© 2016. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2016) 219, 635-648 doi:10.1242/jeb.134445

RESEARCH ARTICLE

Increased muscular volume and cuticular specialisations enhance jump velocity in solitarious compared with gregarious desert locusts, *Schistocerca gregaria*

Stephen M. Rogers*,, Joanna Riley‡, Caroline Brighton§, Gregory P. Sutton‡, Darron A. Cullen¶ and Malcolm Burrows**

ABSTRACT

The desert locust, *Schistocerca gregaria*, shows a strong phenotypic plasticity. It can develop, depending upon population density, into either a solitarious or gregarious phase that differs in many aspects of behaviour, physiology and morphology. Prominent amongst these differences is that solitarious locusts have proportionately longer hind femora than gregarious locusts. The hind femora contain the muscles and energy-storing cuticular structures that propel powerful jumps using a catapult-like mechanism. We show that solitarious locusts jump on average 23% faster and 27% further than gregarious locusts, and attribute this improved performance to three sources: first, a 17.5% increase in the relative volume of their hind femur, and hence muscle volume; second, a 24.3% decrease in the stiffness of the energy-storing semi-lunar processes of the distal femur; and third, a 4.5% decrease in the stiffness of the tendon of the extensor tibiae muscle. These differences mean that solitarious locusts can generate more power and store more energy in preparation for a jump than can gregarious locusts. This improved performance comes at a cost: solitarious locusts expend nearly twice the energy of gregarious locusts during a single jump and the muscular co-contraction that energises the cuticular springs takes twice as long. There is thus a trade-off between achieving maximum jump velocity in the solitarious phase against the ability to engage jumping rapidly and repeatedly in the gregarious phase.

KEY WORDS: Phase change, Phenotypic plasticity, Jumping, Biomechanics, Energy storage, Muscle force

INTRODUCTION

Swarm outbreaks of the desert locust (*Schistocerca gregaria*, Forskål 1775) remain a major agricultural problem across a region spanning from North Africa to northwest India. Swarms may contain billions of individuals covering hundreds of square kilometres, and are occasional events triggered by changing environmental conditions in the arid regions that this species normally inhabits (Steedman, 1990). Central to swarm formation is the ability of locusts to transform reversibly between a lone-living solitarious phase and a group-living gregarious phase, depending upon population density (Uvarov, 1921, 1966; Ellis, 1959; Simpson et al., 1999; Pener and Simpson, 2009). This remarkable phenotypic plasticity results in locusts that differ extensively in many aspects of their behaviour, physiology and morphology (Dirsh, 1953; Roessingh et al., 1993; Roessingh and Simpson, 1994; Simpson et al., 1999; Rogers et al., 2004, 2007, 2014; Lester et al., 2005) (Fig. 1A). Solitarious locusts occur at low population densities and actively avoid other locusts, adopting a life of cryptic inconspicuousness. Increasing population density leads to forced contact between individuals and induces the transformation to the gregarious phase (Simpson et al., 2001; Rogers et al., 2003, 2014). Gregarious locusts walk with a rapid gait, fly during the day, are highly conspicuous with aposematic colouration as nymphs (Sword, 1999, 2002), and, most importantly, are attracted to other locusts, forming coherent migratory bands that may eventually aggregate into vast swarms (Buhl et al., 2006, 2011). Phase change is a multi-stage process occurring over many different time scales; some key changes in behaviour occur within a few hours, but other, principally morphological features emerge over an entire lifespan or even across generations via epigenetic mechanisms (Roessingh and Simpson, 1994; Simpson et al., 1999; Bouaïchi et al., 1995; Islam et al., 1994; Wang and Kang, 2014; Ernst et al., 2015).

Whilst many phase characteristics can be clearly related to lifestyle, the role of others is less clear: solitarious locusts, for example, have proportionately longer hind femora than gregarious locusts (Dirsh, 1951, 1953). The ratio of the hind femur length (F) to head width (C) (F:C ratio) is a metric used to determine the extent of gregarisation in locust populations sampled in the field (Uvarov, 1966, 1977), but the functional consequence of this difference is unknown. The large hind femora of grasshoppers (Acridoidea) are one of their most distinctive features and the source of their prodigious jumping ability. Each hind femur contains a massive, pennate extensor tibiae muscle and a much smaller flexor tibiae muscle (Fig. 1B). The rapid extension of the hind tibiae provides the propulsive force by which locusts jump to avoid predators, initiate flight or, as nymphs, increase their speed of locomotion by hopping (Burrows and Morris, 2001).

Jump take-off velocity is limited by the amount of energy a muscle can generate, but the more rapidly a muscle needs to contract (its strain rate), the less energy it can produce (Zajac, 1989; Burrows and Sutton, 2008). In large animals, long legs provide high lever-arm ratios, allowing direct leg extension produced by contracting muscles to generate long acceleration times and high take-off velocities, whilst maintaining a low muscle contraction rate and maximising the amount of energy available to power the jump (Alexander, 1995). For a large animal, therefore, increasing leg length should allow for faster jumps, all else being equal. Small

---

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK.
*Present address: School of Life Sciences, Arizona State University, PO Box 874601, Tempe, AZ 85287-4501, USA. ‡Present address: School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TH, UK. §Present address: Department of Zoology, The Tinbergen Building, University of Oxford, South Parks Road, Oxford OX1 3PS, UK. ¶Present address: Zoological Institute, KU Leuven, Naamsestraat 59 - Box 2465, Leuven BE-3000, Belgium.

**Author for correspondence (Stephen.m.rogers@asu.edu)

Received 9 November 2015; Accepted 11 December 2015

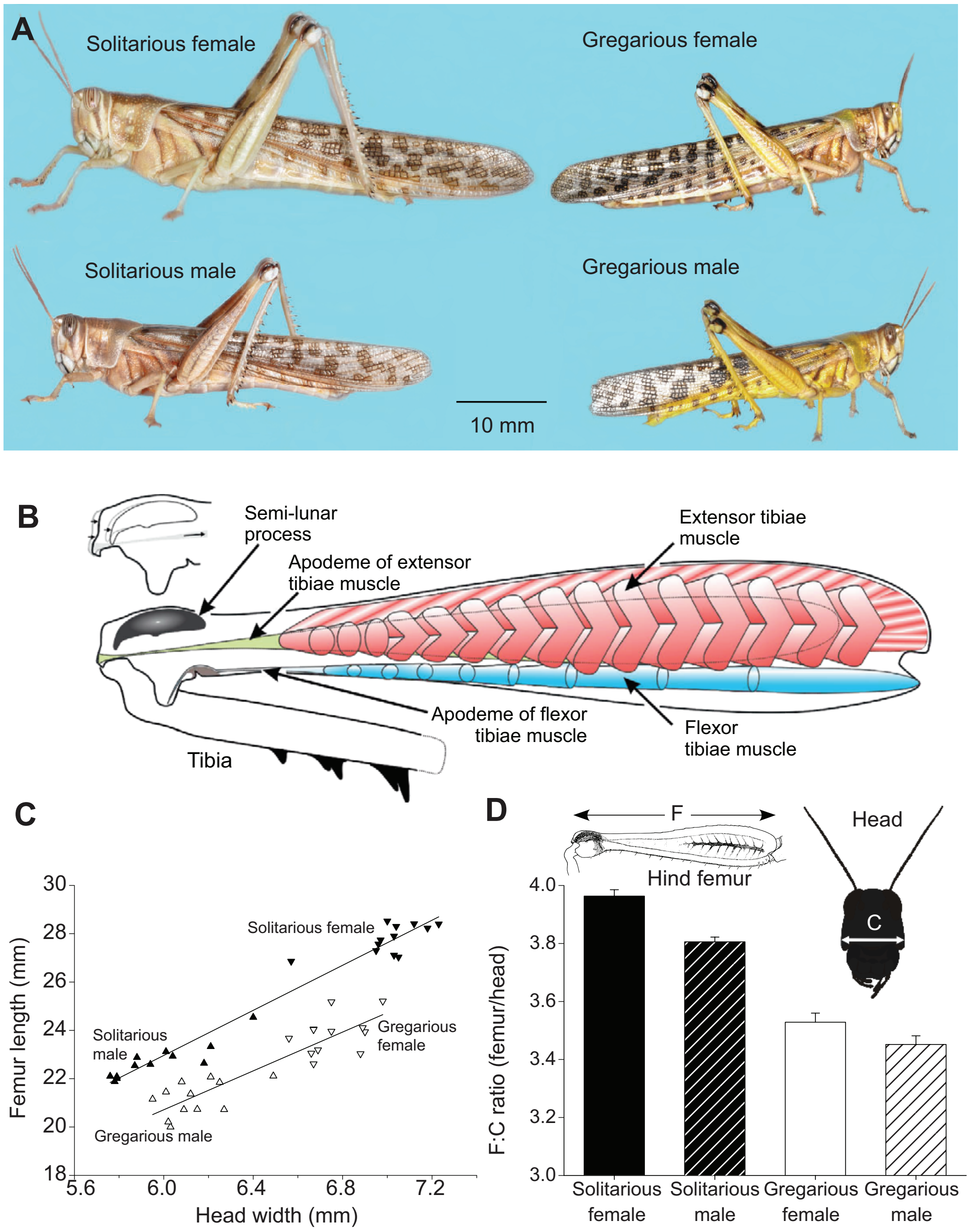

Fig. 1. Morphology, body size and F:C ratios (ratio of hind femur length to head width) in solitarious and gregarious *Schistocerca gregaria*. (A) Photos of mature adult solitarious and gregarious females and males. (B) Diagram of the internal anatomy of a hind femur. Shown are the large pennate extensor tibiae muscle (red), its apodeme (green) and its ribbon-like extension inside the extensor muscle (dotted line), and the smaller flexor tibiae (blue). See Fig. 7C for a mechanical diagram of the interactions between the extensor tibiae muscle, its apodeme and the semi-lunar processes. Inset, during the co-contraction prior to jumping, the extensor apodeme pulls on and distorts the front of the femoro-tibial joint and, in doing so, bends the semi-lunar processes (relaxed state, grey; after co-contraction, black) (based on Bennet-Clark, 1990 and Burrows and Morris, 2001). (C) Scatter plot of the relationship between hind femur length and maximum head width: solitarious females, black downward-facing triangles; solitarious males, black upward triangles; gregarious females, white downward triangles; gregarious males, white upward triangles. (D) Mean± s.e.m. F:C ratio (inset diagrams show how these were measured) in solitarious and gregarious male and female locusts. *N*=12 for each group.

insects, however, are at a severe disadvantage, because their short legs only allow muscles to act for a short time and distance to produce sufficient acceleration. If muscles were to directly extend the legs, then they would have to contract more rapidly than biologically possible to generate the high power and acceleration needed for take-off. Instead, many insects, including locusts, exploit a completely different mechanism that uses slower muscle contraction to distort elastic structures that act as an energy store, the sudden recoil of which drives the rapid extension of the legs (Bennet-Clark, 1975, 1990; Burrows and Sutton, 2008, 2012). To use these catapult-like mechanisms, the leg joints must be first locked into position so that the slow contraction of their jumping muscles deforms the elastic structures without moving the legs.

