Shaken, not stirred: a serendipitous study of ants and earthquakes

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Summary

There is anecdotal evidence for profound behavioral changes prior to and during earthquakes in many organisms, including arthropods such as ants. Behavioral or physiological analysis has often, in light of these reports, been proposed as a means of earthquake prediction. We report here a serendipitous study of the effect of the powerful Landers earthquake in the Mojave Desert, USA (Richter magnitude 7.4) on ant trail dynamics and aerobic catabolism in the desert harvester ant *Messor pergandei*. We monitored trail traffic rates to and from the colony, trail speed, worker mass distributions, rates of aerobic catabolism and temperature at ant height before and during the earthquake, and for 3 days after the earthquake. Contrary to anecdotal reports of earthquake effects on ant behavior, the Landers earthquake had no effect on any measured aspect of the physiology or behavior of *M. pergandei*. We conclude that anecdotal accounts of the effects of earthquakes or their precursors on insect behavior should be interpreted with caution.

Key words: ant behavior, earthquake prediction, *Messor pergande*.

Introduction

Various reports in the popular and technical press have linked changes in animal behavior with earthquakes and precursor temblors (e.g. Ikeya et al., 1998 and references therein; Quammen, 1985; Ulomov and Malashev, 1971). Quantitative observation of animal behavior or physiology might therefore serve a useful predictive function (Schaal, 1988).

Ants are attractive, practical candidates for quantitative behavioral and physiological observations. Traffic kinetics on foraging trails can be characterized by video analysis, and it is possible, with sensitive flow-through respirometry, to measure a foraging trail's aerobic catabolism (Lighton and Duncan, 2002). Traffic kinetics and catabolism, when analyzed in combination, can yield a comprehensive record of a colony's foraging and energy allocation strategies (Lighton and Duncan, 2002). Various earthquake-precursor-related effects have been proposed that may affect insect physiology or behavior (see Ikeya et al., 1998). If anecdotal reports linking earthquakes and their precursors to changes in ant colony activity – even to the extent of colony evacuation (Ulomov and Malashev, 1971) – are correct, then recording and analyzing ant behavior may be an effective means of earthquake prediction, and would yield interesting information on colony-level responses to external, density-independent stimuli.

A testable null hypothesis in this regard would be that ant foraging behavior (and any other readily quantifiable aspects of ant behavior or physiology) does not change immediately prior to or during a major earthquake. Testing such a heuristic hypothesis is not, however, a project for which one might realistically expect to be funded. Earthquakes cannot be predicted at present, so testing the utility of ant behavior as a predictive mechanism is challenging because obtaining detailed ant foraging data by chance prior to and during a large earthquake is unlikely. Yet such an event has happened. We report here a serendipitous field study of ant foraging (undertaken in the course of a field validation of laboratory foraging energetic data; Lighton and Duncan, 2002) that took place in the Mojave Desert, California, when the magnitude 7.4 Landers earthquake struck.

The large S-wave displacements made it difficult for the researchers to stand upright or walk during the event, but 'E' markers were placed in the data acquisition record during the main temblor and during the sporadic aftershocks that occurred during the rest of that recording. We refer below to the Landers earthquake day as E-day. Thus, serendipitously (Merton and Barber, 2003), we had recorded an ant colony's response to a significant earthquake, the most powerful to strike in the USA in four decades (Sieh et al., 1993), and its associated aftershocks. Recordings on 3 subsequent, earthquake-free days served as controls.

Materials and methods

Animals

Data were obtained from a single colony of the harvester ant *Messor pergandei* Mayr a common seed-eating ant in the

xeric areas of the North American southwest (Hölldobler and Wilson, 1990). The colony was located at Zzyzx, California, in the eastern Mojave Desert, on a bajada (alluvial fan) near the edge of a playa (dry pleistocene lake bed) some 100 km from the epicenter of the Landers earthquake. The substrate was sandy and the colony had been foraging on a daily basis for several days prior to our measurements. Measurements (see below) took place in June and July 1992, and were initiated slightly before dawn, when the ants began to forage, until the temperature at ant height reached the maximum for foraging of *ca.* 43°C, which occurred before 09:00 h each day.

