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Locust Migration—A Forced March

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Report

Collective Motion and Cannibalism in Locust Migratory Bands

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Summary

Plagues of mass migrating insects such as locusts are estimated to affect the livelihood of one in ten people on the planet [1]. Identification of generalities in the mechanisms underlying these mass movements will enhance our understanding of animal migration and collective behavior while potentially contributing to pest-management efforts. We provide evidence that coordinated mass migration in juvenile desert locusts (*Schistocerca gregaria*) is influenced strongly by cannibalistic interactions. Individuals in marching bands tend to bite others but risk being bitten themselves. Reduction of individuals' capacity to detect the approach of others from behind through abdominal denervation (1) decreases their probability to start moving, (2) dramatically reduces the mean proportion of moving individuals in groups, and (3) significantly increases cannibalism. Similarly, occlusion of the rear visual field inhibits individuals' propensity to march. Abdomen denervation did not influence the behavior of isolated locusts. When within groups, abdominal biting and the sight of others approaching from behind triggers movement, creating an autocatalytic feedback that results in directed mass migration. This "forced march" driven by cannibalistic interactions suggests that we need to reassess our view of both the selection pressure and mechanism that can result in the coordinated motion of such large insect groups.

Results and Discussion

Effect of Mechanosensory and Visual Stimuli on Collective Motion in *Schistocerca gregaria*

Recently, it has been demonstrated that alignment among nearby moving neighbors allows locusts within aggregates to align spontaneously and start marching once a threshold density of locusts is achieved [2]. This finding raises a key question about the biological process that underlies such collective migration: Why should individuals align with neighbors? An important clue came from field studies of swarming Mormon crickets (*Anabrus simplex*) in the United States [3–5], where individuals' motion is driven by the need to find nutrients such as protein and salt and where cannibalism within migratory bands is rife [3, 4]. If individuals fail to continue moving they are likely to be attacked and risk becoming another cricket's source of these essential resources. Importantly, cannibalism in animals is a widespread and common feeding strategy [6], particularly so among grasshoppers, locusts, and Mormon crickets, in which it can be a major cause of mortality in the field [3, 7–9]. By conducting manipulative experiments combined with detailed analyses of individual and group behavior, we tested the prediction that cannibalism serves as a general mechanism for the transition from relatively disordered and benign aggregations to highly coordinated and mobile bands which are responsible for the devastating impact of marching locusts [10].

We experimentally manipulated the degree to which individuals could detect mechanosensory (tactile) and visual information about conspecifics approaching from behind under controlled laboratory conditions. In addition, we investigated the importance of insects having sight of those insects ahead. Experiments were performed in a ring-shaped arena (80 cm in diameter) with a central dome, to restrict the perception of other individuals on the opposite side of the arena (as described in [2] and shown in Figure S1 available online). Individuals in such arenas select collectively a (randomly determined) rotational direction of travel. This simulates, in a reasonable space, the persistent collective marching of nymphs in sparse desert conditions [2]. Automated digital tracking software [2] was used to obtain the position, speed, and direction of all individuals concurrently five times per s (see the Experimental Procedures and Figure S1).

To manipulate the sense of physical contact from conspecifics approaching from behind, we constructed two treatment categories consisting of locusts that could sense tactile cues from their abdomen and locusts that could not. To denervate individuals, we severed the abdominal connectives of the ventral nerve cord (immediately posterior to the metathoracic ganglion, responsible for conveying sensory information from abdominal exterceptors, such as cerci, to the brain and thoracic centers [1]) through a small, hinged window cut in the cuticle (Figure S2). This denervates the majority of the abdomen. All operated locusts were checked for healthy movement, and were left to recover for 20–30 min with food ad libitum. For control insects, we performed a sham operation, where the ventral connectives were surgically exposed but not severed.