Jumping using these mechanisms requires specialisations in both the musculo-skeletal and nervous systems. The extremely large extensor tibiae muscle of locusts is combined with mechanical specialisations of the hind femoro-tibial joint in such a way as to give the much smaller flexor-tibiae muscle a mechanical advantage over the extensor when the tibia is fully flexed (Heitler, 1974, 1977). The principal energy-storage structures are the tendon (apodeme) of the extensor tibiae muscle and two bow-like semi-lunar processes, specialised cuticular structures found on either side of the femoral-tibial joint (Bennet-Clark, 1975). These are made of hard sclerotized cuticle backed internally by a layer of the highly elastic protein resilin, combining the capacity to store the large amounts of energy generated when bending hard materials with the elastic capacity to rapidly restore shape (Burrows and Sutton, 2012).

The motor pattern for jumping has three phases (Burrows and Morris, 2001; Burrows, 1995, 1996; Godden, 1975; Heitler and Burrows, 1977). First, during the cocking phase, the hind tibiae are fully flexed and locked into position against the hind femora. Second, during the co-contraction phase, both the extensor tibiae muscle and its antagonistic flexor tibiae muscle of each hind leg contract together, but no movement occurs (Heitler, 1974, 1977). Instead, both the semi-lunar processes and extensor apodeme are steadily deformed, storing the energy produced by the prolonged muscle contraction (Burrows and Morris, 2001). Third, during the jump phase, the flexor-tibiae motor neurons are inhibited, freeing the tibiae to move, and the energy stored in the semi-lunar processes and extensor apodemes is suddenly released to power the jump (Brown, 1967; Burrows and Morris, 2001).

One consequence of using catapult-like mechanisms is that jumping performance becomes largely decoupled from the length of the legs, because the energy that is released from the elastic structures is nearly independent of the muscle contraction rate preceding it (Burrows and Sutton, 2008; Alexander, 1995; Bennet-Clark, 1990). Burrows and Sutton (2008) found no difference in jump take-off velocity in long- and short-legged species of leafhopper (Hemiptera: Cicadellidae). However, the longer-legged species produced lower ground reaction forces and were therefore able to jump more effectively from compliant surfaces such as leaves, whereas shorter-legged species required a firmer substrate from which to jump. This does not appear to be an ecologically relevant consideration for why solitarious and gregarious locusts have different leg lengths. We therefore analysed the jumping of solitarious and gregarious desert locusts to determine whether differences in leg structure had functional consequences for performance. We show that solitarious locusts are capable of jumping faster and further than gregarious locusts, and we then show how differences in structure of the hind leg combine to produce the apparently paradoxical result of the longer-legged solitarious phase out-performing the shorter-legged gregarious phase when both phases are dependent upon a catapult mechanism.

MATERIALS AND METHODS

Locusts

Experimental locusts were taken from a colony at the University of Cambridge reared under crowded conditions for many generations, with 200+ locusts kept in 50×50×60 cm cages. Solitarious locusts were obtained by isolating eggs and rearing the progeny in visual, tactile and olfactory isolation from other locusts in individual cages for three generations. All locusts ate fresh wheat seedlings and dry wheat germ *ad libitum* and were kept under a 12 h:12 h light:dark cycle at 30±0.5°C. Locusts were starved for 24 h and weighed just prior to observation. Separate groups of 12 female and 12 male adult locusts of each phase were used for the morphometric and kinematic analyses, 1 to 2 weeks after their final moult. All data from all locusts were included in the analyses with no outlier exclusion.

Jumping arena

Jumping distance was measured in a corridor (2.2×0.7×1 m, length×width×height) of white card at 30±0.5°C. A black target 600 mm high and 300 mm wide was at one end. At the opposite end was a 250 mm-high platform made of 30 mm diameter dowel covered in sandpaper from which locusts jumped, either spontaneously or encouraged by stimulation with a fine paintbrush. Three jumps by every individual were recorded with 5 min intervals between each. Only the longest jump of each locust was used for analysis, as an estimate of maximum performance. The wing tips were glued together with cyanoacrylate so that wing movements could not affect take-off velocity or distance jumped.

Jumping kinematics

Jumps viewed from the side were recorded at a frame rate of 1000 s^{-1}, exposure time of 0.2 ms and 1024×1024 pixel resolution with a Photron Fastcam SA3 camera (Photron Europe, High Wycombe, Bucks, UK). The saved images were analysed with Motionscope camera software (Redlake Imaging, Tucson, AZ, USA) or with Canvas 14 (ACD Systems International, Seattle, WA, USA). The time to take-off was defined as the period from the first detectable propulsive movement of the hind legs to when they lost contact with the ground and the locust became airborne. Measurements of distances moved were made from jumps that were nearly parallel to the image plane of the camera. Jumps that deviated from the image plane of the camera by more than 30 deg were not analysed. Peak velocity of the locust was calculated from the distance moved by a reference point on the body in a rolling three-point average of successive images just before take-off.

Morphometric analysis

Photographs of whole locusts were taken with a Nikon D90 camera and of the hind legs with a Nikon DXM 1200 camera attached to a Leica MZ16 stereo microscope (Wetzlar, Germany). Measurements were made with digital callipers either directly from a locust or from digital images with reference to a calibration image of a steel ruler. The depth (thickness) of the semi-lunar processes and apodeme of the extensor tibiae muscle were measured from cross-sections of the femur cut with microtome blades.

Data were analysed using ANOVA, general linear models (GLMs) using body mass as covariate and phase and sex as factors, or non-parametric Mann–Whitney tests as appropriate with SPSS Statistics (version 22, IBM, Armonk, NY, USA). Where it was necessary to account for error variances in both *x*- and *y*-axes, we performed standardised major axis regressions in R (R Development Core Team, 2008) using the package SMATR (Warton et al., 2012). Data were tested for normalcy and homogeneity of variance, and transformed as appropriate prior to statistical testing.

Electrophysiology

Myogram electrodes, made from pairs of 30 µm diameter steel wires, insulated except for their tips, were inserted into the left hind femur approximately 5 mm apart. They were secured to the femur with beeswax and then looped and fixed to the lateral nota of thorax to allow free movement of the leg. The wires then ran dorsally to the pronotum, where they were fixed. From the pronotum, the wires and an additional cotton thread were attached to a clamp above the locust so that it was able to jump freely. The data were digitised using a Cambridge Electronic Design (CED, Cambridge, UK) data acquisition system and analysed using Spike 2 software (version 7, CED). The high-speed imaging and electrophysiological recordings were synchronised by activating a small LED light on the take-off platform with an electrical pulse that was also recorded on a separate channel with the myogram spikes. This enabled measurements of take-off velocity to be correlated with the electrophysiological data from 10 locusts of each phase split equally between males and females.

RESULTS

Our laboratory populations of lone- and crowd-reared locusts showed a morphological differentiation resembling the solitarious and gregarious phases of wild locusts (Fig. 1A). There was a close relationship between maximum head width and the length of the hind femora (r^2=0.96, $F_{1,44}$=641.422, P<0.001) in both phases [standardised major axis regression of $\log_e$-transformed data; slope of regression 1.23 (range 1.14 to 1.33) with no difference in slope gradient between phases; likelihood ratio=0.251, d.f.=1, P=0.616; Fig. 1C]. Solitarious locusts, however, always had longer hind femora for any given head width (i.e. the slope was the same but the intercept was higher; Wald statistic=185.7, P<0.001). The hind femur to head width (F:C) ratios were 3.96±0.02 for solitarious females and 3.81±0.02 for solitarious males (Fig. 1D). For the gregarious locusts, the F:C ratios were 3.53±0.03 and 3.45±0.03 for females and males, respectively. There was a significant effect of both phase and sex on the F:C ratios (ANOVA, phase, $F_{1,44}$=235.40, P<0.001; sex, $F_{1,44}$=20.78, P<0.001), but no non-additive effects of sex and phase (phase×sex interaction $F_{1,44}$=2.475, P=0.123).

Jumping performance

The average take-off velocity of solitarious locusts was 23% faster than that of gregarious locusts (3.26±0.4 and 2.65±0.34 m s^{-1}, respectively; ANOVA: $F_{1,44}$=32.5, P<0.001) (Fig. 2A). There was no significant difference between the sexes ($F_{1,44}$=3.17, P=0.082) nor any interaction between phase and sex ($F_{1,44}$=0.001, P=0.982). Take-off velocity was not influenced by either their body mass ($F_{1,44}$=1.67, P=0.204) (Fig. 2B), or by hind femur length (data not shown; $F_{1,44}$=1.41, P=0.243).

The time to take-off was 16.7% greater in females (35±4.8 ms) than in males (30±3.4 ms; $F_{1,44}$=15.8, P<0.001), but did not differ with the phase of the locust (phase, $F_{1,44}$=2.1, P=0.155; phase×sex interaction, $F_{1,44}$=0.80, P=0.375; Fig. 2C). The acceleration of the jump, derived from the final take-off velocity and the time taken to achieve it, differed with both phase and sex (Fig. 2D). Solitarious locusts underwent greater acceleration than gregarious locusts when they jumped ($F_{1,44}$=8.3, P=0.006), and males accelerated faster than females ($F_{1,44}$=10.7, P=0.002), but there was no significant interaction

