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Not everything that counts can be counted: ants use multiple metrics for a single nest trait

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There are claims in the literature that certain insects can count. We question the generality of these claims and suggest that summation rather than counting (*sensu stricto*) is a more likely explanation. We show that *Temnothorax albipennis* ant colonies can discriminate between potential nest sites with different numbers of entrances. However, our experiments suggest that the ants use ambient light levels within the nest cavity to assess the abundance of nest entrances rather than counting *per se*. Intriguingly, Weber's Law cannot explain the ants' inaccuracy. The ants also use a second metric, independent of light, to assess and discriminate against wide entrances. Thus, these ants use at least two metrics to evaluate one nest trait: the configuration of the portals to their potential homes.

Keywords: ants; counting; decision-making; house hunting; Weber's Law; social insects

> Not everything that can be counted counts, and not everything that counts can be counted.
>
> Albert Einstein (attributed)

1. INTRODUCTION

Counting can be defined as determining the number of items in a group by assigning successive numbers to its members (Shorter Oxford English Dictionary 2002). Two aspects of this definition need further clarification. First, counting is based on an abstract notion of number (e.g. it may proceed irrespective of item size and even item type). Second, summation is not counting. For example, the odometer of a car does not count kilometres: it merely sums a continuous variable (distance covered) and, obviously, an odometer does not use an abstract notion of number. This is an important distinction because parts of the literature on 'counting' in insects may confuse true counting and summation (see below).

Can animals count? Evidently, a number of vertebrates can count, including chimpanzees, dolphins, racoons, rats and a parrot (Dehaene 1999). Consider one of the clearest examples of counting in animals. Studies of rats imply that they can form an abstract concept of number. Rats can assess the total number of mixed stimuli they have just witnessed. A rat can learn to assess the number of light flashes it has seen or the number of audible tones heard. It can be trained to press a lever for the same number of times as the number of stimuli it has just witnessed, to get a reward. Most impressively, a rat can respond to the total number of a mixture of light flashes and discrete sounds with the appropriate number of lever presses (Meck & Church 1983; Church & Meck 1984).

The ability to mix different sensory inputs, in these cases, seems to imply some abstract notion of number. Psychologists use this to separate proto-counting (i.e. an assessment of numerousness with neither abstraction nor application to different contexts) from true counting (Davis & Pérusse 1988). The beautiful work on rats (Meck & Church 1983; Church & Meck 1984) has controlled meticulously for other continuous cues such as duration of stimuli or duration of sets of stimuli (i.e. including inter-stimuli durations). Furthermore, because the rats were isolated they do not have access to unwitting signals from their trainer—as in the infamous case of the horse 'Clever Hans' (see Dehaene 1999).

Can invertebrates count? Chittka & Geiger (1995) claim that honeybees can proto-count landmarks. The honeybees were first trained to forage at an artificial feeder after they had flown over a certain number of landmarks (yellow tents) in a longer line of such landmarks. When the spacing of the landmarks was changed, a proportion of the bees flew down to land on a control feeder after they had flown over the critical number of landmarks, whether or not the landmarks were closer together or further apart than before. Thus, the bees were not simply using distance to the feeder instead of counting landmarks. To rule out other possible cues such as scents, the control feeder did not contain a reward. The landmarks were relatively small and Chittka & Geiger (1995) reason plausibly that bees do not have the visual acuity to see all or many of the landmarks within a single field of vision. Thus, subitizing seems unlikely, i.e. detecting immediately, without counting, the number of items in a small sample. Nevertheless, in Chittka & Geiger's (1995) experiments, the honeybees might have been using a continuous variable. Chittka & Geiger (1995) do not discuss this possibility. The bees, possibly using optical flow (Esch & Burns 1995; Tautz *et al.* 2004), might have been summing the amount of yellow, or the number of contrasting edges they had flown over, up to a learned threshold, to determine the location of the feeder.

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Karban *et al.* (2000) claim that 17 year-old periodical cicadas can count 17 annual cycles as larvae before developing into the adult form. Their ingenious experiments involved shortening the annual cycles of the cicada's host trees. The cicadas emerged after the appropriate number of such shortened 'years'. It is thus clear that the cicadas are not measuring continuous time. However, the cicadas might have been monitoring the yearly ebb and flow of amino acids or other compounds in the xylem juices of their host plants. Hence, the cicadas may have some physiological system that adds a quantity of some chemical token, in response to the passage of real or artificial seasonal cycles, until a threshold is encountered. Thus, as with the honeybees, we suggest that the cicadas may not be truly counting.