Effect of Abdomen Denervation on the Behavior of Isolated Locusts

The removal of sensation from the abdomen did not inherently influence individual motion. Tracking of the motion of both control and denervated individuals in isolation in the arena for 4 hr revealed no difference in the proportion of time spent moving (Figure 1A, t test, $p = 0.742$, $T = -0.336$, $Df = 12$) or

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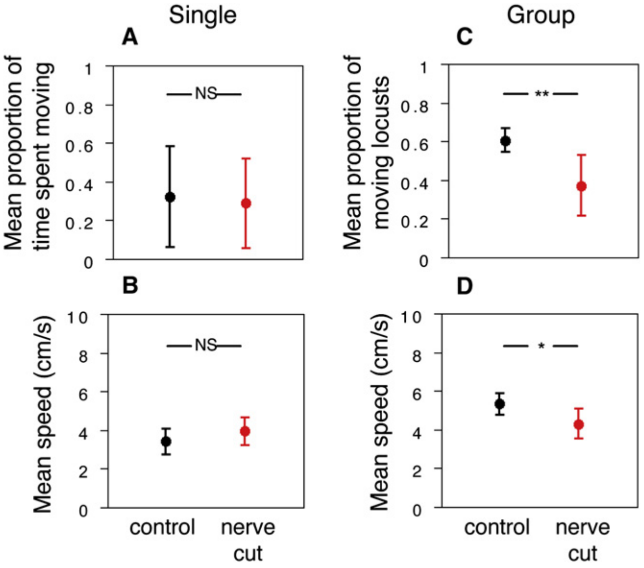

Figure 1. Sensing Contact from Behind Stimulates Marching

Measures of locust behavior when isolated or within groups in response to control (black) and nerve-cut (red) treatments. Seven experimental trials were carried out for each treatment in the single locust experiments. Ten experimental trials were carried out for each treatment in locust group experiments. Trial duration was 4 hr. For all experiments, the mean proportion of time spent moving and the mean proportion of moving insects, for single and group experiments, respectively, and the mean speed of moving locusts, were calculated for each trial and averaged within treatment. Error bars show ± 1 standard deviation (SD).

(A) Mean proportion of time spent marching by single locusts: control = 0.32, SD = 0.26; nerve cut = 0.29, SD = 0.23; n = 7.

(B) Mean speed (cm/s) of single locusts: control = 3.39, SD = 0.68; nerve cut = 3.93, SD = 0.72; n = 7.

(C) Mean proportion of moving locusts in a group: control = 0.60, SD = 0.06; nerve cut = 0.37, SD = 0.16; n = 10.

(D) Mean speed (cm/s) of moving locusts in a group: control = 5.32, SD = 0.56; nerve cut = 4.28, SD = 0.76; n = 10.

mean speed of movement (Figure 1B, t test, p = 0.176, T = 1.437, Df = 12) despite the sensitive nature of our data acquisition and analysis. Thus, there was no discernable effect of the nerve-cut surgery on locust motion when insects were alone in the arena.

Effect of Abdomen Denervation on the Behavior of Locusts within Groups

We investigated the motion of sham-operated and denervated individuals in groups of 15 individuals, a density for which strongly coordinated marching readily occurs in our experimental arena [2]. Reduction of the sensation of individuals approaching from behind had a very strong negative influence on marching behavior in groups; the mean proportion of moving locusts and their mean speed when moving were significantly lower in abdomen-denervated groups (Figure 1C, t test assuming unequal variance, p = 0.001, T = −4.236, Df = 11, and Figure 1D, t test, p = 0.003, T = −3.430, Df = 18, respectively).