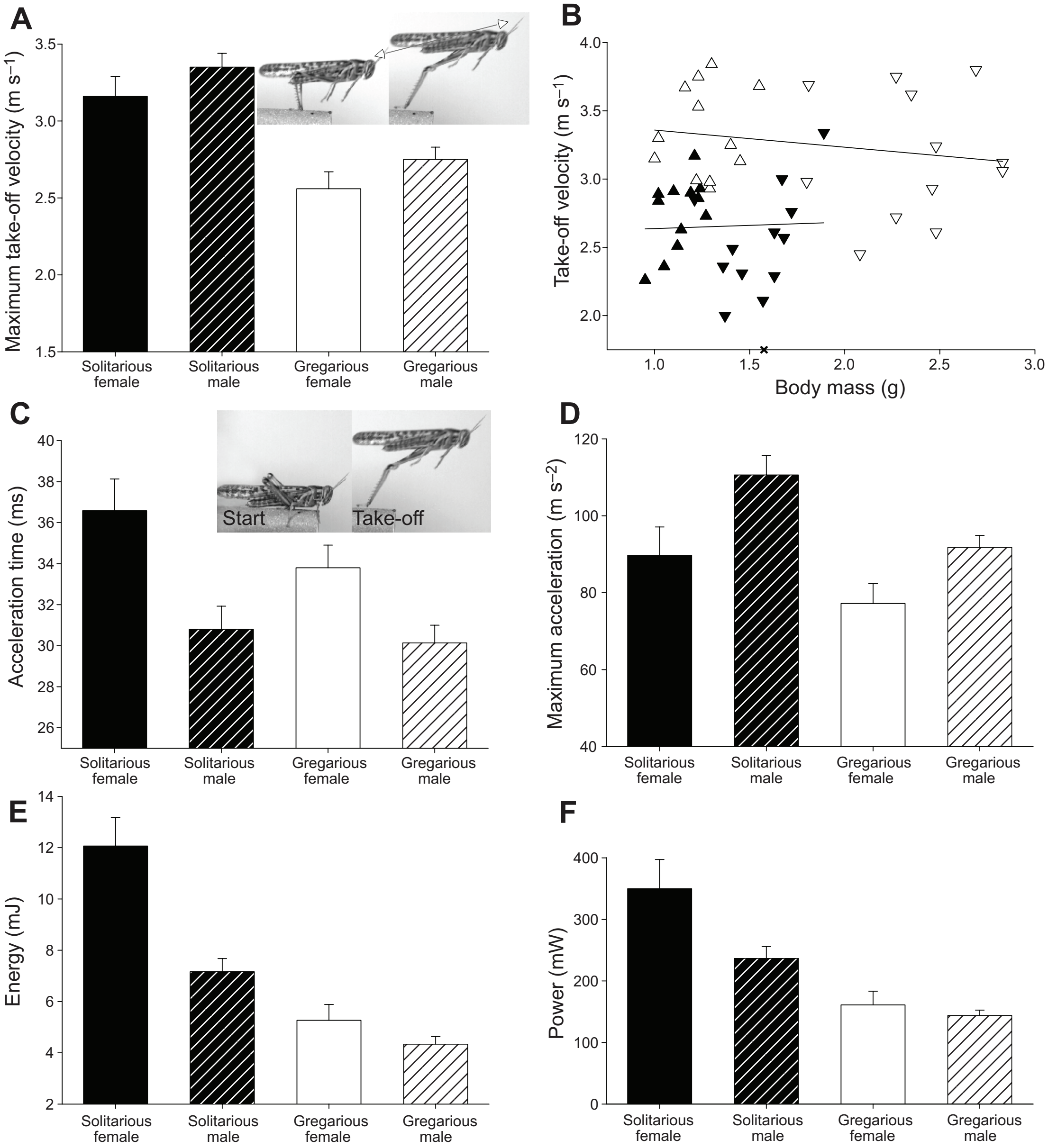

Fig. 2. Jumping performance of solitarious and gregarious locusts. (A) Maximum take-off velocity of female and male solitarious and gregarious locusts (means±s.e.m.). Inset frames from a high-speed video of a jump show the time during which velocity was measured. (B) Scatter plot of maximum take-off velocity against body mass. Solitarious females, black downward-facing triangles; solitarious males, black upward triangles; gregarious females, white downward triangles; gregarious males, white upward triangles. (C–F) Means±s.e.m. (N=12 for each group) of female and male solitarious and gregarious locusts for: (C) acceleration time, (D) maximum acceleration at take-off; (E) energy expended by each jump; and (F) power output of each jump. The inset frames in C from a high-speed video show the point at which the hind legs first moved and when they lost contact with the ground, thus defining acceleration time.

between sex and phase ($F_{1,44}$=0.34, P=0.565). Therefore, the greatest acceleration was shown by solitarious males (111±17.8 m s^{-2}) and the slowest by gregarious females (77±18 m s^{-2}), with solitarious females and gregarious males having broadly similar accelerations (90±25.7 and 92±10.6 m s^{-2}, respectively).

The kinetic energy released by jumps of solitarious locusts was approximately twice that of gregarious locusts (Fig. 2E). The energy expended by solitarious females (12.1±3.8 mJ) was 128% greater than that of gregarious females (5.3±2.1 mJ), and the energy expended by solitarious males (7.2±1.8 mJ) was 67% greater than that of gregarious males (4.3±1.0 mJ; phase, $F_{1,44}$=57.9, P<0.001; sex, $F_{1,44}$=13.8, P=0.001; phase×sex interaction, $F_{1,44}$=3.7, P=0.061; analysis performed on $\log_e$-transformed data). The power of jumps also differed with phase, with solitarious locusts (293.3±27.6 mW) using 92.3% more power than gregarious locusts (152.5±11.8 mW; Fig. 2F), but the difference between the sexes was less than with energy expended because females took longer to extend their hind legs than males (phase, $F_{1,44}$=33.9, P<0.001; sex, $F_{1,44}$=3.03, P=0.089; phase×sex interaction, $F_{1,44}$=1.75, P=0.193; analysis performed on $\log_e$-transformed data).

The increased take-off velocity by solitarious locusts was reflected in a 27% increase in distance jumped compared with that for gregarious locusts (means: solitarious, 108±16 cm; gregarious, 85± 12 cm; GLM, $F_{1,43}$=6.559, P=0.014; Fig. 3A,B). There was no difference between males and females (sex, $F_{1,43}$=2.716, P=0.107; phase×sex interaction, $F_{1,43}$=0.283, P=0.597). As with take-off velocity, body mass did not have a significant effect on jump distance ($F_{1,43}$=2.156, P=0.149; Fig. 3B).

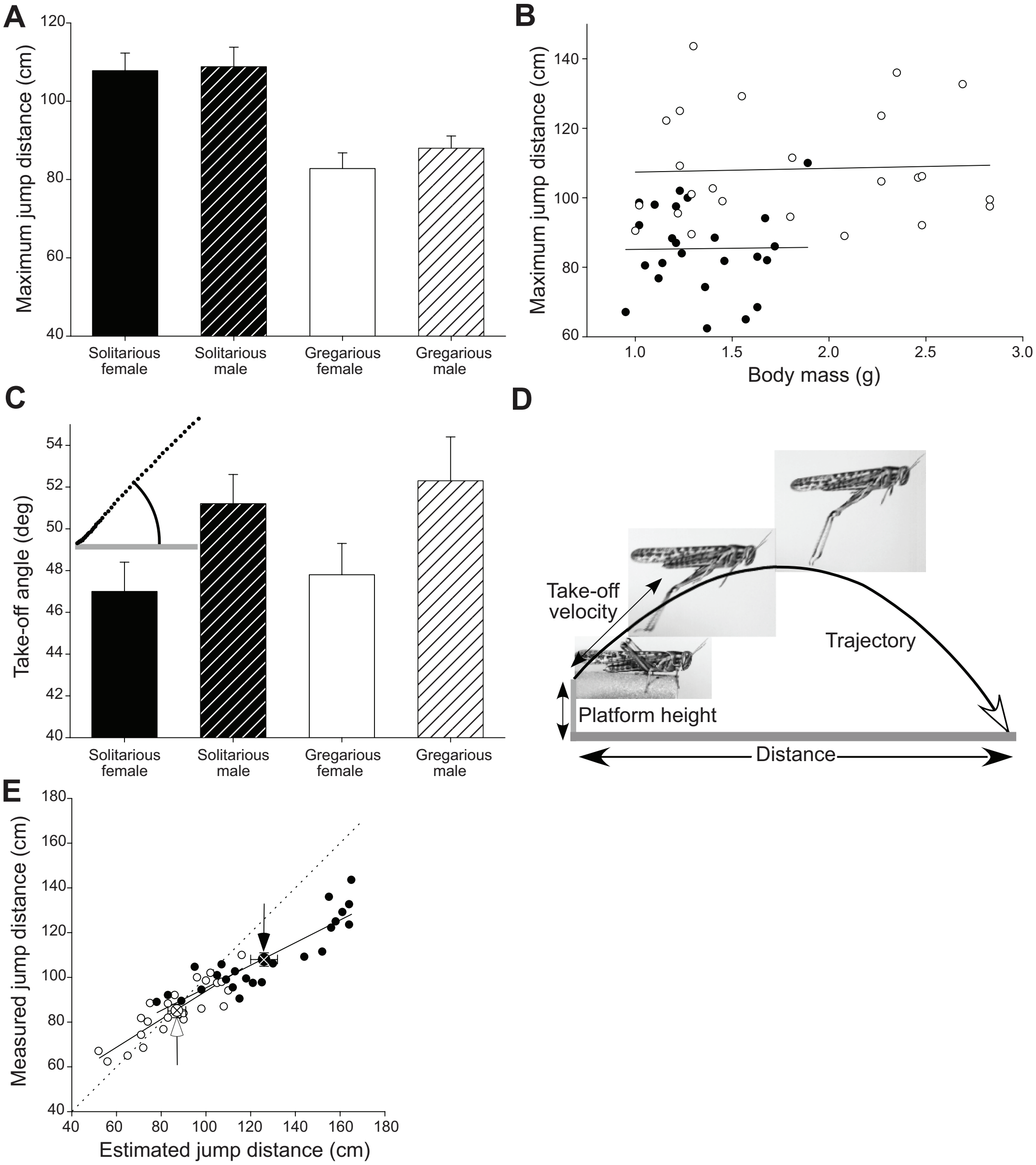

Fig. 3. Jump distance achieved by solitarious and gregarious locusts. (A) Maximum distance jumped by female and male solitarious and gregarious locusts (means±s.e.m.). (B) Scatter plot of maximum distance jumped against body mass. (C) Trajectory angle of jumps by female and male solitarious and gregarious locusts (means±s.e.m.). (D) Diagram of how take-off velocity, trajectory angle and platform height were measured to calculate predicted jump distances. (E) Scatter plot of actual versus predicted maximum jump distance. Solitarious locusts, white circles; gregarious locusts, black circles. The solid lines are regressions fitted to the solitarious and gregarious data; the dashed line shows measured distance=estimated distance. Arrows point to group means. *N*=12 for each group.

The angle of take-off was generally greater than the optimum of 45 deg to achieve the maximum distance for a simple ballistic trajectory (Fig. 3C), with males having a greater take-off angle (52±6.1 deg to horizontal) than females (47±5.1 deg; $F_{1,44}$=7.1, P=0.011). There was no difference between solitarious and gregarious locusts ($F_{1,44}$=0.34, P=0.563).

Air resistance will curtail maximum jump distance and, because it is proportional to the velocity squared (Bennet-Clark and Alder, 1979), this should disproportionately affect solitarious locusts. In gregarious locusts, the jump distances estimated from take-off velocity, take-off angle and height of the jumping platform (Fig. 3D), assuming negligible air resistance, were similar to the measured distances (estimated distance: 87±17 cm; paired t-test against measured distances, t_{23}=0.718, P=0.48; Fig. 3E). For solitarious locusts, however, the actual measured distance measured was significantly less than the estimated distance (estimated distance: 126±28 cm; t_{23}=5.36, P<0.001; Fig. 3E).

Explaining the difference in jumping performance between solitarious and gregarious locusts

Take-off velocity and distance jumped did not differ with mass, but many of the leg structures that are important in generating jumping show a strong correlation with body size. Most of the differences between the sexes reduce to differences in body size, and sex has thus not been analysed independently of body mass. In analyses of covariance, with body mass as a covariate and phase as a main effect, the regressions fitted to data from solitarious and gregarious locusts typically take the form of two parallel (or near parallel) lines. Solitarious locusts tend to be heavier than gregarious locusts, but this alone cannot explain the difference in size between phases: there are significant effects of both mass and phase (Fig. 4A). In our analyses, we separated the effects of body mass from phase. The effect of body mass on a morphological character is explained by the slope of fitted regressions, and that of phase by the difference in intercept between the two lines (Fig. 4A). The values of phase differences at the intercept are where mass equals zero, and are therefore of limited use. Where regressions are parallel, the pure effect of phase can be determined by comparing locusts of equal body mass. As our benchmark for comparison we have used the estimated marginal mean (EMM), which is the predicted value of the y-variable (body dimension) at the average value of the covariate (body mass) for each level of the factor (phase).