The honeybees might have been summing the landmarks they had flown over up to some learned threshold and the cicadas may have been recording the number of cycles in their host plant's physiology up to some innate threshold equivalent to 17 years. Such summation is not counting (*sensu stricto*) any more than an odometer in a car has counted when it signals that it is time to have the car serviced at a set mileage interval.

Here we test if ants can determine the abundance of entrances in potential nest sites. We used the intensively studied model system of house hunting by *Temnothorax albipennis* ant colonies (Franks *et al.* 2002, 2003*a*,*b*; Pratt *et al.* 2002; Dornhaus *et al.* 2004). We presented colonies with binary choices between nests that differed only in the number, configuration or size of their entrances. We tested two main hypotheses: (i) the ants discriminate the abundance of entrances by counting (*sensu stricto*); and (ii) the ants discriminate the abundance of entrances by sensing light levels. The second hypothesis is based on the notion that the ants do not count *per se*, but use the light entering the nest through its entrances to determine the abundance of these holes in the nest wall.

If the ants are using the strength of a continuously variable stimulus such as light intensity, their behaviour might be consistent with Weber's Law (Shettleworth 1998). Many organisms exhibit a difference threshold (or the phenomenon of 'just noticeable difference'). This is the minimum amount by which the intensity of a stimulus must be changed in order to produce a noticeable variation in sensory experience (Shettleworth 1998). Weber's Law states that the size of the *just noticeable difference* is a constant proportion of the original stimulus value. For example, imagine that an observer in a large room could just tell, from ambient illumination, when 11 light bulbs were glowing rather than 10. Then, if that observer was exhibiting Weber's Law, one would predict that they would only be able to discriminate between, say, 20 and 22 incandescent bulbs. Thus, under Weber's law, the just detectable difference ratio is constant. We, therefore, also examine the ants' choices to determine if they are consistent with Weber's Law.

Finally, we tested if the ants were using additional metrics to assess nest entrances.

2. MATERIAL AND METHODS

Colonies of *T. albipennis* were collected in early October 2003 and 2004 from the Dorset coast, UK. A total of 57 colonies were used in these experiments. They had a median number of 116 workers (with an interquartile range of 63–172) with a median of 146 brood items (interquartile range 89–212). Seventy-two percent of the colonies had queens. These numbers are consistent with unbiased field samples from collections in October (Partridge *et al.* 1997).

The colonies were cultured in the lab in standard nests constructed from a piece of cardboard sandwiched between two clear glass microscope slides, 75×50 mm. The headroom within the nest cavity, determined by the thickness of the cardboard, was 1.9 mm in all nests. The floor area of nests was 46×32 mm^2. Each standard nest had a single entrance, 2 mm wide and 3 mm long, in the middle of the 75 mm side. Standard nests did not have light filters (see below), i.e. they were 'bright' nests (see Franks *et al.* 2003*a*,*b*). Between experiments, each nest was housed in a square Petri dish, 100×100×17 mm. A layer of Fluon was applied to the walls of the dish to prevent the ants from escaping. The colonies were fed with *Drosophila* and provisioned with honey solution and a separate water supply, except during experiments.

(a) *Alternative potential nest sites*

In total, nests with 14 different entrance configurations were presented to the ants in different combinations. All new nests were constructed in the same way as the standard nests. However, filters covering the whole of the top microscope slide controlled the amount of light entering the cavity of the potential new nests. Certain nests had no filters, others were covered with black cardboard and others had red or orange filters (LEE filters: 105 orange and 106 primary red, respectively). Such filters covered not just the nest cavity but also extended above any entrances to that cavity. These different filters allowed different amounts of ant-visible light to enter the nest cavity through the roof of the nest. The red filters should have cut out almost all ant-visible light, i.e. light of wavelengths below about 600 nm (Briscoe & Chittka 2001). The orange filters allowed ingress by some ant-visible wavelengths of light (i.e. between about 550 and 600 nm). The black filter was cardboard and thus impervious to light. We used coloured filters rather than neutral density filters, because the red filters should have been 'totally black' for the ants but allowed us to see into the nests to count their occupants.