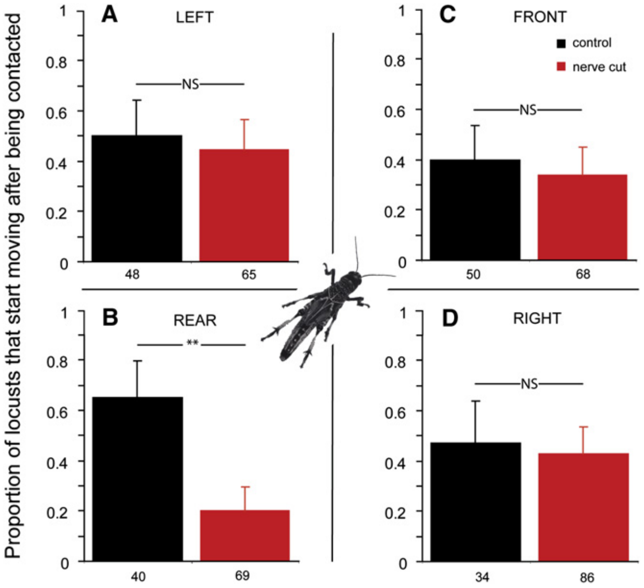

Figure 2. Individual Behavior Analysis

All physical contacts among mobile individuals approaching those that were stationary (had not moved in at least 5 s) were analyzed for the first 10 min of the experiment. The mean proportion of stationary locusts that started to move when contacted from each of four different directions—left side (A), rear (B), front (C), and right side (D)—was calculated for control (black) and nerve-cut (red) treatments. The numbers below the bars indicate the number of replicates. Error bars show 95% confidence intervals.

These results demonstrate that sensation of contact of others from behind plays an important role in determining the extent to which locusts will move, as well as the resulting degree of coordinated movement among individuals in marching bands [2]. Despite the fact that only abdomen sensation was removed, the proportion of time spent moving by denervated individuals in a group was very similar to that expected if they were not influencing each other at all (Figures 1A and 1C).

Tactile Activation of Inactive Locusts Is Specifically through Abdominal Contact

To test further whether this lack of reactivity was the specific result of abdominal denervation rather than some global effect of surgery, we investigated the response of stationary individuals within groups to tactile contact from conspecifics approaching from different directions during the experiments. A significant difference between the control and the nerve-cut locusts appeared during the first 10 min of the experiments. This difference was in the probability to start moving after being contacted from the rear (Figure 2B, chi-square = 21.78, Df = 1, p = 3.05 × 10^{-6}) but not when contacted from the left (Figure 2A, chi-square = 0.321, Df = 1, p = 0.571), the front (Figure 2C, chi-square = 0.475, Df = 1, p = 0.491), or the right (Figure 2D, chi-square = 0.161, Df = 1, p = 0.688). Relative to contact from conspecifics approaching in other directions, contact from behind resulted in the highest probability (0.65) of movement among the sham-operated insects. The opposite occurred among the nerve-cut locusts, where contact from behind resulted in the *lowest* probability (0.2) of subsequent movement. Thus, the lack of collective activity in the nerve-cut animals is not the consequence of animals that are globally less reactive, i.e., unhealthy due to surgery, but rather due to insects that are specifically less responsive to interactions from behind.

Cannibalistic Interactions within Groups

Successful cannibal attacks were more common among denervated locusts (see Figure S3). The mean proportion of

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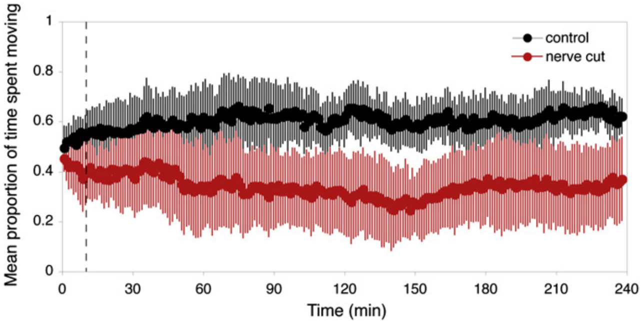

Figure 3. Time Series of the Mean Proportion of Moving Locusts

The mean proportion of moving locusts in groups was calculated for every minute of each 4 hr experiment. The minute average was then calculated for control (black) and nerve-cut (red) experiments. The dashed line at 10 min indicates the point at which the rate of divergence between the control and nerve-cut groups has stabilized. A significant difference between control and nerve-cut groups was found for this time period: t test, p = 0.009, T = −2.943, Df = 18. Ten experimental trials were carried out for each treatment. Error bars show ± 1 SD.