Muscle force

The maximum force that a muscle can produce is proportional to its cross-sectional area (Zajac, 1989). In addition, a longer muscle can apply force over a larger distance, contract a greater amount and hence produce a larger displacement in an attached spring. This can be approximated as an increase of the effective force proportional to muscle length. The total force exerted by a jumping muscle (F_{muscle}) that shows minimal length change during its contraction will thus be proportional to its volume (cross-sectional area×length), which in turn is proportional to the volume of the hind femora, assuming both phases have similar distributions of sarcomere lengths in their muscle fibres:

$$F_{\mathrm{muscle}} = \alpha f_{\mathrm{width}} f_{\mathrm{depth}} f_{\mathrm{length}}, \tag{1}$$

where α is a proportionality constant, f_{width} is the maximum dorsal-ventral width, f_{depth} is the maximum anterior-posterior depth and f_{length} is the proximal-distal length of the hind femur.

There was a strong correlation between body mass and hind femur length (r^2=0.845, $F_{1,45}$=134.7, P<0.001; Fig. 4B), but phase still had an effect additional to that of body mass ($F_{1,45}$=11.545, P=0.001), with solitarious locusts having proportionately longer hind femora than gregarious locusts. The average body mass of all locusts was 1.81 g and the EMM for femur length was 24.8±0.03 mm for solitarious and 23.7±0.03 mm for gregarious locusts, a 4.7% difference ($F_{1,45}$=11.545, P=0.001).

The maximum dorso-ventral width of the hind femur also scaled significantly with body mass (r^2=0.775, $F_{1,45}$=90.355, P<0.001; Fig. 4C): the EMM of solitarious locusts was 4.86±0.004 mm and that of gregarious locusts 4.72±0.004 mm, a 3.0% difference between phases ($F_{1,45}$=5.022, P=0.030). The anterior-posterior depth of the hind femur likewise scaled with body mass (r^2=0.764, $F_{1,45}$=49.209, P<0.001) (Fig. 4D): the EMM was 2.6±0.03 mm in solitarious locusts and 2.4±0.03 mm in gregarious locusts, a 9.2% difference ($F_{1,45}$=25.435, P<0.001). When hind femur width, depth and length were multiplied to give an estimate of possible maximum muscle force, the relative difference between phases became far greater (relationship to body mass, r^2=0.88, $F_{1,45}$=159.127, P<0.001), with an EMM of solitarious and gregarious locusts of 32.0±0.66 and 27.27±0.66 mm^3, respectively. This amounted to a 17.5% difference between phases ($F_{1,45}$=22.504, P<0.001; Fig. 4E).

Elastic energy storage

The energy released by the muscle force is stored in the femoral semi-lunar processes and in the apodeme of the extensor tibiae muscle. The relationship between applied force and distortion of a simple linear spring is given by Hooke's Law, where the force (F) is proportional to spring stiffness (s) times the displacement of the spring (d):

$$F = sd. \tag{2}$$

The elastic energy (e_{elastic}) stored by a spring when it is stretched or compressed is given by:

$$e_{\mathrm{elastic}} = \frac{1}{2} sd^2. \tag{3}$$

The displacement produced in the springs of the locust leg is not known, but substituting d for F/s from Eqn 2 above gives:

$$e_{\mathrm{elastic}} = \frac{1}{2}\frac{F^2}{s}. \tag{4}$$

The stiffness of a spring is related to its dimensions, specifically its cross-sectional area (A) divided by its length (L), the Young's modulus of the material it is made from (E), and a proportionality constant (β) that corrects for the difference in the shape of the spring from a rectangular prism:

$$s = \beta E \frac{A}{L}. \tag{5}$$

The shape of the semi-lunar processes is the same in both phases (Fig. 5), and an assumption is made that they consist of the same materials in the same relative proportions so that the Young's modulus is also the same. Therefore, any difference in semi-lunar process stiffness between phases can be attributed to the difference in the relative cross-sectional area and length between phases (A/L).

The dorso-ventral width of the semi-lunar process was correlated with body mass (r^2=0.642, $F_{1,45}$=59.738, P<0.001; Figs 5, 6A,B) and also differed between phases ($F_{1,45}$=60.989, P<0.001), but gregarious locusts (1.04±0.2 mm) had larger structures than

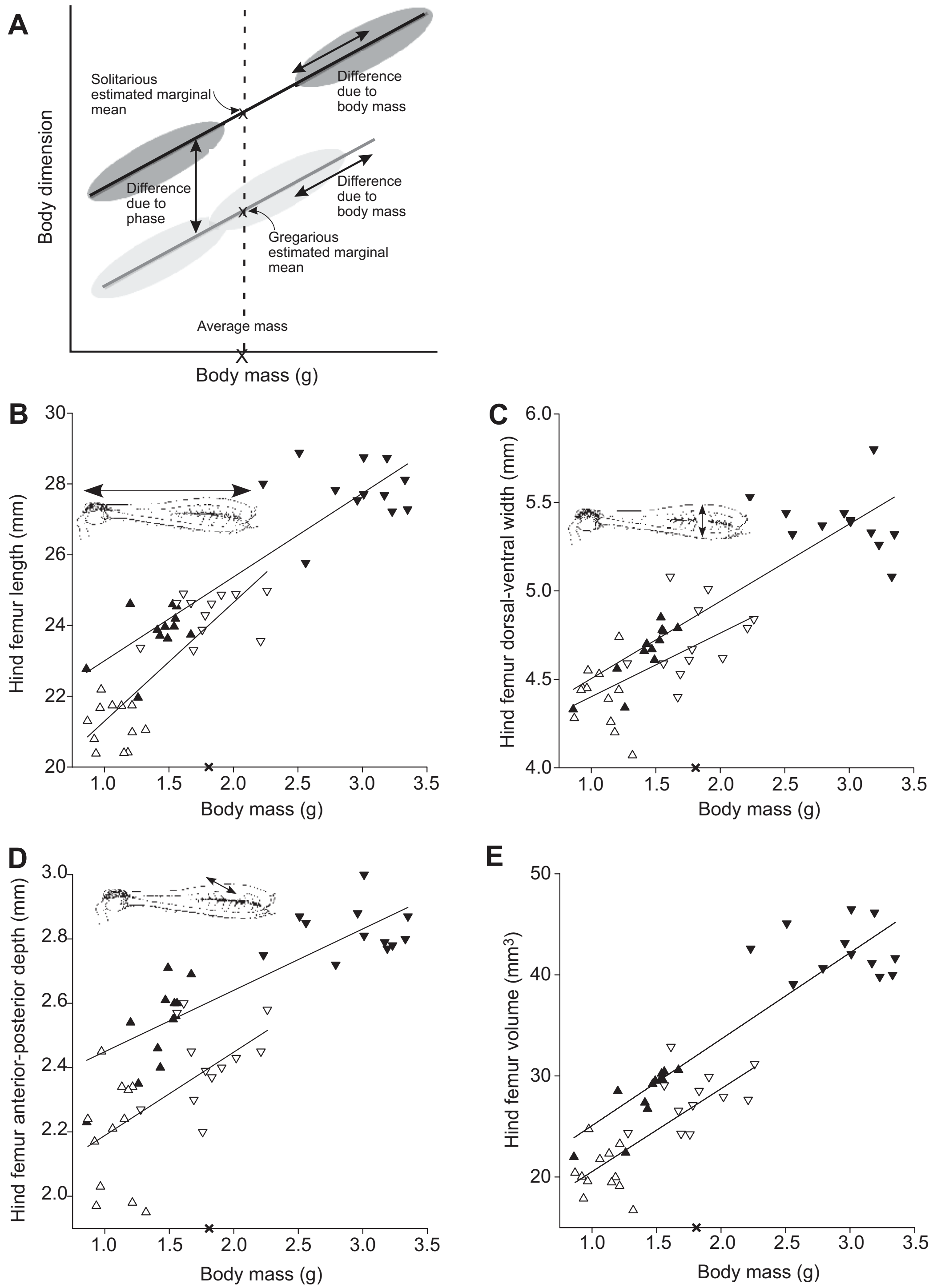

Fig. 4. Scaling of the dimensions of the leg with body mass. (A) Diagram illustrating the separation between variation in a body dimension ascribed to phase as opposed to body mass. The distribution of data is represented by the grey ellipses, to which regressions for each phase have been fitted. Differences that scale to body mass follow the slope of the regression; differences that are purely phase-related are described by the vertical displacement between the two regression lines. The estimated marginal mean (EMM) values for phase are the values of *y* from the regressions at the mean body mass for all locusts indicated by the small × on the horizontal axes. (B–E) Scatter plots of hind femur dimensions against body mass: (B) hind femur proximo-distal length; (C) dorso-ventral width; (D) anterior-posterior depth (all dimensions are as indicated in the inset diagrams); and (E) hind femur volume (length×width×depth). *N*=12 for each group. Solitarious females, black downward-facing triangles; solitarious males, black upward triangles; gregarious females, white downward triangles; gregarious males, white upward triangles.

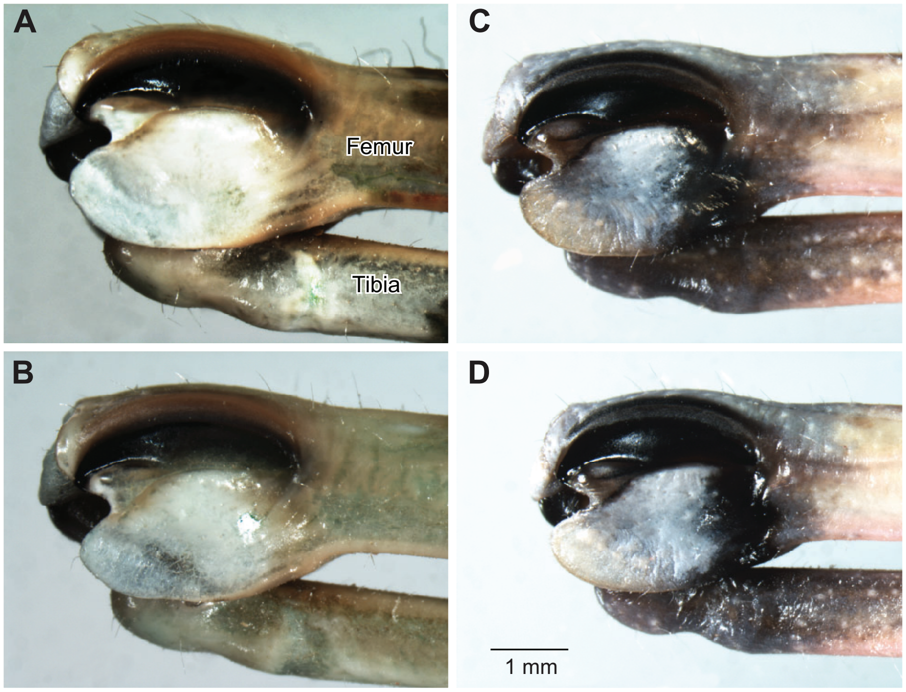

Fig. 5. Photographs of the lateral surface of the femoro-tibial joint of the right hind leg showing the semi-lunar process in solitarious and gregarious locusts. (A) Solitarious female. (B) Solitarious male. (C) Gregarious female. (D) Gregarious male.

solitarious locusts (0.78±0.2 mm) at the EMM. The semi-lunar processes of solitarious locusts were therefore 25% narrower than those of gregarious locusts of the same size. By contrast, overall there was only a weak correlation between body mass and proximo-distal length of the semi-lunar process (r^2=0.188, $F_{1,45}$=9.789, P=0.003) and no difference between phases (solitarious EMM 3.02±0.1 mm, gregarious EMM 3.15±0.1 mm; $F_{1,45}$=0.723, P=0.400; Figs 5, 6C). There was evidence, however, for a different scaling relationship between the length of the semi-lunar process and body mass in each phase: the slopes were significantly different for solitarious and gregarious locusts (phase×body mass interaction term, $F_{1,44}$=12.435, P=0.001; within gregarious phase, r^2=0.616, $F_{1,23}$=35.293, P<0.001; within solitarious phase, r^2=0.08, $F_{1,23}$=1.934, P=0.178). By sectioning the distal end of the femur we were able to obtain the thickness of the semi-lunar processes (Fig. 6D). The EMM thicknesses were 0.107±0.004 mm for solitarious locusts and 0.115±0.005 mm for gregarious locusts. These did not differ significantly with body mass ($F_{1,42}$=1.484, P=0.230) or with phase ($F_{1,42}$=2.395, P=0.129), nor was there a significant phase×body mass interaction ($F_{1,42}$=3.395, P=0.072).

