoskeleton is strong and kicks can readily be elicited. Before and after the adult moult, when the exoskeleton is weak, kicks can be elicited less frequently, thus avoiding skeletal damage. At these times, animals do not generate the adult motor pattern for kicking, so that extension of the tibia is powered by direct muscle contraction, rather than through the release of stored energy. The muscles of all newly moulted animals are capable of generating sufficient force to damage the leg, but 14 days later the muscles can rarely generate sufficient force to damage the leg.

To mimic the forces generated during the preparation for a kick, when the flexor and extensor tibiae muscles co-contract, the extensor muscle was stimulated electrically at a range of frequencies and the nature and occurrence of the resulting mechanical damage to components of the skeleton were assessed over a 14 day period following the

adult moult. In newly moulted animals, the proximal femur partially collapses and thus protects the leg from damage before the muscles generate sufficient force to damage chronically other components of the leg. This partial collapse of the femur is reversible when the extensor muscle is activated at low frequency, but high frequencies cause permanent damage. The muscles of all animals 1 day after the moult are also capable of generating sufficient force to damage the leg, but the proximal tibia breaks most commonly in the region where the extensor muscle apodeme attaches. 5 days after the moult, the muscles in only 50% of animals can damage the leg and most commonly the extensor muscle apodeme breaks. In mature animals, the only structure that fails is the extensor muscle apodeme, which fractures close to its point of attachment to the tibia. Damaging a metathoracic leg can significantly decrease the ability of a locust to jump and to compete for mates. Changes in the likelihood of damage to a metathoracic leg occur at predictable stages of development. Locust behaviour is modified during development, avoiding such damage.

Key words: motor pattern, jump, kick, development, exoskeleton, insect, behaviour, grasshopper, *Schistocerca gregaria*.

Introduction

The ability to avoid predators and engage successfully in aggressive encounters with rivals is important to an animal's survival. This behaviour is not constant during development, especially in arthropods which must moult in order to grow. Around the time of the moult, the exoskeleton is susceptible to damage, but the likelihood of damage can be reduced by adopting behavioural strategies appropriate to the developmental stage of the animal (Cromarty *et al.* 1991; Tamm and Cobb, 1978; Steger and Caldwell, 1983; Adams and Caldwell, 1990).

Locusts kick and jump to avoid predation, but jumping performance changes during a moult cycle (Gabriel, 1985*a,b*;

Queathem, 1991). In insects specialised for jumping, energy generated by the muscles is stored, thus enabling the available power to be amplified (e.g. locust: Heitler, 1974; flea: Bennet-Clark and Lucey, 1967; click beetle: Evans, 1972). The metathoracic (hind) leg of the locust is mechanically specialised to store energy, which is used to extend the tibia rapidly in kicking, jumping, swimming and launching into flight. Initial flexion of the femoro-tibial joint is followed by a period of co-contraction of both the flexor (FITi) and extensor (ETi) tibiae muscles, enabling the extensor to develop maximum tension and energy to be stored in specialised structures in the leg. This stored energy is released when the

*Present address: Department of Zoology, School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK.

flexor is inhibited, thus allowing the tibia to extend much more rapidly than it could if it were driven by direct muscle action alone (Bennet-Clark, 1975; Heitler, 1974, 1977). The main sites of energy storage are the ETi apodeme and the semilunar processes. Fibres of the extensor muscle insert onto the apodeme along most of the length of the femur before it attaches onto the proximal tibia. The semilunar processes are paired ridges of thickened cuticle in the distal femur, near the point of articulation with the tibia, that store strain energy during muscle co-contraction by bending. A small amount of additional energy is stored in the femur, in the region where the ETi muscle inserts proximally, and in the tibia, which bends during co-contraction and can therefore recoil like a spring (Katz and Gosline, 1992).

The safety factors of the energy storage components of the locust metathoracic leg are extremely low, ranging between approximately 1.2 and 2.0 (Bennet-Clark, 1975). The forces generated during kicking by locusts are only slightly smaller than those necessary to break cuticular components of the femoro-tibial joint. 'Safety factor' is an engineering term for the ratio between the load that would break a structure and the maximum predicted load. Alexander (1981, 1984) proposed that evolution of the safety factor of skeletal structures depends both upon the costs of growth and use of the skeleton and upon the probability and costs of failure. In a comparative study, Brandwood *et al.* (1986) argued that data from a range of taxa confirmed Alexander's predictions. The incidence of healed fracture was found to be higher in molluscs, where the costs of failure are likely to be low, than in mammals and birds, where they argue that the costs are likely to be higher. There appear to be no data available on the incidence of fracture in arthropods. If chitin synthesis is prevented following the adult moult in locusts, the hind leg breaks when a kick is generated (Ker, 1977). Two types of hypothesis have been proposed to explain the extremely low safety factors in the locust metathoracic leg. First, proprioceptive afferents, which monitor strain in the cuticle as a result of the forces generated by the muscles, could regulate the activity of the muscles (Burrows and Pflüger, 1988). This feedback may prevent the muscles from exerting sufficient force to damage the leg. Second, energy storage is optimised in structures that have low safety factors. The evolutionary drive behind the low safety factors in the locust metathoracic leg may be that energy storage is optimised (Alexander, 1981).

In the light of the known developmental changes in locust jumping performance (Gabriel, 1985*a,b*; Queathem, 1991), and in the deposition and reabsorption of the exoskeleton during a moult cycle (Andersen, 1973, 1974), it is necessary to determine whether behaviour is also modified. It might be expected that moulting increases the risk of damaging the leg when generating a jump. Is locust behaviour modified during development so that damage to the leg is prevented? This study analyses the changes in locust kicking behaviour that occur during development and assesses the risks and costs of damaging a hind leg, to determine how flexibility in this behaviour is adaptive.

Materials and methods

Final-instar locusts, *Schistocerca gregaria* (Forskål), were taken from a crowded culture and kept individually in compartments (10 cm×15 cm×15 cm) so that the day on which each animal moulted to adulthood was known. To maintain the animals in gregarious phase, the compartments were constructed from wire mesh and were situated adjacent to each other so that air could move freely between the animals.

Behaviour

A standard paradigm was designed to compare the probability with which animals would kick at different stages of the moult cycle. Each animal was stroked 10 times at a fixed site on the wings with a small paintbrush (Fig. 1A), and its responses were recorded. The number of kicks evoked in animals of each age was used to calculate the relative frequency of kicking over the moult cycle. To confirm that the observation of kicks accurately reflected the generation of the motor pattern of the kick (Heitler and Burrows, 1977), electrical activity in the flexor and extensor tibiae muscles during the moult cycle of a second series of animals was recorded, whilst movement about the femoro-tibial joint was monitored (Miall and Hereward, 1988).