injured locusts was significantly higher in those experiments conducted with denervated insects together in the arena (0.08 ± 0.08 were injured in the control and 0.45 ± 0.22 in the nerve-cut group; t test, p < 0.001, T = −4.983, Df = 18, see Figure S4). Because cannibalism was more pronounced in groups of nerve-cut locusts, it is possible that injuries due to cannibalism could account for the lower mean proportion of moving insects per unit of time in these groups. If so, we would expect the mean proportion of moving locusts initially to be the same as for control experiments but progressively to decline as individuals became injured. We found no evidence for such a pattern. The mean proportions of moving locusts in both treatments were initially very similar, but a difference between the two treatments emerged very early in the experiments (within 5–10 min, too soon, our observations indicate, to have incurred injuries that would significantly decrease their level of marching) with sham-operated individuals increasing and operated individuals decreasing in activity (Figure 3).

Visual Detection of the Approach of Others from Behind Strongly Stimulates Marching Behavior

Visual stimuli are also potentially important in marching coordination [10]. To investigate this, we restricted the visual input of each individual under solitary conditions and within a group completely (totally blind), partially (back- or front blind), or not at all (control) by using black acrylic paint (Figure S5). The locusts were left for 20–30 min with food ad libitum before being placed in the experimental arena. We found no significant difference between visual treatments in the proportion of time spent marching for locusts under solitary conditions (One-way analysis of variance: p = 0.356, F = 1.116, within-groups Df = 36, between-groups Df = 3). However, groups of individuals with no restriction of visual input (control) showed significantly higher levels of marching than those with a complete restriction of visual input (totally blind) (Figure 4, t test, p < 0.001, T = 8.913, Df = 18). Furthermore, the proportion of moving locusts in groups where individuals had no visual input from behind (back blind) was not significantly different from that in groups of individuals that were totally blind (Figure 4, t test, p = 0.584, T = 0.557, Df = 18). Individuals that could see behind but not ahead (front blind) exhibited a propensity to march intermediate between blind and sighted groups.

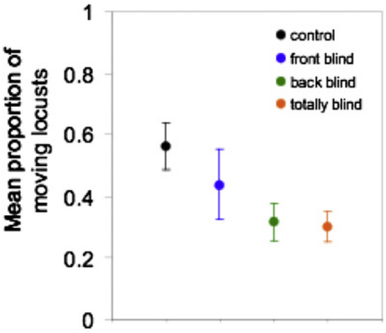

Figure 4. The Role of Vision

Mean proportion of moving locusts for visual treatments. Individuals in a group had no restriction of visual input (control), restricted visual input from the front (front blind), restricted visual input from behind (back blind), or a complete restriction of visual input (totally blind). The mean proportion of moving locusts was calculated for each experiment and then averaged for each treatment. Ten experimental trials were carried out for each treatment; error bars show ± 1 SD (control = 0.56, SD = 0.08; front blind = 0.44, SD = 0.11; back blind = 0.32, SD = 0.06; totally blind = 0.30, SD = 0.05; n = 10). One-way analysis of variance: p < 0.001, F = 22.680, within-groups Df = 36, between-groups Df = 3.

These results demonstrate how the visual perception of individuals from behind in particular influences the level of marching of a group. In addition, a lack of vision from behind and denervation of the abdomen show quantitatively similar effects in the proportion of moving locusts (t test assuming unequal variances, p = 0.271, T = −1.159, Df = 11).

Conclusions

Our study suggests that cannibalistic interactions among individuals, and the threat of attack by those approaching from behind, is a principal factor in the onset of collective movement among locusts. Individuals increase the propensity of others to march as they approach toward, or contact, their abdomen. Those that don't move in response face an increased risk of cannibalism. This demonstrates that coordinated mass migration in animal groups may be driven by highly selfish and aggressive behavior. In the case of locusts, both tactile and visual stimuli from behind are necessary, and the major source of these in a group will come from other locusts, which are demonstrably cannibalistic. Migration is widely viewed as an adaptation to exploit spatiotemporally variable environments in which animals undertake straightened-out directional movements while temporarily suppressing routine station-keeping behaviors such as foraging (including cannibalism [3, 6–9]) or mating [11–13]. However, cannibalism is perhaps one of the mechanisms that catalyzes the alignment of individuals and subsequently drives the directional mass movement of insects in migratory bands. This suggests a new perspective to our understanding of collective motion [14–19], a topic of increasing interest to physicists, mathematicians, engineers and biologists [20].