Combining these measurements (width×thickness/length) gave the stiffness of the semi-lunar processes (Fig. 6E); in solitarious locusts (0.028±0.0205 mm) the stiffness was only 75.7% of that in gregarious locusts at the EMM (0.037±0.002 mm; $F_{1,44}$=7.704, P=0.008), and did not differ significantly with body mass (r^2=0.148, $F_{1,45}$=1.183, P=0.283).

The other major energy-storing component is the apodeme of the extensor tibiae muscle. A longer hind leg with a larger area for muscle attachment will also have a longer apodeme. This will give it a different stiffness and, therefore, altered energy storing properties. The extensor apodeme has a complex shape (Bennet-Clarke, 1975, 1990), being narrowest and thickest distally near its insertion onto the tibia, but wider and thinner more proximally in the femur. We were able to measure apodeme dimensions in the majority of locusts (nine solitarious females, 10 solitarious males, eight gregarious females and 11 gregarious males). The anterior-posterior depth of the apodeme at its distal end scaled with body mass (r^2=0.406, $F_{1,28}$=76.474, P<0.001; Fig. 7A), but there was no additional effect of phase ($F_{1,28}$=0.04, P=0.842). The depth of the apodeme at the EMM was 0.31±0.01 mm. The dorso-ventral width of the apodeme was 0.99±0.01 mm and did not scale with body size (r^2=0.025, $F_{1,28}$=0.583, P=0.451), nor did it differ by phase ($F_{1,28}$=0.048, P=0.829; Fig. 7B). If it is assumed that the apodeme extends for the same relative proportion of the femur in solitarious and gregarious locusts (approximately 80% of femur length; Gabriel, 1985a), then the change in apodeme stiffness between phases can be ascribed solely to the change in length and will be proportional to $1/f_{\mathrm{length}}$. The hind femora of solitarious locusts were 1.047 times longer than those of gregarious locusts; therefore, the stiffness of the apodeme is predicted to be 95.5% as great.

The extensor tibiae muscle acts on two semi-lunar processes that operate in parallel with each other but in series with the extensor apodeme (Fig. 7C). To determine the total elastic energy stored, the equivalent stiffness (s_{eq}) of all the springs working together must be calculated. For springs in parallel:

$$s_{\mathrm{eq}} = s_1 + s_2. \tag{6}$$

For springs in series:

$$\frac{1}{s_{\mathrm{eq}}} = \frac{1}{s_1} + \frac{1}{s_2}. \tag{7}$$

Therefore, the equivalent stiffness of the entire spring system within a femur (s_{f}) is:

$$\frac{1}{s_{\mathrm{f}}} = \frac{1}{s_{\mathrm{apo}}} + \frac{1}{2s_{\mathrm{slp}}}, \tag{8}$$

where s_{apo} is the stiffness of the extensor apodeme and s_{slp} is the stiffness of a semi-lunar process. If gregarious locusts are given a nominal value of 1 for both s_{apo} and s_{slp}, then the equivalent figures for solitarious locusts are 0.955 and 0.757, respectively. Inserting these values into Eqn 8 above gives the s_{f} of gregarious locusts a value of 0.667, and that of solitarious locusts 0.586; the s_{f} of solitarious locusts is thus 87.8% that of gregarious locusts.

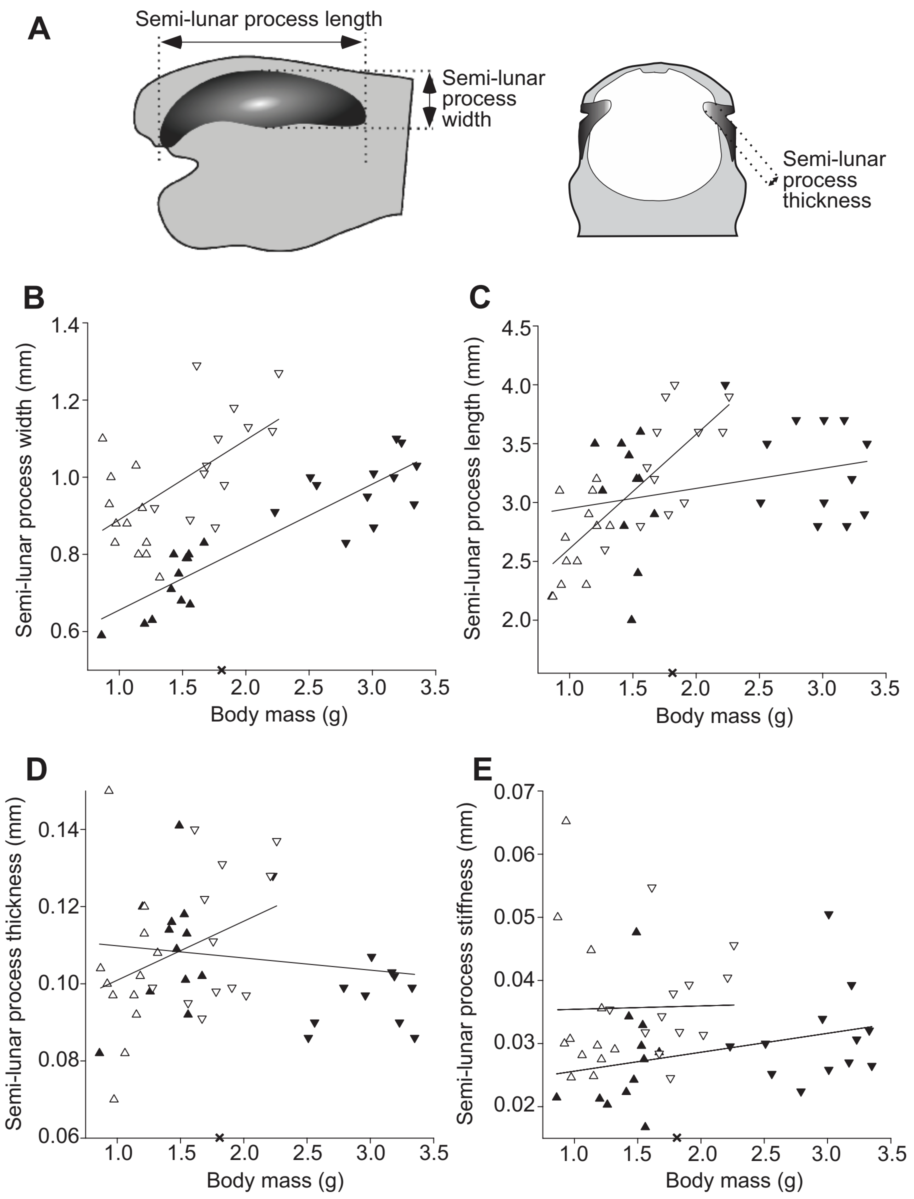

Fig. 6. Dimensions of the semi-lunar process in solitarious and gregarious locusts. (A) Diagrammatic lateral view and cross-section of the distal femur illustrating maximum length, width and thickness of a semi-lunar process. (B) Width. (C) Length. (D) Semi-lunar process cross-sectional thickness. (E) Stiffness (width×thickness/length). N=12 for each group. Solitarious females, black downward-facing triangles; solitarious males, black upward triangles; gregarious females, white downward triangles; gregarious males, white upward triangles. The small × on the horizontal axis indicates the location of the EMM.

The take-off velocity can be predicted from the kinetic energy (e_{kinetic}) released during a jump:

$$v = \sqrt{\frac{2e_{\mathrm{kinetic}}}{m}}. \tag{9}$$

By conservation of energy, the energy released from the jump must be equivalent to the energy put into it from the elastic energy stored in the semi-lunar processes and extensor apodeme. Substituting in the expression for elastic energy (Eqn 4) above gives:

$$v = \sqrt{\frac{F^2}{sm}}. \tag{10}$$

The muscle force (F) is related to muscle volume as discussed above, and s is the s_{f} calculated above. Substituting in leg volume leaves:

$$v = \sqrt{\frac{(f_{\mathrm{volume}})^2}{s_{\mathrm{f}}m}}. \tag{11}$$

Comparing the relative size of these terms in solitarious and gregarious locusts at the EMM cancels out body mass. If f_{volume} and s_{f} are both given nominal values of 1 in gregarious locusts, then the equivalent values for solitarious locusts are 1.175 and 0.88, respectively. Calculating velocity (v) from these values gives gregarious locusts a value of 1 and solitarious locusts a value of 1.253; therefore, it would be expected that the take-off velocity of solitarious locusts would be 25.3% faster than gregarious locusts. The measured maximum take-off velocity of solitarious locusts at the EMM was 3.28 m s^{-1}, or 24.7% faster than that of gregarious locusts at 2.63 m s^{-1}. The predicted and measured values are thus within 2.5% of each other, indicating that this model explains most of the observed differences in jumping performance between phases.