Mechanical failure of the metathoracic leg

The pattern of activity of the muscles involved in generating the kick was mimicked by electrically stimulating the ETi muscle, and the resultant forces were measured. Animals at a range of ages were restrained ventral side uppermost in Plasticine with the left metathoracic femur fixed anterior side uppermost and the femoro-tibial joint free to move. A window of thoracic cuticle was removed to expose the metathoracic ganglion, and nerves 3 and 5 (Campbell, 1961) were cut to denervate the distal parts of the leg. The exposed tissue was covered with a mixture of Vaseline and paraffin oil to prevent desiccation. A window of cuticle approximately 0.5 mm×1.0 mm was removed from the antero-distal femur and the FITi apodeme was cut. This was necessary because the ETi muscle could not be selectively stimulated, because electrical stimulation could also excite the FITi muscle. The window was sealed with a wax/resin mixture. The few experiments in which mechanical failure of the leg occurred in the region of the window as a result of this surgery were discarded. Damage to structures in other regions of the leg did not occur as a result of surgery.

To stimulate the ETi muscle, two 50 µm diameter silver wires were inserted into the muscle through pinholes made in the cuticle at fixed sites. Stimuli were controlled using a BBC computer. A force transducer was positioned perpendicular to the tibia to measure relative ETi tension. The femoro-tibial joint was positioned at 15° and the distal tibia (2–3 mm proximal to the distal end of the tibia) was attached to the force transducer with a wax/resin mixture (Fig. 2A). During the co-contraction phase of a kick, the fast extensor tibiae motor neurone, which innervates the ETi muscle, spikes at a maximum frequency of 100 Hz (Heitler

and Burrows, 1977). To produce a range of forces in the leg, up to the maximum that the muscles can generate, the ETi muscle was therefore stimulated at a range of frequencies between 5 and 100 Hz, for periods between 1.0 and 1.3 s, while the forces generated were measured. Locusts were used at four ages after the adult moult (0, 1, 5 and 14 days). Ten animals were tested at each age. Failure of the ETi apodeme was accompanied by a loud snapping sound, and the nature of any damage was confirmed by dissection. Data were stored on magnetic tape (Racal store 4) and displayed on a Gould digital oscilloscope and chart recorder. The significance test used throughout was a Student's *t*-test and values are given as mean \pm S.E.M.

The incidence of skeletal damage in the locust

The incidence of non-fatal skeletal damage incurred during an animal's life was assessed by placing 100 first-instar animals in a communal cage. The 67 animals which survived

to sexual maturity were examined, and the number of missing limbs and limb segments was recorded and used to calculate the percentage of animals showing different types of damage. In order that a comparison could be made with published data, the fracture incidence (*p*), or the ratio between the number of fractures and the number of major limb segments (femur and tibia) was calculated after Brandwood *et al.* (1986).

The consequences of skeletal damage

A comparison was made between the jumping ability of intact animals and that of animals that were missing one metathoracic leg. Sixteen male animals were taken from a crowded culture shortly after the adult moult, and autotomy of the left metathoracic leg was induced in half of them by touching the leg with a hot wire. Intact and autotomised animals were placed in a communal cage until sexual maturity. The wings were fixed closed with adhesive tape and animals were induced to jump by touching their wings. Each animal

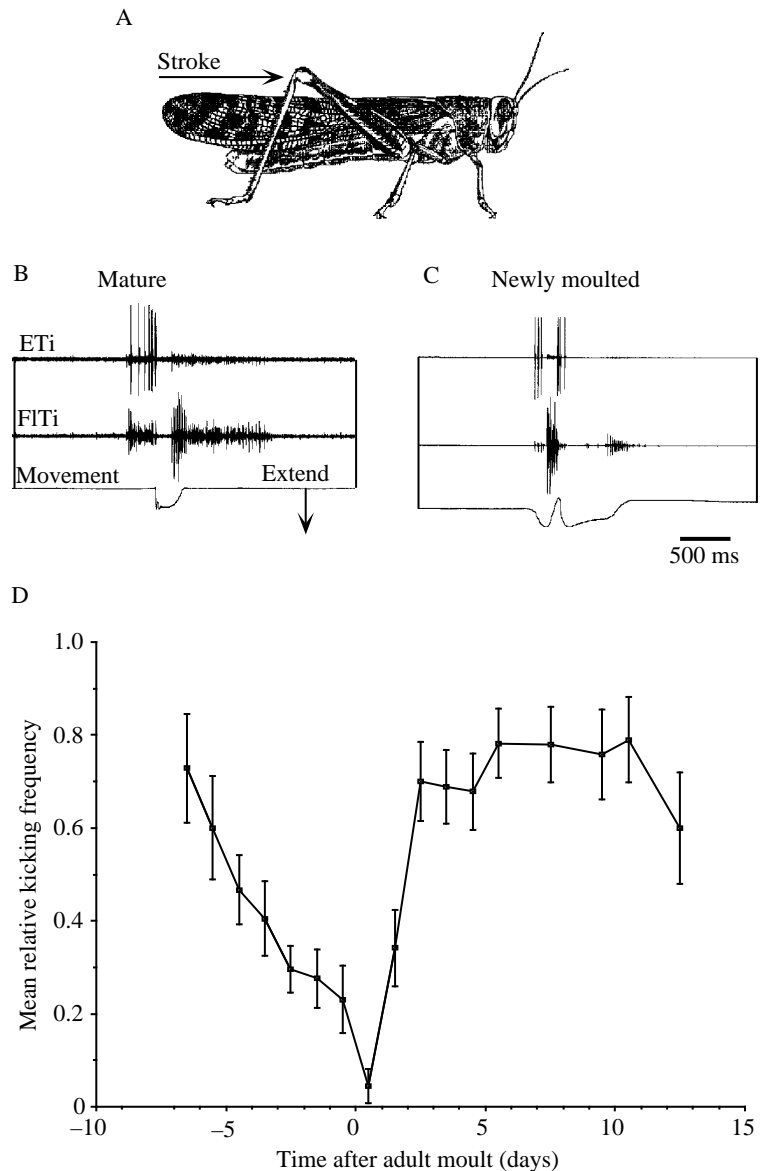


Fig. 1. (A) Kicks were elicited by stroking animals with a small paintbrush, in the direction indicated by the arrow. Myogram recordings of the activity of the extensor (ETi) and flexor (FITi) tibiae muscles whilst movements of the metathoracic leg were monitored showed that on the day of the moult animals did not kick. (B) A kick generated by a 3-day-old animal in which a period of co-contraction was followed by a very rapid extension of the leg. Scale bar refers to B and C. Arrow shows direction of extension and applies to B and C. (C) Newly moulted animals did not kick but did alternately extend and flex the leg. Co-contraction did not occur, so extension here was much slower than in older animals. (D) The relative frequency with which kicks were elicited declined gradually as the adult moult (day 0) approached. Maximum kick frequency was reached 3 days after the moult and remained constant on subsequent days (mean \pm S.E.M., $N=7-25$).

was weighed, its first jump measured and the energy used was calculated using the method of Bennet-Clark (1975).