At high population densities, individuals in migratory bands can benefit by reducing predation risk [5] but can find themselves serving as a source of potentially limiting food or water for cannibalistic conspecifics [4]. Our results indicate that the defensive response to this risk, movement away from the attack, provides a general mechanism that results in marching bands being autocatalytic: Aggressive interactions stimulate motion in others, which increases encounter probabilities, and thus further aggressive acts. Furthermore, individuals that do become damaged by conspecifics may suffer increased risk of further cannibalism; as abdominal receptors are damaged, locusts may be less likely to respond to contact from behind. The strongly coordinated motion of migratory bands thus serves not only to facilitate migration from nutrient-poor habitats but also as a delicate balance between minimizing the risk of cannibalism by others and allowing attacks on those ahead.

Experimental Procedures

Locusts

Desert locusts (*Schistocerca gregaria*) of both sexes, 2 days after ecdysis in the fifth stadium, reared under conditions described in [21], were used. All locusts were in the gregarious phase [22]. At this age, the level of marching is high and consistent [23]. All experimental insects were fed ad libitum prior to experiments with seedling wheat and wheat germ. Only completely intact, healthy insects were used for experiments. The condition of all insects after each trial was assessed, and signs of cannibalism were recorded. Injuries were classified as damage to any abdominal tissue and loss of haemolymph from the site of damage.

Experimental Arena

An 80 cm diameter ring-shaped arena (with walls 52.5 cm high) was used for each experiment, as described in [2] and shown in Figure S1. The room was maintained at a temperature of 28°C–32°C.

Ventral Nerve Cutting

Surgery was carried out on the morning of the day of experimentation. Each locust was immobilized ventral-side up with Plasticine and placed under a light microscope. The ventral connectives were exposed by cutting of a small, hinged window in the cuticle and sectioned immediately posterior to the metathoracic ganglion, hence denervating the majority of the abdomen. The cuticular flap was closed and sealed with molten wax (a bee wax and rosin mixture). In sham-operated insects, the connectives were exposed but left intact (see Figure S2). All insects were checked for damage to the abdomen and healthy movement before being put into the experimental arena.

Motion Analysis

The motion of the locusts in the experimental arena was filmed with a digital video camera (Canon XM2 Digital Video Camcorder) connected to a computer. Eciton Software icBiovision 1.5, developed by I.D.C., captured images (at a rate of five times per s) of the entire arena and its contents. This software extracts information from real-time or stored video by using computer vision methods. The live video footage is digitized with a Matrox MeteorII framegrabber in an IBM-compatible PC. The video sequence is processed automatically frame by frame, and image segmentation techniques are used to locate the positions of all locusts in each frame. Quantitative measures of locust behavior were obtained from the raw data produced by the tracking analysis with Matlab Version 7.0 (Mathworks, 2004). An individual locust was considered moving if it moved greater than 0.3 cm per frame of video footage [2]. The speed of moving individuals was calculated by examination of their distance moved in successive frames, fulfilling the criteria above, divided by the interframe time interval, 0.2 s.

Group Behavioral Analysis

Locusts that moved a distance greater than 2 pixels (0.3 cm) between successive frames were considered moving, and those that moved less were considered stationary [2]. Moves less than 2 pixels were associated with image noise and slight adjustment of posture by nonmoving individuals. Both the proportion of moving locusts and their mean speed, between subsequent frames, were calculated and then averaged over all frames to give a single data point for the mean proportion of moving locusts, and mean speed, respectively, for each trial. Ten experimental trials were carried out for control and nerve-cut treatments.