Compensating for changing body mass

A notable feature of the jumping performance of locusts is how little it was affected by the considerable range in body mass (in solitarious locusts from 0.86 to 3.35 g, a 3.9-fold range, and in gregarious locusts from 0.87 to 1.89 g, a 2.2-fold range). From Eqn 11 it is clear that, all else being equal, an increase in mass should lead to a decrease in take-off velocity. This detrimental effect

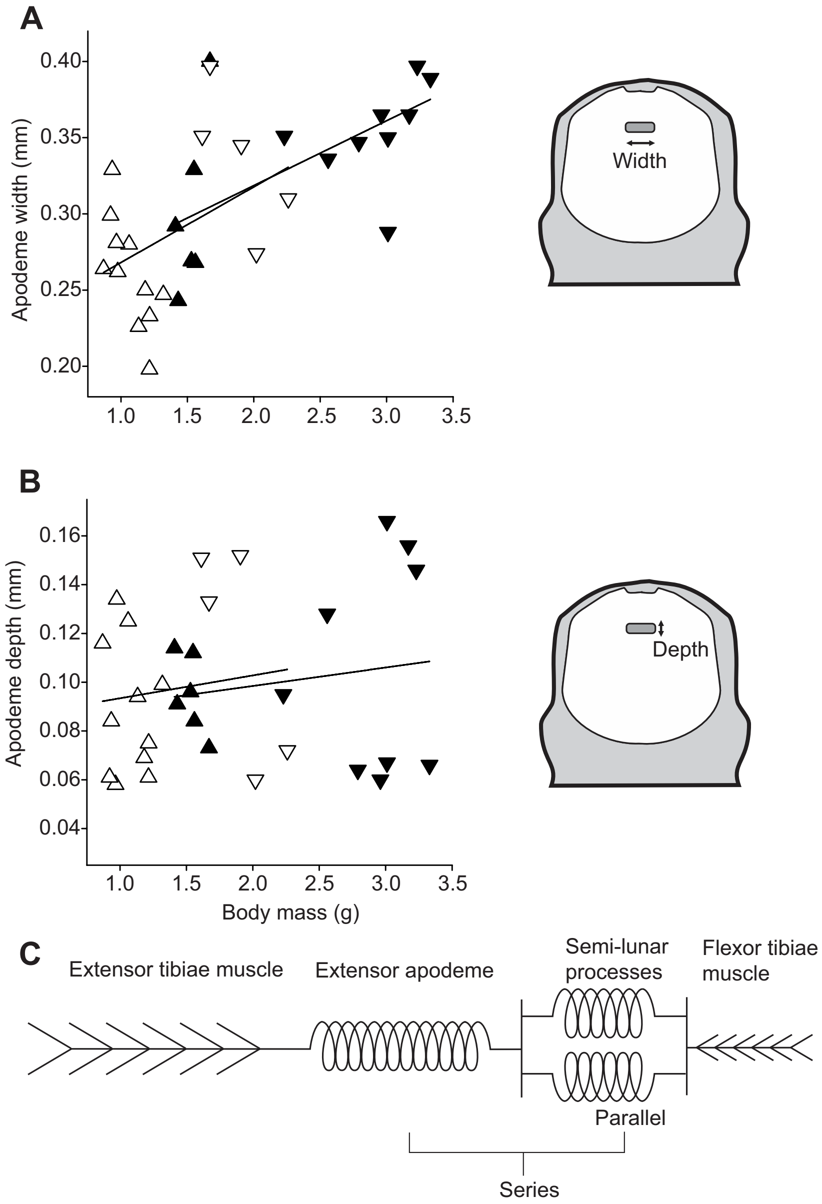

Fig. 7. Dimensions of the apodeme of the extensor tibiae muscle in the distal femur. Scatter plots of the depth (A) and width (B) of the extensor apodeme against body mass (*N*=9 solitarious females, 10 solitarious males, 8 gregarious females and 11 gregarious males). Solitarious females, black downward facing triangles; solitarious males, black upward triangles; gregarious females, white downward triangles; gregarious males, white upward triangles. (C) Diagram of the arrangements of the muscles and the two elements of the springs upon which they act (muscle apodeme and semi-lunar processes) to store energy for the jump.

of increased body mass could in principle be compensated by decreasing the stiffness of the cuticular springs and/or increasing the muscular force (femur volume).

Individually, the length, and in particular the width, of a semi-lunar process scaled with body mass (Fig. 6A,B). Overall, however, the dimensions of the semi-lunar process internally compensate and cancel out these linear mass-dependent differences to produce a constant stiffness that is characteristic of each locust phase (Fig. 6E). The length of the hind femur (Fig. 4B), and hence the apodeme of the extensor tibiae muscle, increased in length with increasing body mass, tending to decrease its stiffness. Counteracting this, the depth of the apodeme increased with increasing body mass (Fig. 7A), which would tend to increase its stiffness. We calculated the relative stiffness of the extensor apodeme (apodeme area/femur length) after dividing the length of the hind femora of solitarious locusts by 1.047 to bring them into register with those from gregarious locusts. The stiffness of the apodeme did not scale significantly with body mass (r^2=0.032, $F_{1,29}$=0.946, P=0.339). Therefore, it seems that neither element of the cuticular springs powering the jump can provide the mass-dependent variation needed to correct for changes in body mass.

The volume of the hind femur showed a strong correlation with body mass (Fig. 4E). From Eqn 11 it is apparent that to compensate fully for body mass, the change in femoral volume squared (and hence maximum possible muscle force) would have to scale with changes in body mass with a slope of 1. Fig. 8A shows femoral volume squared against body mass, and Fig. 8B shows a normalised plot of change in body mass against relative change in femoral volume squared. The minimum body mass in the sample was normalised to 1, and all other body masses scaled as multiples of this; femoral volume squared was normalised so that the mean was scaled to be the same as mean body mass. Femoral volumes from solitarious locusts were also divided by 1.175 to bring them into register with volumes from gregarious locusts. The slope for the fitted regression was 1.01±0.07 and the intercept 0.03±0.16 (r^2=0.82, $F_{1,46}$=210.473, P<0.001). Therefore, we conclude that changes in femoral volume are sufficient to fully counteract changes of body mass.

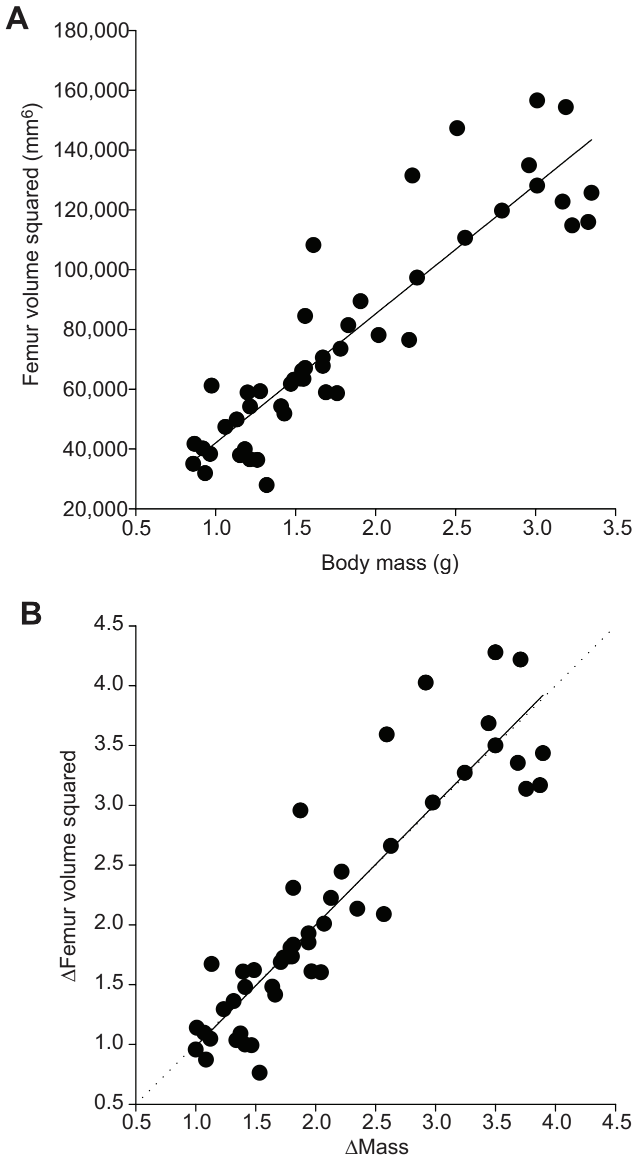

Fig. 8. Femoral volume squared scales isometrically with body mass. (A) Scatter plot of the square of femoral volume against body mass. (B) Normalised data, plotting the change in femur volume squared against change in body mass. The solid line is a regression fitted to the data; the dotted line is the equation *y*=*x*. Femur volumes from solitarious locusts have been reduced by 17.5% to bring them into the same register as volumes from gregarious locusts.

The neurophysiology of jumping

Myogram recordings from the femur revealed the pattern of motor spikes that preceded a jump (Fig. 9A). The recordings were dominated by the large potentials from the single fast extensor tibiae (FETi) motor neuron; potentials from the many flexor tibiae (FlTi) motor neurons were much smaller (Godden, 1975; Heitler and Burrows, 1977). In many jumps, locusts did not produce a full co-contraction (defined as simultaneous activity in both extensor and flexor motor neurons), but instead produced a short burst (three to seven) of spikes in FETi only, resulting in a low-velocity (approximately 1.5 m s^{-1}) hop, much below their best performance. Jumps with a take-off velocity below 2 m s^{-1} were not analysed, leaving us with recordings from five different solitarious and eight different gregarious locusts. The take-off velocities achieved under these conditions (Fig. 9B) were slightly lower than those of free locusts (Fig. 2A), but solitarious locusts (2.95±0.23 m s^{-1}) were still on average 26.6% faster than gregarious locusts (2.33 ±0.09 m s^{-1}; Mann–Whitney, *U*=5.5, *N*=5, 8, *P*=0.034). The duration of the co-contraction preceding the jump (Fig. 9C) was on average 72±19% longer in solitarious locusts (391±44 ms) than in gregarious locusts (228±22 ms; Mann–Whitney, *U*=3.0, *N*=5, 8, *P*=0.013), and in this period more than twice as many FETi spikes were produced (solitarious locusts 47.2±10.8 spikes, gregarious locusts 19.9±2.9 spikes; Mann–Whitney, *U*=2.0, *N*=5, 8, *P*=0.008; Fig. 9D). The peak (Fig. 9E) and average spike rate (Fig. 9F) of FETi, however, did not differ significantly between phases, even though the highest values were seen in solitarious locusts (peak spike rate: median value 177 spikes s^{-1}, Mann–Whitney, *U*=13.0, *N*=5, 8, *P*=0.306; average spike rate: median value 99 spikes s^{-1}, Mann–Whitney, *U*=18, *N*=5, 8, *P*=0.770). The increase in jump performance in solitarious locusts thus comes at the cost at taking nearly twice as long to load the energy storage mechanism in preparation for take-off.

DISCUSSION

Solitarious locusts, with their disproportionately longer hind femora, can jump almost 25% further and faster than gregarious locusts. The improved performance of solitarious locusts comes from two structural differences: first, from an increased hind femoral volume relative to total body mass, and hence the capability of producing greater force in the extensor tibiae muscle; and second, from differences in the structure, and hence elasticity, of the energy-storing springs of the hind femora. As the extensor tibiae muscle is highly pinnate and its fibres insert onto its apodeme at an angle of approximately 20 deg (Bennet-Clark, 1975), there is a complex relationship between the area and length of the femur and that of the muscle within it. Increased femoral length will increase both muscular cross-sectional area, increasing the maximum force that can be produced, and muscle length, increasing the amount by which the muscle can distort the energy-storing springs. Longer hind femora give rise to increased jump performance in solitarious locusts because the muscles powering the jump are entirely within the femur rather than spanning between the body wall and trochanteral joints of the legs, as in long- and short-legged leafhoppers (Burrows and Sutton, 2008).

The F:C ratios of solitarious locusts (Fig. 1D), agreed closely with published values for wild solitarious locust populations (Dirsh, 1951, 1953). For the gregarious locusts, however, the values were 11% higher than those reported for wild gregarious locust populations (means 3.18 and 3.11, respectively; Dirsh, 1951).