The ability of intact and autotomised male locusts to compete for mates was compared by placing 10 intact males, 10 males which had autotomised their left hind legs (see above) and 10 intact females in a communal cage shortly after the adult moult. Once sexual maturity had been reached, the animals were inspected daily for 4 days, copulation lasted for 3–14 h (*The Locust Handbook*, 1971), and the proportion of intact and autotomised males which were mounted on females was recorded.

Results

Changes in kicking behaviour during development

When the cuticle was hard, stroking the wings (Fig. 1A) readily elicited powerful kicks which had a characteristic motor pattern; newly moulted animals did not kick. Six newly moulted locusts and six locusts that had moulted 3 days earlier were stroked 10 times with a small paintbrush whilst the electrical activity of the ETi and FITi muscles and movements about the femoro-tibial joint were monitored. The proportion of kicks generated by locusts of each age was used to calculate the relative frequency with which kicks were generated. There was a significant difference ($P < 0.01$) between the responses of newly moulted locusts, which never kicked (mean relative kick frequency \pm S.E.M., 0.00 ± 0.00), and 3-day-old animals, which commonly kicked (0.27 ± 0.04). In mature animals, the ETi and FITi muscles co-contracted, and the kick was triggered following inhibition of the FITi muscle, allowing the tibia to extend very rapidly (Fig. 1B). The motor pattern elicited in newly moulted animals by the same stimulus differed from that

seen in older animals (Fig. 1C). Co-contraction did not occur; instead, alternate bouts of activity in the FITi and ETi muscles generated alternate flexion and extension movements of the leg. Extension of the leg was driven by direct muscle action alone, so the movement was much slower than in the kicks generated by mature animals in which stored energy was also released.

The relative frequency with which tactile stimulation could elicit kicks between 7 days before and 12 days after the adult moult was assessed by tactile stimulation, as described above, but kicks were detected visually rather than by recording the activity pattern of the muscles. The relative frequency of kicking declined gradually over a period of days approaching the adult moult and then reached a maximum frequency again within 3 days following the moult (Fig. 1D, $N = 7$ –25 locusts on each day).

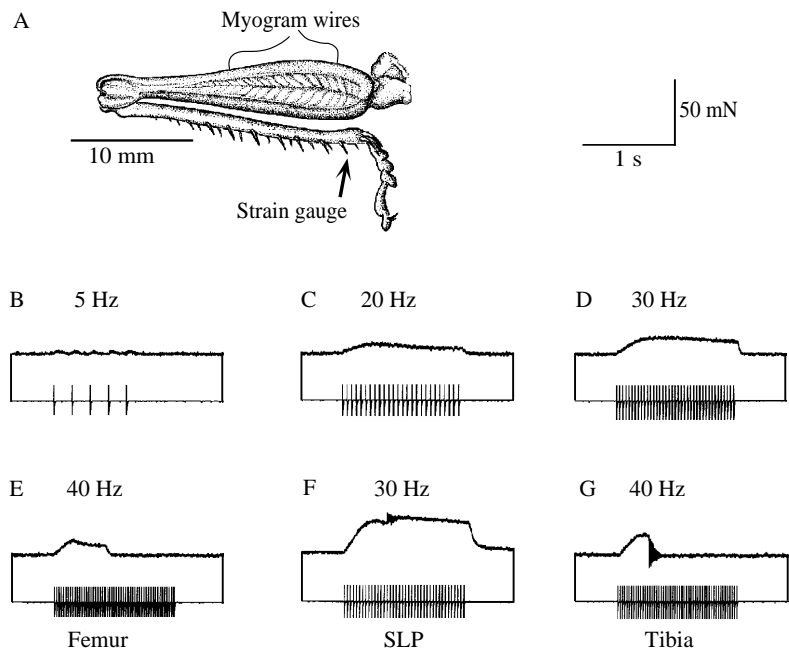
Failure of the metathoracic leg

Mimicking the pattern of activity of the muscles involved in generating the kick in animals at a range of ages indicated that the nature and frequency of mechanical failure of the leg was characteristic for each age, and that the forces generated by newly moulted animals were significantly less than those generated by older animals.

Day 0

In all animals tested on the day of moulting, stimulating the ETi muscle (Fig. 2A) generated sufficient force to damage the leg in one of three ways. The force generated by the ETi muscle increased as the stimulus frequency was increased (Fig. 2B–D), until the inward component of the force was sufficient to cause the anterior and posterior faces of the

Fig. 2. Stimulation of the ETi muscle while holding the tibia flexed simulated co-contraction. (A) The leg was restrained by its attachment to the strain gauge (indicated by an arrow). (B–D) In a newly moulted animal, the force transmitted by the tibia (upper traces) increased as the stimulus frequency (lower traces) was increased from 5 to 30 Hz until, as shown in E, the proximal femur collapsed in the region of the ETi muscle attachments at a stimulus frequency of 40 Hz. This was the most common failure at this age. Following failure of the femur, there was a decline in the force transmitted by the tibia even though the stimulus persisted. Two less common types of failure were also observed at this age and are shown in F and G. (F) Following failure of the semilunar processes (SLP), force continued to be transmitted by the tibia, although there was a small deflection of the force record when the energy stored in the SLP was released. (G) Failure of the proximal tibia occurred very rapidly and force was then no longer transmitted to the strain gauge because the muscle was detached from the tibia. The high-frequency oscillation of the force record following this failure was produced by oscillations of the strain gauge. B–E are from a single locust; F and G are from different individuals.



proximal femur to collapse inwards in the region of the point of attachment of the ETi muscle (Fig. 2E). At low stimulus frequencies, the femur recovered once the stimulus ceased, but at high stimulus frequencies (40 Hz in Fig. 2E) the collapse could cause permanent damage, so that the femur did not recover its original shape. Once the femur had failed, little force was generated in the presence of the stimulus, presumably because the inward movement of the anterior and posterior faces of the femur was sufficient to encompass a large proportion of the range of movement of the ETi muscle fibres. Damage of this nature was the most common failure at this age. Less commonly, the semilunar processes (SLP) snapped and the stored energy that was released caused a small deflection of the force record (Fig. 2F). Following failure of these important energy stores, force continued to be transmitted to the tibia because the muscle still had functional attachments at both ends. In the third type of failure, the force declined very rapidly when the proximal tibia broke in the region of the attachment of the ETi apodeme (Fig. 2G). Following this type of damage, no further force was detected because the muscle was detached from the tibia.