Data acquisition

We measured kinematic and catabolic parameters in a 15 cm section of the foraging trail approximately 50 cm from the nest entrance. The trail passed over a Masonite board, painted flat white, under a transparent respirometer chamber on which an orthogonal S-VHS video camcorder was trained. The chamber length (150 mm) served as the dimensional calibration. An identical chamber, through which no ant trail passed, served as the baseline for the respirometry system. Calibration markers established the dimensional scale at ant level. Kinematic data (number of ants in the chamber, length of each ant, speed and direction of each ant) were obtained by analysis of the video recordings, using a program written by J.R.B.L. The video recordings were synchronized with a prototype Sable Systems field portable TR-2 respirometry and data acquisition system (www.sablesystems.com). Catabolic and kinematic data were synchronized by noting the acquired number of samples of the catabolic/temperature recording on the sound track of the video recorder, which was turned on for *ca.* 30 s at intervals of 5–10 min. A flow rate of $1\,l\,m^{-1}$ was maintained through both chambers by means of mass flow control valves. Simultaneously, temperature was measured using a copper–constantan thermocouple at 'ant height', 3 mm above ground level, and also recorded by the data acquisition system. The measurement of aerobic catabolism in insects *via* CO_2 production is well-validated and details have been published elsewhere (Lighton, 1991; for more details, see especially Lighton and Duncan, 2002).

Using this system, we obtained data on traffic patterns (number and speed of ants entering and leaving the colony), mass distributions (from body length data *via* a separately obtained body length/body mass allometric regression), ant temperature and aerobic catabolism (*via* carbon dioxide production) of the foraging trail, all as functions of time. Because temperature continuously increased within each of the 4 days reported here, it served as a convenient abscissa for data analysis (we could alternatively have used time of day, but temperature is of more direct biological significance to the ants). Because E-day was characterized by not only by the Landers quake itself but by several aftershocks, any and all of which could have affected ant activity (Ulomov and Malashev, 1971), our analysis treats E-day as a discrete earthquake-affected entity for purposes of comparison with the 3 subsequent control days, which were seismologically uneventful.

Tests of earthquake effects

All of our null hypotheses generated for the purpose of assessing the effect of the Landers earthquake on our *Messor pergandei* colony are necessarily *a posteriori*. We had no rational reason to formulate them in advance of the earthquake.

Our primary test for an earthquake effect involved traffic direction ratio (TDR). We define TDR as the ratio of inbound ants to total traffic (inbound plus outbound), with 0.5 denoting an equal number of inbound and outbound ants. We analyzed TDR as a function of ambient temperature on E-day and the 3 subsequent days. Because earthquakes and/or their precursors have allegedly caused disturbances of ant colony activity up to and including colony evacuation (e.g. Ulomov and Malashev, 1971), we considered it plausible that the Landers quake would have changed the ratio of inbound to outbound foragers if, indeed, the colony reacted to the Landers earthquake or its precursors. Thus, our TDR *a posteriori* null hypothesis was that TDR would, as a function of temperature and thus time of day, not differ between E-day and the 3 control days.

We next examined 'motivational state', which we define as the component of ant running speed not explained by temperature, which is the primary determinant of ant running speed (Rissing, 1982). Motivation can therefore be quantified by examining the residuals of the linear regression between traffic speed and temperature at ant height. Any stimulus that elicits escape or panic behavior will drive measured running speeds up or down from the running speed/temperature line. This corresponds to a subjective impression of the ants being more or less active 'than usual'. Thus, our motivational state *a posteriori* null hypothesis was that ant running speed, as a function of temperature, would not differ between E-day and the 3 control days.

Next, we looked for earthquake-related changes in body size polymorphism on the trail. Adult workers of *Messor pergandei* vary in body mass from about 1 to 10 mg, and tend to differ in behavior (e.g. picking up heavier or lighter loads), depending on their mass (Davidson, 1978). If seismic activity affects the mass distribution of workers leaving the nest, perhaps by causing a reallocation of work tasks within the nest, then the mean mass of ants on the trail (as determined from body length by video analysis and length–mass regression analysis) will change. Thus, our body size polymorphism *a posteriori* null hypothesis was that body size polymorphism, i.e. minimum, maximum and mean worker body mass as a function of temperature and thus time of day, would not differ between E-day and the 3 control days.

Finally, we examined the aerobic catabolism of the trail on a mass-specific basis. Trail aerobic catabolism is largely a function of temperature and running speed, with running speed itself also being a function of temperature (Rissing, 1982). If earthquake-related effects modulated aerobic catabolism at a given temperature and activity rate, this would lead to

anomalous catabolic data on E-day. Thus, our catabolic *a posteriori* null hypothesis was that trail aerobic catabolism, as a function of temperature and thus time of day, would not differ between E-day and the 3 control days.