The 4.5% difference in the stiffness of the apodeme of the extensor tibiae muscle between phases was much less than the 25.7% change in the stiffness of the semi-lunar processes. To achieve a comparable reduction in stiffness, the apodeme (and hence the femur) would have to be 33% longer in solitarious locusts. Reducing the stiffness of the apodeme by decreasing its cross-sectional area is probably not viable, as its safety factor (the ratio of a material's breaking strength to its applied load) is already only approximately 1.2 (Bennet-Clark, 1975). Decreasing the area of the apodeme further would increase the stress on it (which is proportional to force/area) and hence increase the likelihood of a break occurring.

How much do the changes in the muscle volume and energy storage structures individually contribute to the difference in jumping performance between phases? Considering a theoretical arrangement in which the properties of the cuticular springs changed but were not accompanied by any changes in femoral volume, then the expected

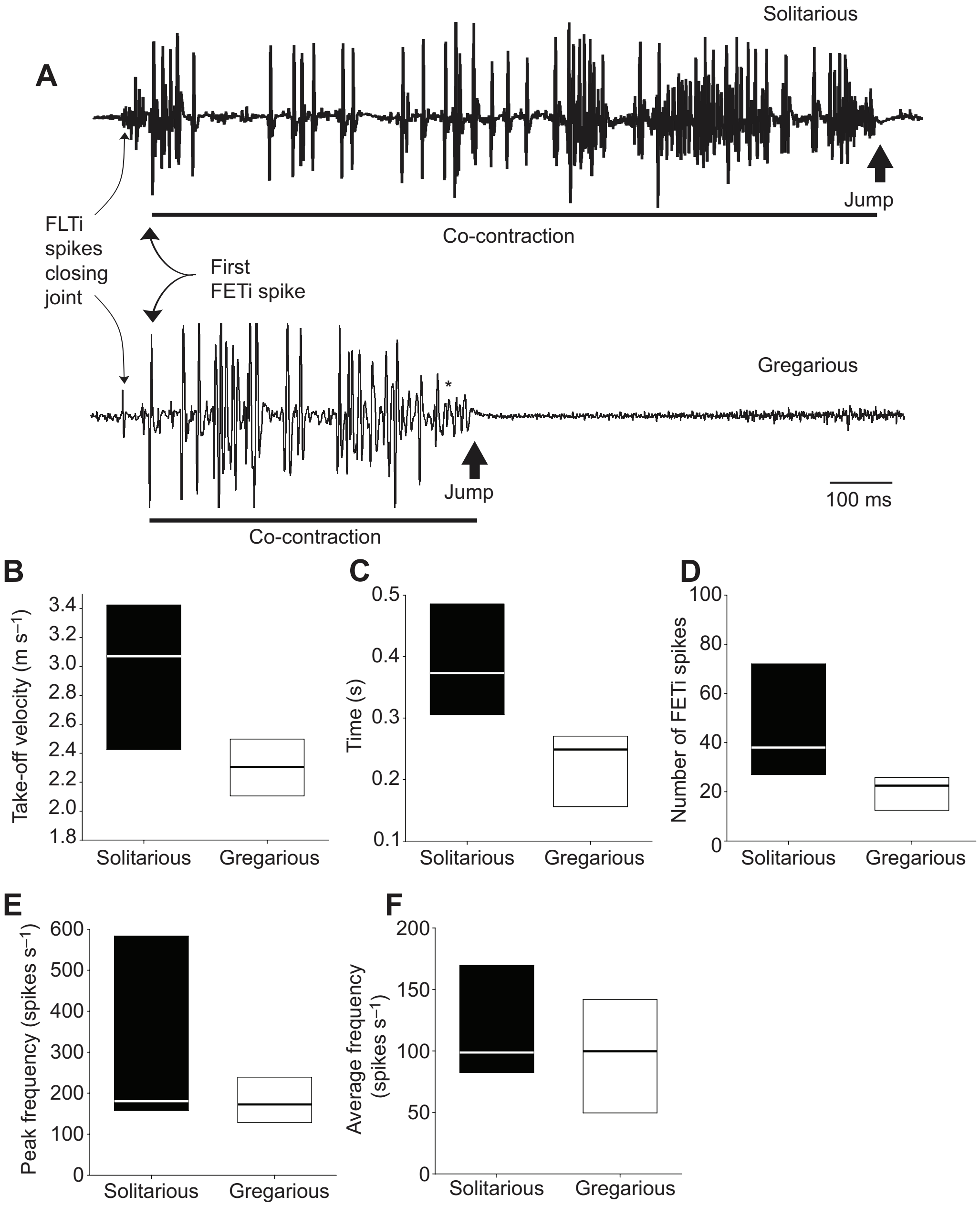

Fig. 9. The co-contraction phase in preparation for a jump lasts nearly twice as long in solitarious locusts. (A) Representative myogram recordings of neuro-muscular activity in hind extensor and flexor tibiae muscles prior to jumping by solitarious (top trace) and gregarious (bottom trace) locusts. The largest amplitude spikes are from the fast extensor tibiae (FETi) motor neuron. The two traces are aligned by the first FETi spikes. A burst of smaller amplitude spikes in flexor tibiae (FlTi) motor neurons precedes co-contraction and fully flexes and locks the femoro-tibial joint. Co-contraction is characterised by activity in both FETi and FlTi. Towards the end of co-contraction the high frequency of spiking leads to destructive interference between successive spike waveforms and a decrease in overall amplitude (asterisk). A jump is released when co-contraction ends. (B–F) Box plots showing the median (line) and interquartile ranges (boxes) of: (B) take-off velocity of locusts with implanted myogram wires; (C) duration of co-contraction; (D) total number of FETi spikes; (E) peak spike frequency of FETi; and (F) average spike frequency of FETi during co-contraction. Data are independent measurements from five solitarious and eight gregarious locusts.

increase in jump velocity in solitarious locusts would be 6.7%, or just 26% of the calculated or observed difference in performance between phases. Conversely, if femoral volume in solitarious locusts was increased by the observed 17.5% but there was no accompanying change in the stiffness of the cuticular springs, then the expected difference in take-off velocity would also be 17.5%, or still only 69% of the total calculated difference. The majority of the increased performance in solitarious locusts therefore comes from the increase in volume of the femoral muscle relative to body mass, but the altered properties of the semi-lunar processes also make a significant contribution; the effect of changing both is marginally greater than the sum of their individual effects. Solitarious locusts expended on average 100±16% more energy during a jump than gregarious locusts, and the co-contraction preceding jumping lasted on average 72±19% longer, suggesting that the power output of the muscles delivering energy to the springs was the same in both phases, or at best only marginally higher in solitarious locusts.

The phenotypes that characterise each phase are entirely environmentally determined and depend upon exposure to other locusts. It might then be expected that all locusts, regardless of phase, would adopt the properties of a solitarious femur and therefore benefit from faster and longer jumps. The improved jumping performance of solitarious locusts, however, incurs substantial costs, offsetting its advantages. For example, the 25% improvement in take-off velocity in solitarious locusts (Fig. 2A) entails expending 100% more energy (Fig. 2E). Furthermore, the duration of the muscular co-contraction preceding a jump is nearly twice as long in solitarious locusts as it is in gregarious locusts; therefore, improved jump velocity is offset by a much longer lead-in time before the jump can be released.

These costs can also be understood in terms of the number of jumps required to move a particular distance. A gregarious locust requires four successive jumps (predicted average 341.5 cm, 4 times average single jump distance of 85.4 cm) to cover the same

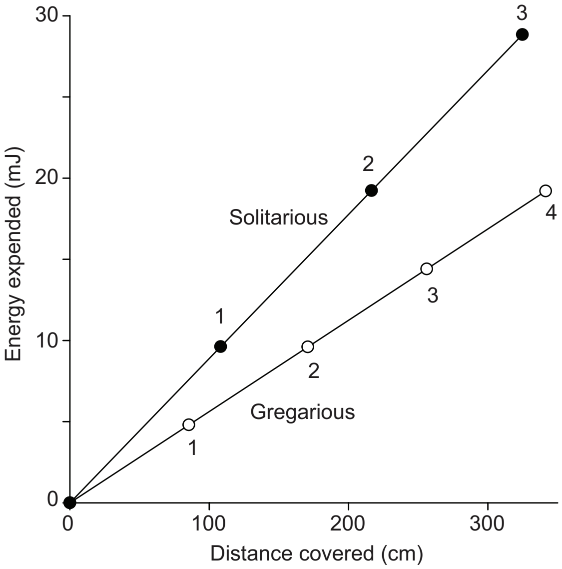

Fig. 10. Energy used in jumping a fixed distance by solitarious and gregarious locusts. To cover the same distance, solitarious locusts (filled circles) require only three jumps compared with four by gregarious locusts (open circles). Their energy expenditure is, however, higher.

distance that a solitarious locust can cover in three (predicted average 324.8 cm, 3 times average single jump distance of 108.3 cm), but in doing so will only expend an average of 19.2 mJ of energy compared with the average of 28.8 mJ by a solitarious locust. This is an energy saving of 33% (Fig. 10A). Jumping in grasshoppers is a metabolically costly activity, and in the first minute of repetitive jumping a substantial oxygen debt is incurred with a corresponding accumulation of lactate in the extensor tibiae muscle (Zebe and McShan, 1957; Gade, 1984; Harrison et al., 1991; Kirkton et al., 2005). *Schistocerca americana*, a closely related non-swarming species that shows limited phase change (Sword, 2003; Gotham and Song, 2013), undergoes a two-thirds decrease in its jumping rate during 5 min of sustained jumping (Kirkton and Harrison, 2006).

Solitarious locusts do not use jumping as a primary means of locomotion, whereas gregarious locusts, particularly nymphs, do (Ellis, 1951; Gabriel, 1985a). The primary defence of solitarious locusts against predation is to remain undetected, but if found they will be a direct target. Solitarious locusts need therefore to escape from a predator's strike as fast and as far as possible, so that they land far enough away to settle and hide again; they rarely need to make consecutive escape jumps.

Adult gregarious locusts migrate by flying, but still spend much of the day on the ground (Uvarov, 1966). They are therefore still vulnerable to ground-based predators, and jumping remains an important defence. Individual predation risk is mitigated by being part of a large group, even though animals are more exposed (Hamilton, 1971; Foster and Treherne, 1981), but protection depends on remaining within the group. Being able to jump repeatedly with little respite is likely to be crucial to remaining responsive to the activity of other locusts and maintaining group cohesion. Absolute jump velocity and distance may be less important; indeed, a jumping performance better than conspecifics' may take a locust outside the group, or make it more conspicuous, and therefore be counterproductive. Moreover, gregarious locusts live in a complex sensory environment dominated by stimuli produced by neighbouring locusts (Rogers et al., 2007, 2010; Ott and Rogers, 2010; Burrows et al., 2011). Their ability to detect approaching danger from long distances may therefore be limited by this environment so that they may need a jumping mechanism that requires shorter preparation. Solitarious locusts, however, may have greater forewarning and thus be able to co-contract for longer, releasing a high-velocity jump at the last possible moment to forestall a predator altering its approach strategy. Locust nymphs are less proficient jumpers than adults (Gabriel, 1985a,b), but differences in femur morphology between phases are still apparent in locust nymphs. It is therefore likely that differences in relative jumping performance exist between non-adult solitarious and gregarious locusts, even though the absolute distances jumped are likely to be less.