Day 1

One day after the moult, stimulating the ETi muscle still caused mechanical failure of the legs of all animals tested. As the stimulus frequency was increased, the force produced by the leg increased (Fig. 3A–C). The most common failure was a break in the proximal tibia in the region of the ETi apodeme attachment (Fig. 3D), leading to a rapid decline in force, similar to that seen when this type of damage occurred in newly moulted animals. Other types of failure were observed less often. Failure of the ETi apodeme resulted in a rapid decline in force similar to that following failure of the tibia (Fig. 3E). When the semilunar processes snapped, the energy stored in them was lost, causing a small deflection of the force record, but force continued to be transmitted to the tibia (Fig. 3F). The proximal femur never failed at this age.

Day 5

Five days after the moult, stimulating the extensor muscle caused failure in only 50% of legs. As the stimulus frequency was increased, the force generated by the leg increased to a maximum (Fig. 4A–D), beyond which further increases resulted in the production of slightly less force (Fig. 4E). Two types of damage were observed in the legs that failed: failure of the ETi apodeme (Fig. 4F) or of the proximal tibia (Fig. 4G). Both types of failure were followed by a characteristic rapid decline in force. The semilunar processes and the proximal femur never failed at this age.

Day 14

By day 14 following the moult, the majority of legs (80%) remained intact throughout the full range of stimulus frequencies used. Again, as the stimulus frequency was increased, the force produced by the leg increased to a maximum (Fig. 5A–D); further increases resulted in the production of slightly less force (Fig. 5E). The only type of damage to the leg that was observed at this age was failure of the extensor apodeme (Fig. 5F).

The susceptibility of a hind leg to damage as a result of force generated by the muscles, therefore, declined over a 14 day period following the adult moult. On the day of moult and on the subsequent day, all animals were capable of generating sufficient force to damage the leg. Damage occurred in only 50% ($N=10$ for all incidents of stimuli-induced damage) of animals 5 days after the moult and 20% of animals 14 days after the moult ($N=10$ for all ages, Fig. 6A). The nature of the most common damage also changed during this period. On the day of moult, most commonly the femur collapsed (70%), less commonly the tibia snapped (20%) or, least often, the semilunar processes broke (10%). One day after the moult, the tibia broke in 80% of animals, the semilunar processes broke in 10% and the ETi apodeme broke in 10%. Five days after the moult, the ETi apodeme broke in 40% of animals and the tibia broke in 10%. Fourteen days after the moult, the ETi

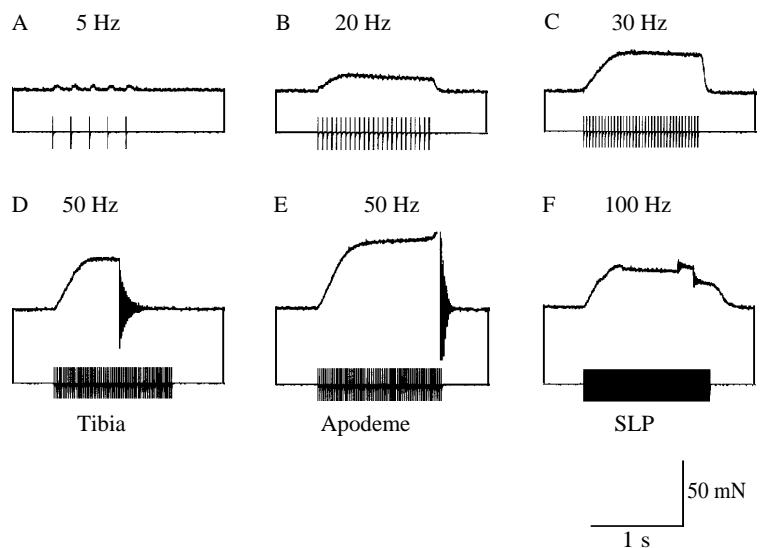


Fig. 3. In animals 1 day after the moult, mechanical failure of the leg occurred in characteristic ways which differed from failures in newly moulted animals. (A–D) As the stimulus frequency was increased from 5 to 50 Hz (lower traces), more force was generated (upper traces) until, at 50 Hz (D) the proximal tibia snapped. This was the most common failure at this age. (E) Less commonly, the ETi apodeme snapped and force was no longer transmitted to the strain gauge. (F) As in newly moulted animals, failure of the semilunar processes (SLP) was accompanied by a small upward deflection of the force record as their stored energy was released. A–D are from a single locust; E and F are from different individuals.

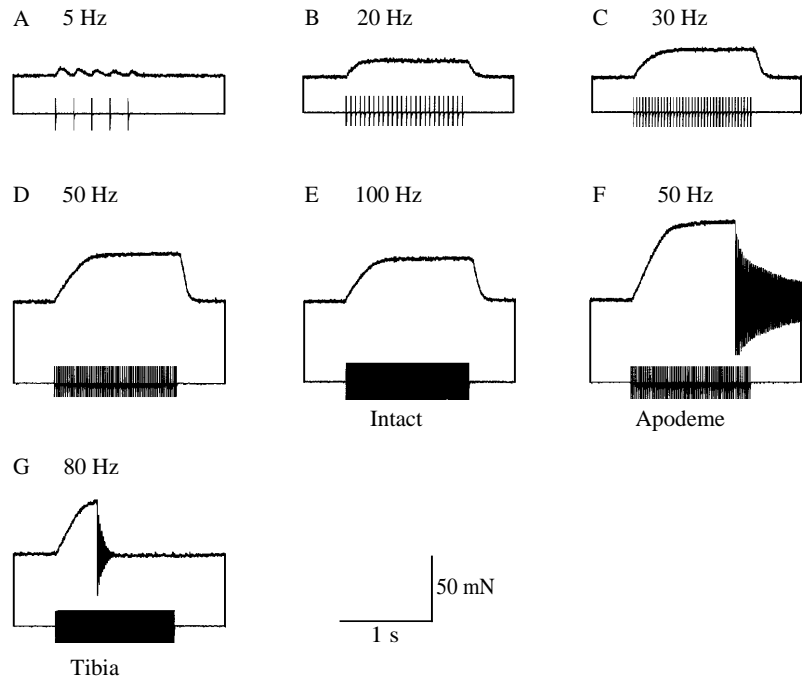


Fig. 4. In animals 5 days after the moult, electrical stimulation of the ETi muscle did not always result in failure of the legs. (A–D) Increasing the stimulus frequency from 5 to 50 Hz (lower traces) resulted in an increase in the force generated (upper traces), with force reaching a maximum at 50 Hz. (E) On a further increase in stimulus frequency to 100 Hz, there was a slight decline in the amount of force generated. Failures of either the ETi apodeme (F) or the proximal tibia (G) resulted in a rapid decline in force. A–E are from a single locust; F and G are from different individuals.