Statistics

Data analysis was performed using Sable Systems Datacan software, and with statistical programs written by J.R.B.L. and validated against SYSTAT version 4 (Wilkerson, 1988). Means are accompanied by standard deviations (S.D.) and *N*, and were compared using Student's *t*-test or by analysis of variance (ANOVA). Regressions were calculated by the method of least squares and were compared using analysis of covariance (ANCOVA).

Results

Our first recording on 28 June 1992 started at 05:50 h. At 05:58 h, the Landers earthquake struck. An 'E' for earthquake marker noted the event, which was accompanied by S-wave displacements large enough to prevent one of us (F.D.D.) from standing at the time. 40 s before the S-wave reached us, a violent but brief excursion occurred in the channel monitoring trail CO_2 emission. The genesis of this event is unknown, but it is possible that the gas analyzer may have received an EMF spike generated piezoelectrically by
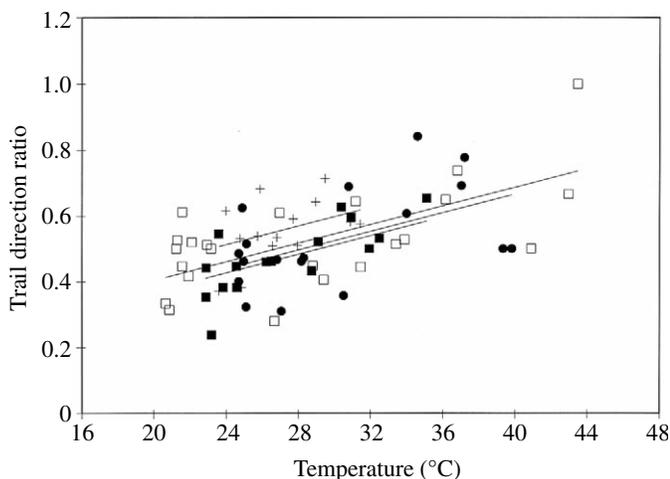

Fig. 1. Trail direction ratio (TDR; see text) as a function of temperature at ant height (4 mm) in a foraging trail of a *Messor pergandei* colony. Filled circles: data from E-day; Landers earthquake and subsequent aftershocks. The earthquake struck at the lowest temperature (05:58 h, 28 June, 1992). Temperature is a primary determinant of ant behavior, and also serves to separate data points in time; higher temperatures correspond to later times on all days. Other symbols: control days, all recordings starting at approximately the same time as on E-day. Empty squares, 29 June 1992; filled squares, 2 July 1992; crosses, 3 July 1992. Testing the null hypothesis by ANCOVA (slopes equal) yielded *P*>0.2. The common slope is 0.0142. Testing the null hypothesis (intercepts equal) yielded *P*>0.15. The common intercept is 0.138. The regression line for E-day is third from the top.

stressed rocks at the Landers fault (see Finkelstein et al., 1973). The main temblor was followed by several aftershocks over the next few hours, which were marked in the same way on the recordings. Following E-day, we recorded the same colony's foraging activity for a further 3 days which, for the purposes of this study, served as controls. After the third control day the colony stopped foraging temporarily, which is normal *Messor pergandei* behavior, and our work moved on to other colonies.

Traffic direction ratio

Temperature at ant height explained almost 40% of TDR variance in *Messor pergandei* (Fig. 1). TDR was about 0.2 at the initiation of recordings at ca. 05:30–06:00 h, with most traffic outbound and an ant height temperature of 22–25°C. TDR approached unity in the heat of the day when most traffic was inbound. Traffic ceased at 35–45°C ant height temperature, typically before 09:00 h. Had the earthquake and its aftershocks increased outward traffic from the nest as claimed in anecdotal reports (e.g. Ulomov and Malashev, 1971), the TDR would have fallen prior to, and/or during, the earthquake and its aftershocks. The earthquake and its aftershocks had no effect on TDR (Fig. 1; *P*=0.2), or on the absolute numbers of foragers (*P*>0.3; data not shown). It might be objected that we only began recording data shortly before the earthquake, and may have missed an earlier, predictive outbound pulse of ants. This is not the case, however, because such an ant pulse would have returned to the nest when rising ambient temperatures drove it back, thus elevating the TDR in the hours following the earthquake. Fig. 1 shows no such effect relative to non-quake days. Our TDR *a posteriori* null hypothesis is not falsified.