Despite the considerable developmental plasticity evinced by phase change in locusts, the jumping strategy falls into two clear classes, and it is notable that within each phase there is little variation in jump performance despite considerable differences in body size. This suggests that the necessary developmental coordination between body size, relative muscular growth, cuticular specialisations and neuronal control to produce a viable jumping mechanism limits the possible variation between these factors and leads to the canalised growth trajectories characteristic of each phase.

Competing interests

The authors declare no competing or financial interests.

Author contributions

S.M.R. and M.B. conceived the project. S.M.R. performed the quantitative analysis, and wrote the manuscript. J.R. and C.B. conducted the jumping experiments and wrote an initial report. G.P.S., assisted by S.M.R., performed the biomechanical analysis. S.M.R., D.A.C. and M.B. performed the electrophysiological experiments. M.B. conducted writing, analysis and presentation of data.

Funding

S.M.R., J.R. and C.B. were supported by a grant from the Biotechnology and Biological Sciences Research Council (BBSRC) (UK) to M.B. and S.M.R. (BB/H002537/1). G.P.S. is supported by a Royal Society (UK) University Research Fellowship.

References

Alexander, R. M. (1995). Leg design and jumping technique for humans, other vertebrates and insects. *Philos. Trans. R. Soc. B Biol. Sci.* **347**, 235-248.

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. (1990). Jumping in Orthoptera. In *Biology of Grasshoppers* (ed. R. F. Chapman and A. Joern), pp. 173-203. New York: John Wiley and Sons.

Bennet-Clark, H. C. and Alder, G. M. (1979). The effect of air resistance on the jumping performance of insects. *J. Exp. Biol.* **82**, 105-121.

Bouaïchi, A., Roessingh, P. and Simpson, S. J. (1995). An analysis of the behavioural effects of crowding and re-isolation on solitary-reared adult desert locusts (*Schistocerca gregaria*) and their offspring. *Physiol. Entomol.* **20**, 199-208.

Brown, R. H. J. (1967). Mechanism of locust jumping. *Nature* **214**, 939.

Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J., Despland, E., Miller, E. R. and Simpson, S. J. (2006). From disorder to order in marching locusts. *Science* **312**, 1402-1406.

Buhl, J., Sword, G. A., Clissold, F. J. and Simpson, S. J. (2011). Group structure in locust migratory bands. *Behav. Ecol. Sociobiol.* **65**, 265-273.

Burrows, M. (1995). Motor patterns during kicking movements in the locust. *J. Comp. Physiol. A* **176**, 289-305.

Burrows, M. (1996). *The Neurobiology of an Insect Brain*. Oxford, UK: Oxford University Press.

Burrows, M. and Morris, G. (2001). The kinematics and neural control of high-speed kicking movements in the locust. *J. Exp. Biol.* **204**, 3471-3481.

Burrows, M. and Sutton, G. P. (2008). The effect of leg length on jumping performance of short- and long-legged leafhopper insects. *J. Exp. Biol.* **211**, 1317-1325.

Burrows, M. and Sutton, G. P. (2012). Locusts use a composite of resilin and hard cuticle as an energy store for jumping and kicking. *J. Exp. Biol.* **215**, 3501-3512.

Burrows, M., Rogers, S. M. and Ott, S. R. (2011). Epigenetic remodelling of brain, body and behaviour during phase change in locusts. *Neural Sys. Circuits* **1**, 11.

Dirsh, V. M. (1951). A new biometrical phase character in locusts. *Nature* **167**, 281-282.

Dirsh, V. M. (1953). Morphometrical studies on phases of the desert locust. *Anti-Locust Bull.* **16**, 1-34.

Ellis, P. E. (1951). The marching behaviour of hoppers of the African migratory locust, *Locusta migratoria migratorioides* (R. & F.), in the laboratory. *Anti-Locust Bull.* **7**, 1-48.

Ellis, P. E. (1959). Learning and social aggregation in locust hoppers. *Anim. Behav.* **7**, 91-106.

Ernst, U. R., Van Hiel, M. B., Depuydt, G., Boerjan, B., De Loof, A. and Schoofs, L. (2015). Epigenetics and locust life phase transitions. *J. Exp. Biol.* **218**, 88-99.

Foster, W. A. and Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* **293**, 466-467.

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.

Gade, G. (1984). Anaerobic energy metabolism. In *Environmental Physiology and Biochemistry of Insects* (ed. K. H. Hoffmann), pp. 119-136. Berlin: Springer-Verlag.

Godden, D. H. (1975). The neural basis for locust jumping. *Comp. Biochem. Physiol. A* **51**, 351-360.

Gotham, S. and Song, H. (2013). Non-swarming grasshoppers exhibit density-dependent phenotypic plasticity reminiscent of swarming locusts. *J. Insect Physiol.* **59**, 1151-1159.

Hamilton, W. D. (1971). Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295-311.

Harrison, J. F., Phillips, J. E. and Gleeson, T. T. (1991). Activity physiology of the two-striped grasshopper, *Melanoplus bivittatus*: gas exchange, hemolymph acid base status, lactate production, and the effect of temperature. *Physiol. Zool.* **64**, 451-472.

Heitler, W. J. (1974). The locust jump. Specialisations of the metathoracic femoral-tibial joint. *J. Comp. Physiol.* **89**, 93-104.

Heitler, W. J. (1977). The locust jump. III. Structural specializations of the metathoracic tibiae. *J. Exp. Biol.* **67**, 29-36.

Heitler, W. J. and Burrows, M. (1977). The locust jump. I. The motor programme. *J. Exp. Biol.* **66**, 203-219.

Islam, M. S., Roessingh, P., Simpson, S. J. and McCaffery, A. R. (1994). Effects of population density experienced by parents during mating and oviposition on the phase of hatchling desert locusts*, Schistocerca gregaria. Proc. R. Soc. B Biol. Sci.* **257**, 93-98.

Kirkton, S. D. and Harrison, J. F. (2006). Ontogeny of locomotory behaviour in the American locust, *Schistocerca americana*: from marathoner to broad jumper. *Anim. Behav.* **71**, 925-931.

Kirkton, S. D., Niska, J. A. and Harrison, J. F. (2005). Ontogenetic effects on aerobic and anaerobic metabolism during jumping in the American locust, *Schistocerca americana*. *J. Exp. Biol.* **208**, 3003-3012.

Lester, R. L., Grach, C., Pener, M. P. and Simpson, S. J. (2005). Stimuli inducing gregarious colouration and behaviour in nymphs of *Schistocerca gregaria*. *J. Insect Physiol.* **51**, 737-747.

Ott, S. R. and Rogers, S. M. (2010). Gregarious desert locusts have substantially larger brains with altered proportions compared with the solitarious phase. *Proc. R. Soc. B Biol. Sci.* **277**, 3087-3096.

Pener, M. P. and Simpson, S. J. (2009). Locust phase polyphenism: an update. *Adv. Insect Physiol.* **36**, 1-272.

R Development Core Team (2008). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at https://www.R-project.org.

Roessingh, P. and Simpson, S. J. (1994). The time-course of behavioural phase change in nymphs of the desert locust*, Schistocerca gregaria. Physiol. Entomol.* **19**, 191-197.

Roessingh, P., Simpson, S. J. and James, S. (1993). Analysis of phase-related changes in behaviour of desert locust nymphs. *Proc. R. Soc. B Biol. Sci.* **252**, 43-49.

Rogers, S. M., Matheson, T., Despland, E., Dodgson, T., Burrows, M. and Simpson, S. J. (2003). Mechanosensory-induced behavioural gregarization in the desert locust *Schistocerca gregaria*. *J. Exp. Biol.* **206**, 3991-4002.

Rogers, S. M., Matheson, T., Sasaki, K., Kendrick, K., Simpson, S. J. and Burrows, M. (2004). Substantial changes in central nervous system neurotransmitters and neuromodulators accompany phase change in the locust. *J. Exp. Biol.* **207**, 3603-3617.

Rogers, S. M., Krapp, H. G., Burrows, M. and Matheson, T. (2007). Compensatory plasticity at an identified synapse tunes a visuomotor pathway. *J. Neurosci.* **27**, 4621-4633.

Rogers, S. M., Harston, G. W. J., Kilburn-Toppin, F., Matheson, T., Burrows, M., Gabbiani, F. and Krapp, H. G. (2010). Spatiotemporal receptive field properties of a looming-sensitive neuron in solitarious and gregarious phases of the desert locust. *J. Neurophysiol.* **103**, 779-792.

Rogers, S. M., Cullen, D. A., Anstey, M. L., Burrows, M., Despland, E., Dodgson, T., Matheson, T., Ott, S. R., Stettin, K., Sword, G. A. et al. (2014). Rapid behavioural gregarization in the desert locust, *Schistocerca gregaria* entails synchronous changes in both activity and attraction to conspecifics. *J. Insect Physiol.* **65**, 9-26.

Simpson, S. J., McCaffery, A. R. and Hägele, B. F. (1999). A behavioural analysis of phase change in the desert locust. *Biol. Rev. Camb. Philos. Soc.* **74**, 461-480.

Simpson, S. J., Despland, E., Hägele, B. F. and Dodgson, T. (2001). Gregarious behavior in desert locusts is evoked by touching their back legs. *Proc. Natl. Acad. Sci. USA* **98**, 3895-3897.

Steedman, A. (ed.) (1990). *Locust Handbook*, 3rd edn. Chatham, UK: Natural Resources Institute.

Sword, G. A. (1999). Density-dependent warning coloration. *Nature* **397**, 217-217. .

Sword, G. A. (2002). A role for phenotypic plasticity in the evolution of aposematism. *Proc. R. Soc. B Biol. Sci.* **269**, 1639-1644.

Sword, G. A. (2003). To be or not to be a locust? A comparative analysis of behavioral phase change in nymphs of *Schistocerca americana* and *S. gregaria*. *J. Insect Physiol.* **49**, 709-717.

Uvarov, B. P. (1921). A revision of the genus *Locusta*, L. (=*Pachytylus*, Fieb.), with a new theory as to the periodicity and migrations of locusts. *Bull. Entomol. Res.* **12**, 135-163.

Uvarov, B. P. (1966). *Grasshoppers and Locusts*, Vol. 1. London: Cambridge University Press.

Uvarov, B. P. (1977). *Grasshoppers and Locusts*, Vol. 2. London: Centre for Overseas Pest Research.

Wang, X. and Kang, L. (2014). Molecular mechanisms of phase change in locusts. *Annu. Rev. Entomol.* **59**, 225-244.

Warton, D. I., Duursma, R. A., Falster, D. S. and Taskinen, S. (2012). smatr 3 – an R package for estimation and inference about allometric lines. *Methods Ecol. Evol.* **3**, 257-259.

Zajac, F. E. (1989). Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. *Crit. Rev. Biomed. Eng.* **17**, 359-411.

Zebe, E. C. and McShan, W. H. (1957). Lactic and α-glycerophosphate dehydrogenases in insects. *J. Gen. Physiol.* **40**, 779-790.