apodeme broke in 20% of animals and no other type of damage occurred (Fig. 6A). At all stimulus frequencies above 5 Hz, newly moulted locusts generated less force than all older groups of locusts (Fig. 6B). 14-day-old locusts produced a peak force at a stimulus frequency of 50 Hz. The force produced by the leg at 30 Hz was significantly less on day 0 than on subsequent days ($N=10$, $P<0.01$). The force at which failures did occur also changed over this period. The force at failure was significantly less on the day of moult (16.7 ± 2.0 mN) than on the following day (42.2 ± 2.0 mN, $N=10$, $P<0.01$) and increased gradually over a 14 day period following the moult (Fig. 6C).

The incidence of skeletal damage in the locust

During a locust's life, accidental damage to the skeleton was common. 45% of animals which survived to sexual maturity (i.e. 30 out of 67 survivors, from an initial group of 100) in a crowded colony sustained skeletal damage, much of which was relatively minor. Animals which had damaged any part of their skeleton were included in this category (Fig. 7A). In 9% of surviving animals, however, at least one metathoracic leg was missing. In 1%, both metathoracic legs were present, but at least one was damaged sufficiently for it to be dysfunctional. Severe damage was defined as functional loss of a metathoracic leg due to damage sustained to either a femur or tibia, or loss of the entire

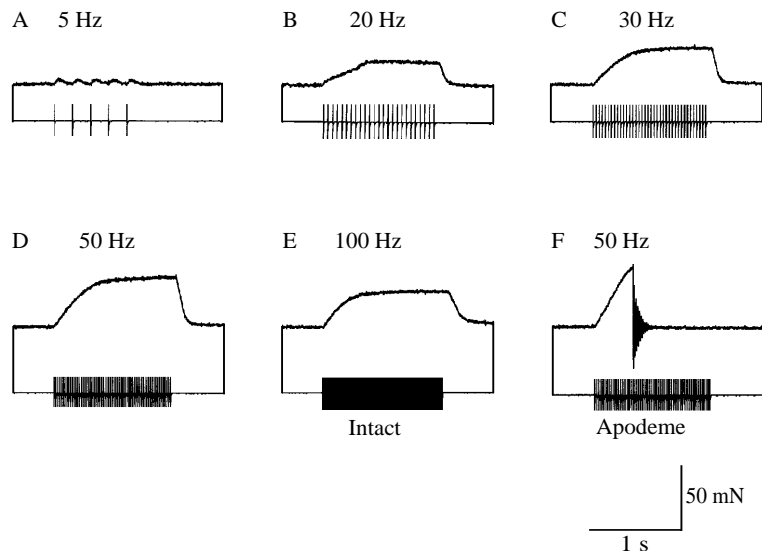
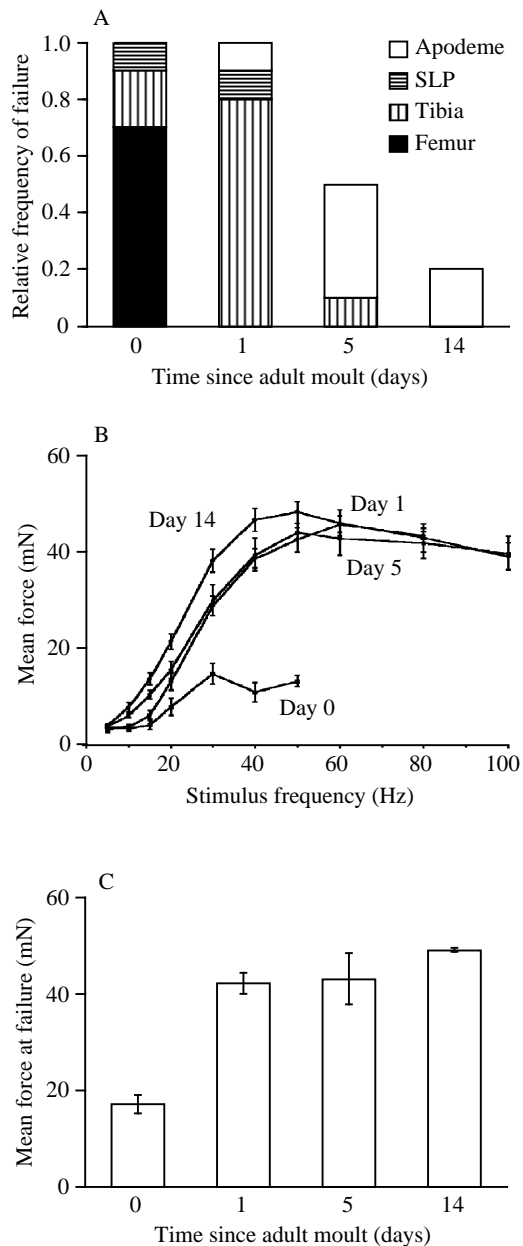


Fig. 5. In animals 14 days after the moult, electrical stimulation of the ETi muscle rarely resulted in mechanical failure of the leg, and the ETi apodeme was the only structure to fail. (A–D) As the stimulus frequency was increased from 5 to 50 Hz (lower traces), the force generated increased (upper traces). Further increases in stimulus frequency resulted in a slight decline in force (E). (F) Failure of the ETi apodeme resulted in a rapid decline in force. A–E are from a single locust; F is from a different individual.

leg at the autotomy plane. Minor damage to the metathoracic leg was defined as damage to the distal leg segments (i.e. tarsus and unguis) and was more common (6%) than severe damage. The fracture incidence of the major limb segments of any of the three pairs of legs, as calculated by the method of Brandwood *et al.* (1986; see Materials and methods) was 0.016 and that of the major leg segments of the metathoracic leg was 0.037.

The consequences of skeletal damage

Autotomy of one metathoracic leg significantly decreased both the ability to generate powerful jumps and the ability to compete for mates. The incidence of skeletal damage amongst males mounted on females was recorded in the colony of 67 locusts described above. One or both of the metathoracic legs of four of the 32 surviving males had been severely damaged.