Motivational state

Inbound traffic speeds are higher and less variable than outbound speeds in foraging ants (Rissing, 1982). In *Messor pergandei*, a linear model of the effect of temperature explains 87% of traffic speed variance for inbound workers (Fig. 2). We found no evidence for any earthquake-linked change in motivational state in either inbound ants (Fig. 2) or outbound ants (data not shown). Only 13% of running speed variance remained unexplained by temperature on any day, including E-day. Other workers have documented different but equally dramatic temperature effects on locomotion in ants (Wehner et al., 1992). We also determined the relation between inbound and outbound traffic speed. By linear regression analysis outbound traffic speed was 86% of inbound speed (correlation coefficient 0.92), and was constant at that value on all 4 days (ANCOVA: *P*>0.2). Our motivational state *a posteriori* null hypothesis is not falsified.

Body size polymorphism

For each measurement interval on each day we determined the minimum, maximum and mean masses of the ants traveling through the respirometry chamber towards and away from the nest. E-day did not differ significantly from the three control
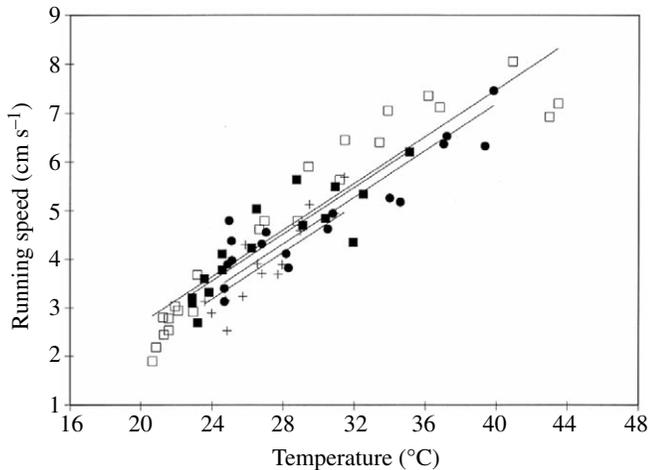
Fig. 2. Trail running speed as a function of temperature at ant height in a foraging trail of the same *Messor pergandei* colony as in Fig. 1. Symbols as in Fig. 1. Testing the null hypothesis by ANCOVA (slopes equal) yielded $P>0.1$. The common slope is 0.241 cm s^{-1} deg.$^{-1}$. Testing the null hypothesis (intercepts equal) yielded $P=0.08$. The common intercept is -2.34 cm s^{-1}. The negative intercept reflects departure, outside the foraging temperature window, from a linear model of running speed/temperature. This figure shows inbound speed (towards the colony), which was slightly (~16%) faster and less variable than outbound speed, which also showed no E-day effect (see text).
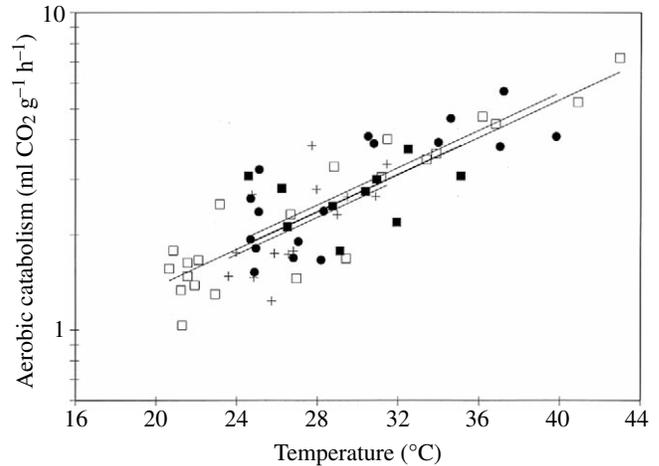

Fig. 3. Aerobic catabolism as a function of temperature at ant height in a foraging trail of the same *Messor pergandei* colony as in Fig. 1. Symbols as in Fig. 1. Trail catabolism measurements were not available early on the second control day (filled squares, 2 July 1992). Testing the null hypothesis by ANCOVA (slopes equal) yielded $P>0.15$. The common slope is 0.295. Testing the null hypothesis (intercepts equal) yielded $P>0.2$. The common intercept is -3.14. The common slope corresponds to a Q_{10} of $10^{(10\times0.295)}$ or 1.97.

days in the values of any of these parameters (ANOVA: $P>0.2$). Our body size polymorphism *a posteriori* null hypothesis is not falsified.

Trail aerobic catabolism

Trail aerobic catabolism increased exponentially with ant-height temperature in *Messor pergandei*, approximately doubling every 10°C, with temperature explaining 70% of the catabolism variance (Fig. 3). E-day did not differ from the control days in this relationship ($P>0.15$). Our trail aerobic catabolism *a posteriori* null hypothesis is not falsified.