Individual Behavior Analysis

For each experiment, all interactions between pairs of locusts consisting of a mobile and stationary individual that had not moved in at least 5 s in the first 10 min of the experiment were analyzed in detail. The first 10 min of the experiment were analyzed because activity of locusts in control and nerve-cut groups differ early in the 4 hr experiment and the rate of divergence between the two groups has stabilized by this point. The positions and orientations of both individuals at the time of the interaction were recorded with the original video recordings and a custom-made Matlab GUI that overlaid the video frames and the tracking points. Each individual's response to the interaction was recorded (whether it moved or remained stationary), as was the direction in which mobile individuals were heading. The part of the stationary locust's body that was contacted (categorized as rear, front, left, and right), and its heading if it started to move, at 1 and 2 s after initiating movement, were also noted. Two hundred and twenty-eight observations were made of interactions where nerve-cut locusts were the stationary individuals, and 172 were made in which control locusts were stationary individuals. The proportion of locusts that started to move after contact from the four different directions (rear, front, left, and right) were compared for control and nerve-cut groups with a (Pearson) chi-square test.

Statistics

All data were checked for normality and homogeneity of variance with the Kolmogorov-Smirnov Test and the Levene's Test, respectively. Where there is unequal variance in the data, the statistical test used assumes unequal variance. All t tests carried out are two-tailed and assume equal variance except when it is specified that there was unequal variance, and alpha is 0.05. All proportion data were transformed with arcsin $\sqrt{p}$ transformation, where p represents the proportion data [24].

Supplemental Data

Five figures are available at http://www.current-biology.com/cgi/content/full/18/10/■ ■ ■/DC1/.

Acknowledgments

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Supplemental Data

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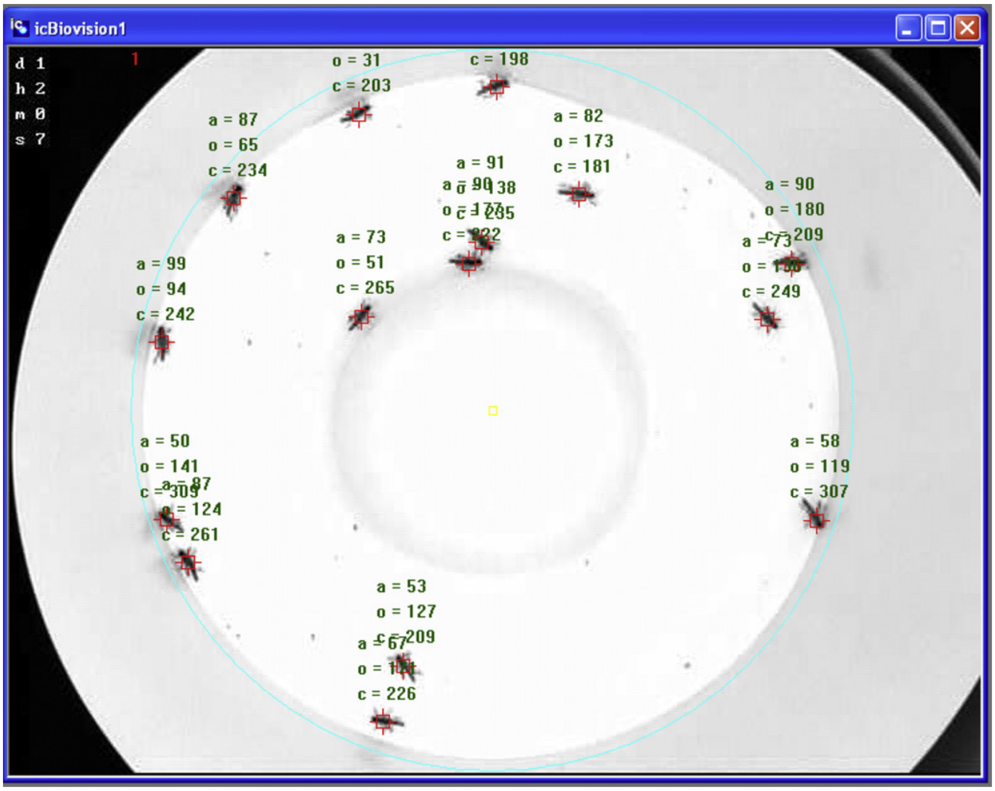

Figure S1. Motion Analysis

Still image of digital tracking software (icBiovision) showing the positions (red crosshair) and area in pixels (a), angle of principal axis in degrees (o), and circularity ($c = P^2/4\pi A$, where P is the perimeter, and A the area of the object, respectively).