None of these four males was observed to be mounted on females when their state of skeletal damage was recorded, whereas nine of the other 28 males without severe damage to a metathoracic leg were mounted on females. In contrast, three of the 35 surviving females had incurred severe damage to one or both metathoracic legs, but two of these were mounted by males. To confirm that there was a reduction in the success of damaged males in comparison with intact males in competing for mates, an artificial population bias towards males was created. Ten intact males, 10 males which had autotomised their left metathoracic leg, and 10 intact females were placed in a communal cage and, once sexual maturity had been reached, they were inspected daily for 4 days and the incidence of mounted males recorded. This competition amongst males revealed that autotomised males spent less time mounted on females ($P < 0.05$, Fig. 7B). Autotomy of one metathoracic leg reduced access to females by 43%. This may have been due to a decrease in the ability to fend off rival males directly resulting from having only one hind leg for kicking. Autotomised males may also have been poorer at competing for food, and hence weaker.

The energy produced when jumping by animals that had one metathoracic leg autotomised was 40% less than that produced by intact animals ($N=8$, $P < 0.01$, Fig. 7C), although the jump range only decreased by 27%. This discrepancy between the reduction in available energy and the reduction in jump range may have been due, in part, to the decrease in mass of autotomised animals, which weighed 16% less (presumably the mass of the missing leg) than intact animals ($N=8$, mean mass \pm S.E.M.; intact, 1.76 ± 0.08 g; autotomised, 1.48 ± 0.05 g).

Fig. 6. The nature and frequency of mechanical failure of the leg and the forces generated by the leg when the ETi muscle was electrically stimulated changed during a 14 day period following the adult moult. (A) During the first 2 days after the moult, the muscles of all animals were capable of generating sufficient force to damage the leg. Most commonly, the femur of newly moulted animals (day 0) collapsed in the region of the ETi muscle attachments. After 1 day, the femur remained intact, but failure of the proximal tibia was common. Five days after the moult, failure occurred in only 50% of animals: most commonly the ETi apodeme broke. In 14-day-old animals, failure was relatively rare, the only type of failure observed being fracture of the ETi apodeme ($N=10$ for each age group). (B) The force generated by the leg was significantly less on the day of the moult (day 0) than on subsequent days (mean \pm S.E.M., $N=10$, $P < 0.01$). In newly moulted animals, there was a gradual increase in force to a maximum at 30 Hz as the stimulus frequency was increased. Further increases resulted in a slight decline in force. The legs of newly moulted animals did not remain intact above a stimulus frequency of 50 Hz. In older animals (days 1–14), there was a more rapid increase in force as the stimulus frequency was increased. Maximum force was generated at approximately 50 Hz. The rate of increase in force as stimulus frequency was increased and the maximum force generated were greatest in the oldest animals. (C) The force at which the legs of newly moulted animals failed was significantly less than for animals 1 day older (mean \pm S.E.M., $N=10$, $P < 0.01$). After this initial rapid increase in the force at which the leg failed, there was a gradual increase for the next 14 days.

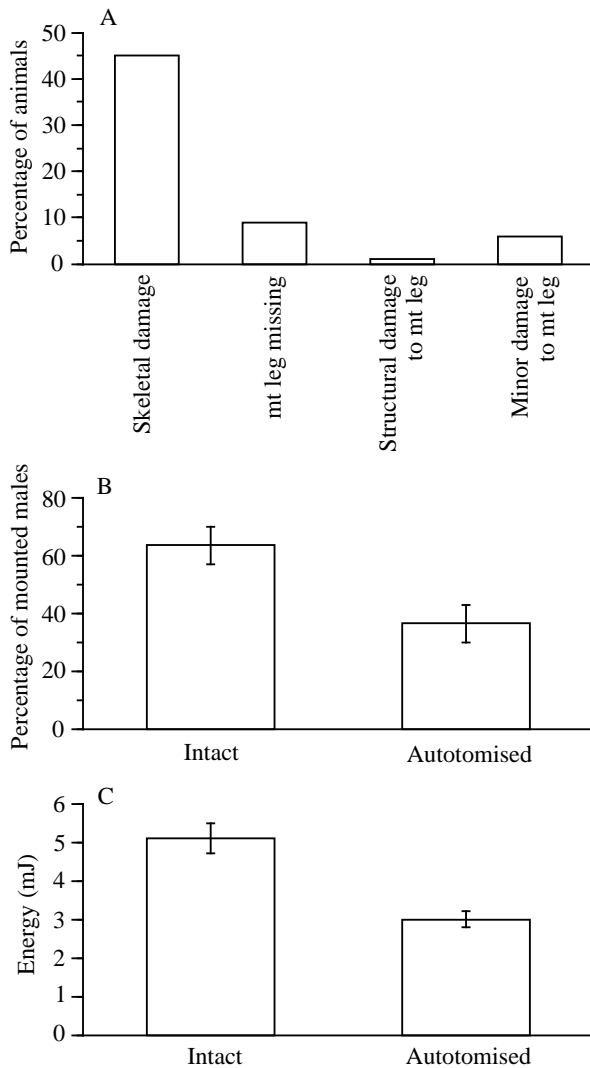


Fig. 7. Skeletal damage incurred during the life of a locust is relatively common and can decrease the animal's ability to avoid predation and compete for resources. (A) Amongst a group of 100 animals which had been raised in a crowded colony since shortly after hatching, 67 survived to sexual maturity; 45% of the survivors (30 animals) had incurred some skeletal damage by the time they reached maturity. Severe structural damage to the metathoracic (mt) legs was rare; more commonly, at least one was missing. Minor damage to the most distal segments of the metathoracic leg was more common than severe damage. (B) Autotomy of one metathoracic leg significantly decreased the ability of males to compete for mates (mean \pm S.E.M., $N=4$, $P<0.05$). (C) Autotomy of one metathoracic leg significantly decreased the amount of energy available for the jump (mean \pm S.E.M., $N=8$, $P<0.01$) and, hence, jumping ability.

Locusts that had one metathoracic leg autotomised might have been expected to produce 50% of the energy produced by intact animals, not 60% as described above. This indicates that intact animals may generate jumps which are shorter than their maximal jump range, so increasing the effective safety factor. Locusts that had one leg autotomised may be generating more energy than expected with their remaining leg to compensate

for the loss of a leg. This would be expected to increase the risk of damage to animals jumping with one leg.

Discussion

Synchrony between behaviour and development

Locust behaviour is flexible, with the result that kicking and jumping are expressed at different developmental stages only when they are appropriate. Structural changes in the exoskeleton, which take place over the moult cycle, leave it weak at particular times and susceptible to damage. A change in behaviour is synchronised with this moult-related change in susceptibility to damage, so that animals do not kick or jump when the cuticle is soft. At these times, animals do not generate the adult motor pattern for kicking; instead, extensions of the tibia are driven by direct muscle action. This prevents damage to the exoskeleton, which would decrease their ability to compete for resources and to avoid predation in the future. The timing of this change in behaviour is also correlated with a decrease in jumping ability (Gabriel, 1985*a,b*; Queathem, 1991) and coincides with developmental stages when old cuticle is being reabsorbed and when new cuticle is being laid down and hardened (Andersen, 1973, 1974). This may reflect a switch in strategy so that the animal remains motionless rather than generating a short ineffective jump that might draw the attention of a potential predator but not displace the locust sufficiently far to avoid capture.