Narrowing the test window

The four analyses we have presented above treat E-day as an entity in itself, during which ant colony behavior and/or physiological state would be affected by precursor events, the Landers earthquake, and the associated aftershocks. What if any possible anomalous behavior was confined only to the times on E-day proximate to the earthquake and its aftershocks? We tested this hypothesis, though not with perfect precision, by examining the residuals of the data points recorded on E-day (see Figs 1–3, filled circles) closest to the time of the earthquake and its aftershocks, and comparing them to residuals generated by equivalent regressions from which those data points were excluded. The E-residuals were tested using Student's *t*-test for significant difference from the non-E-residuals on E-day, and on the control days. No significant difference was found in either case ($P>0.2$).

Discussion

Ants as predictors of earthquakes

By the principle of Occam's razor we assert that any effects of earthquake precursors on ant behavior must also manifest themselves immediately prior to and during the main earthquake itself, and during its aftershocks. Yet the Landers earthquake did not affect the behavior of the desert harvester ant *Messor pergandei* in any way that we could quantify. There is therefore little reason to believe that these ants react to earthquake precursors other, perhaps, than those that may affect colonies directly, by altering physical variables that can be directly measured by other means. Examples of such variables might include groundwater levels or the partial pressures of soil gases. Likewise, ant colonies may react to side-effects of the main earthquake such as flooding or soil liquefaction – both of which are presumably capable of triggering the anomalous changes in ant behavior that have been noted (Ulomov and Malashev, 1971).

Other investigators have studied certain forms of vertebrate behavior prior to earthquakes statistically (Schaal, 1988) and found no significant predictive effects. Our findings are in accordance with theirs. Fascinating though the behavior and physiology of ants may be, we conclude that at least in the species and conditions we examined, they cannot be employed as reliable predictors or even sensors of earthquakes.

References

Davidson, D. W. (1978). Size variability in the worker caste of a social insect (*Veromessor pergandei* Mayr) as a function of the competitive environment. *Am. Nat.* **112**, 523-532.

Finkelstein, D., Hill, R. D. and Powell, J. R. (1973). The piezoelectric theory of earthquake lightning. *J. Geophys. Res.* **78**, 992-993.

Hölldobler, B. and Wilson, E. O. (1990). *The Ants*. Cambridge, MA: Harvard University Press.

Ikeya, M. H., Matsumoto, H. and Huang, Q.-H. (1998). Alignment of silkworms as seismic anomalous behavior (SAAB) and electro-magnetic model of a fault: A theory and laboratory experiment. *Acta Seismol. Sinica* **11**, 365-374.

Lighton, J. R. B. (1991). Measurements on insects. In *Concise Encyclopedia on Biological and Biomedical Measurement Systems* (ed. P. A. Payne), pp. 201-208. Oxford: Pergamon Press.

Lighton, J. R. B. and Duncan, F. D. (2002). Energy cost of locomotion: Validation of laboratory data by *in situ* respirometry. *Ecology* **83**, 3517-3522.

Merton, R. K. and Barber, E. (2003). *The Travels and Adventures of Serendipity: A Study in Sociological Semantics and the Sociology of Science*. Princeton, New Jersey, USA: Princeton University Press.

Quammen, D. (1985). Animals and earthquakes. *San Francisco Chronicle, This World* (21 April), pp. 15-16.

Rissing, S. W. (1982). Foraging velocity of seed-harvester ants, *Veromessor pergandei* (Hymenoptera: Formicidae). *Environ. Entomol.* **11**, 905-907.

Schaal, R. (1988). An evaluation of the animal-behavior theory for earthquake prediction. *California Geology* **41**, 41-45.

Sieh, K., Jones, L., Hauksson, E., Hudnut, K., Eberhart-Phillips, D., Heaton, T., Hough, S., Hutton, K., Kanamori, H., Lilje, A. et al. (1993). Near-field investigations of the Landers earthquake sequence, April to July 1992. *Science* **260**, 171-176.

Ulomov, V. I. and Mavashev, B. Z. (1971). The Tashkent Earthquake of 26 April, 1966. *Acad. Nauk. Uzbek SSR FAN*, 188-192.

Wehner, R., Marsh, A. C. and Wehner, S. (1992). Desert ants on a thermal tightrope. *Nature* **357**, 586-587.

Wilkerson, L. (1988). SYSTAT: The System for Statistics. Evanston, IL: SYSTAT Inc.