Figure S2. Ventral Nerve Cutting

Photographed by Gabriel A. Miller.

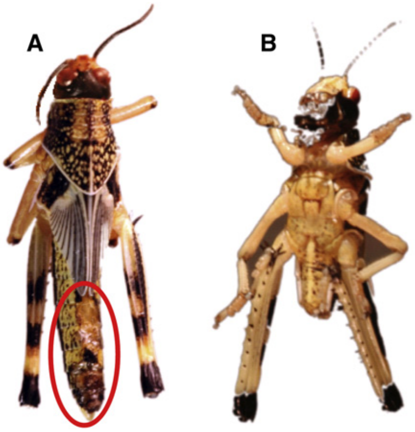

Figure S3. Examples of Injury from Cannibalism

Examples of slight (A) and severe (B) damage resulting from cannibalism in locusts with denervated abdomens kept in groups. Photographed by Gabriel A. Miller.

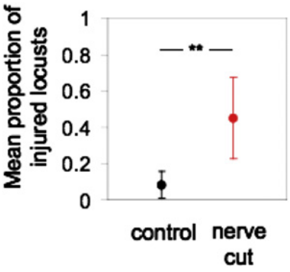

Figure S4. Injury from Cannibalism

The mean proportion of injured insects was calculated for all trials and averaged within control (black) and nerve-cut (red) treatments. Ten experimental trials were carried out for each treatment. Error bars show ± 1 SD.

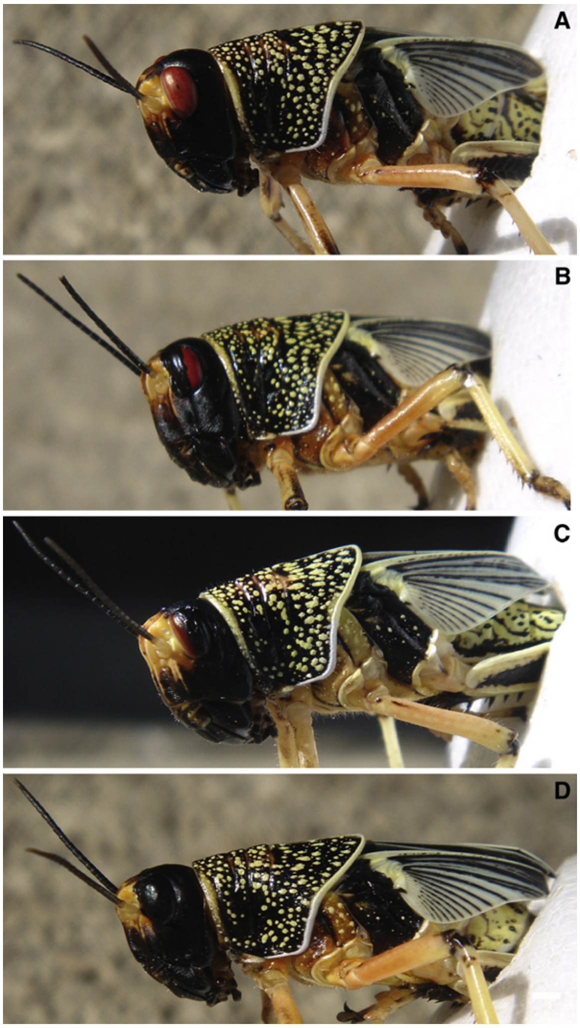

Figure S5. The Role of Vision

Images of control (A), front blind (B), back blind (C), and totally blind (D) treatments. Photographed by S.B.