Mature locusts readily generate powerful kicks and jumps, co-contracting the extensor (ETi) and flexor (FITi) tibiae muscles so that energy is stored in the leg to be released rapidly in a powerful extension movement. Around the time of moult, animals do not store energy in the leg and so do not generate these powerful movements; instead, they generate slower extensions. The jump range of animals approaching the adult moult declines gradually, then, after the moult, increases over a period of days to a consistent level (Gabriel, 1985*a,b*; Queathem, 1991). Instead of co-contracting the leg muscles, as mature animals do, alternate bouts of activity in the ETi and FITi muscles cause the leg to extend and flex alternately (Fig. 1). At such times, the cuticle is weak and the leg is unable to store the energy generated by a co-contraction, which would otherwise cause mechanical failure. Jumps are short and ineffective because they are generated without storing energy in the leg. Flexibility in the timing of the expression of this behaviour prevents damage to the leg. It has been widely noted that arthropods become quiescent around the time of moult. Hughes (1980) identified locusts which were ready to moult by their inability to jump, and Gabriel (1985*a*) reported an increase in the frequency of jumping in newly moulted animals. This latter finding is in contrast to the present study, which found that the frequency of kicking was reduced at the moult, reflecting the different criteria used in the two studies to define kicks and jumps (which share a common motor pattern). Gabriel did not distinguish between jumps generated by co-contraction of the ETi and FITi muscles (the definition used here) and 'jumps' generated solely by ETi activity, which produces slower and weaker extensions of the leg.

The mechanics of the leg protect it from damage

The nature of the most common type of mechanical failure of the leg changes following the adult moult, revealing a mechanism which protects the leg from damage. In newly moulted animals, electrical stimulation of the ETi muscle causes the proximal femur to collapse in the region of the ETi muscle attachments along the anterior and posterior surfaces of the femur, because the cuticle is flexible. At low stimulus frequencies, the femur returns elastically to its original shape once the stimulus ceases. At higher stimulus frequencies, however, the femur does not behave elastically, but becomes permanently damaged. In mature animals, the femur is stiffer and it stores a small amount of the energy generated by the muscles during co-contraction, which is then released when the tibia extends during the kick (Bennet-Clark, 1975). Other types of failure are rare in newly moulted animals (Fig. 6A) because collapse of the femur protects the rest of the leg from mechanical damage by limiting the force that is transmitted to the rest of the leg. Unlike the femur, damage to any of the other components of the leg at any age occurs in an 'all-or-nothing' fashion and is not reversible. When the ETi apodeme, the semilunar processes or the proximal tibia fail, the damage is permanent, so the leg becomes dysfunctional for the rest of the animal's life. The high incidence of animals missing at least one metathoracic leg, and the low incidence of severe damage, indicates that legs may be autotomised if damage renders them dysfunctional.

Incidence of skeletal damage

The incidence of non-fatal skeletal damage in the locust is high. Brandwood *et al.* (1986) compared the incidence of healed fractures in a range of taxa. Comparisons of this nature are complicated by two factors. First, the anatomy of different taxa can be sufficiently different for a direct comparison to be unclear. Second, the available data for different taxa have been sampled at different stages of the animals' lives.

Calculation of the incidence of fracture of a major limb segment (femur or tibia) for all three pairs of legs in the locust, following the method of Brandwood *et al.* (1986), reveals that damage occurs with a similar frequency in locusts as in a number of vertebrate taxa. However, calculation of the incidence of fracture for the metathoracic legs indicates that they fail more frequently than the other two pairs of legs in the locust and in the major limb bones of the vertebrate taxa that have been examined. Shell fracture in molluscs is considerably more frequent than the incidence of limb fracture in either the vertebrates or the locust. This may reflect the method by which the data were calculated for the molluscs, where more than one fracture per shell could be recorded. Data are not available for comparison with other arthropods, but the results presented here indicate that the incidence of skeletal failure in the locust, with the exception of the metathoracic legs, is consistent with those in other taxa that have articulated skeletons. Failure of metathoracic legs is, however, considerably more frequent than

failure of skeletal structures in other animals with articulated skeletons.

The high frequency of failure of the metathoracic legs may be due to the low safety factors of components of the leg which store energy. Kicking may be more dangerous than jumping. When jumping, the forces in the leg are relatively predictable because they are generated by the muscles and the leg is in contact with the ground during the movement. However, when the leg is extending during a kick, it may encounter an obstacle at any point in its extension, exposing it to unpredictable forces. As the loading of a biological structure becomes less predictable, either the safety factor must be increased or failures will become more common (Lowell, 1985). Since the loading of the leg may be less predictable during kicking than during jumping, the risk of damaging the leg may be greater during kicking than during jumping and may occur as a result of sudden changes in the loading of the leg.

The locust's ability to autotomise metathoracic legs may decrease the cost of damaging them. Following loss of one metathoracic leg, a locust's locomotor performance is reduced, but perhaps the reduction in locomotor performance in animals such as mammals, which do not shed damaged limbs, is greater.

During moulting, locusts may fail to extricate themselves completely from the old cuticle and so lose distal leg segments (A. P. Norman, personal observation). A proportion of the minor damage described above may be incurred in this manner. It is possible that the increased length of the metathoracic legs makes it more difficult for the old cuticle to be shed and so leads to an increase in the risk of such damage. In addition, locusts in a crowded colony bite each other (A. P. Norman, personal observation), which may constitute a significant source of damage to the exoskeleton.

There are two sources of error in the assessment presented here of the incidence of failure of the major limb segments of the locust. First, this failure in the locust was not calculated for the whole of an animal's lifetime because the incidence of skeletal damage in the locusts that did not survive to sexual maturity was not available and, for those that did survive, it was not possible to predict what damage might have occurred in the future. Second, the relatively high frequency of autotomy of a metathoracic leg and the relatively low frequency of severe damage suggest that animals autotomise severely damaged legs. Autotomy is probably the best course of action because severe damage to the leg is irreparable, so the leg becomes chronically dysfunctional. Before autotomy, however, a leg might have sustained damage to both major segments, which would bias the sampling towards a low estimate of the incidence of fracture. A more complete description of the nature and occurrence of skeletal damage in the locust could be achieved by examining individually identifiable locusts daily during their entire lifetime and characterising any damage, including that leading to autotomy.

The consequences of skeletal damage

Skeletal damage has a significant effect on the ability of a

locust to compete for resources. Loss of one metathoracic leg decreases both jumping ability (Fig. 7C), which may increase susceptibility to predation, and the ability of males to gain access to mates (Fig. 7B). In adults, the velocity at take-off is important for initiating flight (Pond, 1972; Bennet-Clark, 1975). The loss of one metathoracic leg (leading to decreased velocity at take-off) may prevent the initiation of flight. In addition, the metathoracic legs are used in walking and it might be expected that functional loss of a metathoracic leg would decrease walking performance. The decrease in the success of animals which have incurred damage to the skeleton indicates that there is strong selective pressure for animals to avoid incurring damage.

The evolution of the safety factor of skeletal structures depends upon the costs of growth and use of the skeleton and upon the probability and costs of failure (Alexander 1981, 1984). The costs of mechanical failure of the metathoracic leg are high for two reasons. First, the components of the leg that are at risk of incurring damage are irreparable and, second, loss of function of a metathoracic leg greatly decreases an animal's ability to compete for mates. The energy storage components of the leg are relatively very small, and so the costs of growth and use are likely to be correspondingly small. The control of loading of the leg may be enhanced by mechanosensory feedback sufficiently that damage may be avoided even though the safety factors of some components are low (Bennet-Clark, 1975; Alexander, 1981). During development, changes in the probability of failure of the metathoracic leg occur in a predictable manner. Safety factors in components of the legs of mature animals are low. Around the time of moult, the risk of damaging the leg as a result of forces generated by the muscles is greatly increased. Predictability of changes in the loading which would damage the leg enables damage to be avoided by changes in behaviour so that muscular energy is not stored in the weakened leg.

Flexibility in locust kicking behaviour during development prevents damage to the leg, which would decrease an animal's ability to compete for resources and avoid predation in the future. This study provides the opportunity to investigate the neural basis of this developmental change in kicking and jumping behaviour.

This work was supported by NIH grant 16058 to M. Burrows. I thank M. Burrows, P. L. Newland, T. Matheson, E. Kalogianni, and D. Parker for commenting on earlier drafts of the manuscript.

References

- ADAMS, E. S. AND CALDWELL, R. L. (1990). Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. *Anim. Behav.* **39**, 706–716.
- ALEXANDER, R. MCN. (1981). Factors of safety in the structure of animals. *Scient. Prog.* **67**, 109–130.
- ALEXANDER, R. MCN. (1984). Optimum strengths for bones liable to fatigue and accidental failure. *J. theor. Biol.* **109**, 621–636.
- ANDERSEN, S. O. (1973). Comparison between the sclerotization of adult and larval cuticle in *Schistocerca gregaria*. *J. Insect Physiol.* **19**, 1603–1614.
- ANDERSEN, S. O. (1974). Cuticular sclerotization in larval and adult locusts, *Schistocerca gregaria*. *J. Insect Physiol.* **20**, 1537–1552.
- BENNET-CLARK, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria*. *J. exp. Biol.* **63**, 53–83.
- BENNET-CLARK, H. C. AND LUCEY, E. C. A. (1967). The jump of the flea: a study of the energetics and a model of the mechanism. *J. exp. Biol.* **47**, 59–76.
- BRANDWOOD, A., JAYES, A. S. AND ALEXANDER, R. MCN. (1986). Incidence of healed fracture in the skeletons of birds, molluscs and primates. *J. Zool., Lond. A* **208**, 55–62.
- BURROWS, M. AND PFLÜGER, H. J. (1988). Positive feedback loops from proprioceptors involved in leg movements in the locust. *J. comp. Physiol. A* **163**, 425–440.
- CAMPBELL, I. J. (1961). The anatomy of the nervous system of the mesothorax of *Locusta migratoria migratoides* R&F. *Proc. zool. Soc., Lond.* **137**, 403–432.
- CROMARTY, S. I., COBB, J. S. AND KASS-SIMON, G. (1991). Behavioural analysis of the escape response in the juvenile lobster *Homarus americanus* over the moult cycle. *J. exp. Biol.* **158**, 565–581.
- EVANS, M. E. G. (1972). The jump of the click beetle (Coleoptera, Elateridae) – a preliminary study. *J. Zool., Lond.* **167**, 319–336.
- GABRIEL, J. M. (1985a). The development of the locust jumping mechanism. I. Allometric growth and its effect on jumping performance. *J. exp. Biol.* **118**, 313–326.
- GABRIEL, J. M. (1985b). The development of the locust jumping mechanism. II. Energy storage and muscle mechanics. *J. exp. Biol.* **118**, 327–340.
- HEITLER, W. J. (1974). The locust jump. Specialisations of the metathoracic femoro-tibial joint. *J. comp. Physiol.* **89**, 93–104.
- HEITLER, W. J. (1977). The locust jump. III. Structural specialisations of the metathoracic tibiae. *J. exp. Biol.* **67**, 29–36.
- HEITLER, W. J. AND BURROWS, M. (1977). The locust jump. I. The motor program. *J. exp. Biol.* **66**, 203–219.
- HUGHES, T. D. (1980). The imaginal ecdysis of the desert locust, *Schistocerca gregaria*. I. A description of the behaviour. *Physiol. Ent.* **5**, 47–54.
- KATZ, S. L. AND GOSLINE, J. M. (1992). Ontogenetic scaling and mechanical behaviour of the tibiae of the African desert locust (*Schistocerca gregaria*). *J. exp. Biol.* **168**, 125–150.
- KER, R. F. (1977). Investigation of locust cuticle using the insecticide diflubenzuron. *J. Insect Physiol.* **23**, 39–48.
- LOWELL, R. B. (1985). Selection for increased safety factors of biological structures as environmental unpredictability increases. *Science* **228**, 1009–1011.
- MIAL, R. C. AND HERWARD, C. J. (1988). A simple miniature capacitive position transducer. *J. exp. Biol.* **138**, 541–544.
- POND, C. M. (1972). The initiation of flight in unrestrained locusts, *Schistocerca gregaria*. *J. comp. Physiol.* **80**, 163–178.
- QUEATHAM, E. (1991). The ontogeny of grasshopper jumping performance. *J. Insect Physiol.* **37**, 129–138.
- STEGER, R. AND CALDWELL, R. L. (1983). Intraspecific deception by bluffing: a defense strategy of newly molted stomatopods. *Science* **221**, 558–560.
- TAMM, G. R. AND COBB, J. S. (1978). Behaviour and the crustacean molt cycle: changes in aggression of *Homarus americanus*. *Science* **200**, 79–81.
- The Locust Handbook* (1971). London: Anti-locust Research Centre.