All nests were newly constructed for each of the 22 experiments. All standard entrances were 2 mm wide and 3 mm long, except in experiments where we investigated the relative importance of entrance width versus entrance number and so used 4 mm or wider entrances. In all the experiments, only the light filters and numbers and widths of entrances were variables. Nest entrances were all on the same side of one of the long walls of the new nest sites, except for the following. In experiment 19, the 24-entrance nest had 12 entrances in one long wall and the other 12 in the opposing long wall, and the four-entrance nest had two entrances in one long wall and two in the other long wall. Wherever possible, nest entrances were symmetrically arrayed with equal gaps between them.

(b) *Binary choice experiments*

Experiments were carried out using methods described in Franks *et al.* (2003*b*). All emigrations were carried out in large square Petri dishes (220×220×18 mm), the walls of which were covered with Fluon. A colony in its original nest was placed along the centre of one of the walls. The two new nests, A and B, were placed in opposite corners of the dish

Table 1. Binary choices of ant colonies between nests. The 22 separate experiments ('a', performed in autumn, 's', performed in spring) are grouped according to the hypothesis tested (Roman numerals); * indicates a significant result at $p < 0.005$. In experiment 5, the entrances of nest B were closer together than in experiment 4. Majority choices in experiments used in the meta-analysis are indicated in bold (see text).

			nest entrance design		outcome			
result no.	expt. no.	filter	nest A (entrance no. × width, mm)	nest B (entrance no. × width, mm)	no. of colonies in nest A	no. of colonies in nest B	no. of split colonies	p-value
I	1 s	red vs orange	1×10 (red)	1×10 (orange)	27	3	10	0.000*
II	2 a	red	1×2	10×2	**14**	0	3	0.002*
	3 a	red	1×2	5×2	**10**	1	6	0.012*
	4 a	red	1×2	3×2	**11**	1	5	0.006*
	5 a	orange	1×2	3×2 (close)	**8**	4	8	0.388
	6 a	orange	1×2	3×2	**7**	4	9	0.549
	7 a	orange	1×2	5×2	**6**	3	11	0.508
	8 s	none	1×2	10×2	**10**	5	5	0.302
III	9 a	red	1×4	2×4	5	**9**	3	0.424
	10 a	red	1×2	2×2	0	**2**	15	0.500
IV	11 s	red	2×2	4×2	2	2	13	1.000
	12 s	red	2×2	6×2	**8**	3	6	0.226
	13 s	red	2×2	10×2	**7**	2	8	0.180
	14 a	orange	3×2	9×2	**10**	5	5	0.302
	15 a	orange	4×2	24×2	**14**	6	0	0.115
	16 a	orange	2×2	4×2	5	**6**	9	1.000
V	17 a	red	1×4	2×2	3	11	3	0.057
	18 a	orange	1×20	10×2	0	20	0	0.000*
	19 s	orange	1×20	10×2	0	18	2	0.000*
	20 s	black	1×10	10×2	0	18	2	0.000*
VI	21 s	red	1×2	3×2	**2**	1	14	1.000
	22 s	black	1×2	10×2	**10**	7	23	0.629

equidistant from the old nest (100 mm from entrance to entrance). The two new nests were 90 mm apart (middle entrance to middle entrance), i.e. the paths between all nest entrances created an isosceles triangle.

Colonies were induced to emigrate by removing the upper slide of their current nest. The position, i.e. left or right, of the new nest sites in the arenas was randomized, as was the location of each colony on the laboratory bench to eliminate any chance of directional biases.

The nest that had been 'chosen', i.e. the nest the ants were occupying, was noted 48 h after the start of the experiment, and a colony split was recorded when at least one brood item was present in the alternative nest. After 48 h, all colonies were returned to the standard Petri dishes in the nest that the majority of the colony currently inhabited.

To determine if choices were significantly different from random, the data were analysed with two-tailed binomial tests on each binary choice dataset. Those colonies classified as split were not included in the analysis.

3. RESULTS

All results are presented in table 1. In the following summary, Roman numerals refer to sets of experiments as indicated in table 1.

Result I is an important control for the later experiments. It shows, all else being equal, that the ants prefer a nest with red filters to those with orange filters. This is consistent with them perceiving nests with red filters as darker than nests with orange filters. Previous work has shown that the ants prefer darker nests (Franks *et al.* 2003*a*,*b*).

The second set of results (II) shows that under red filters the ants can distinguish between one and ten, or one and five, or one and three entrances (see experiments 2–4), and prefer a lower number of entrances. Under orange filters they do not make these discriminations (see experiments 5–8). Their perception of the number of entrances is, thus, disturbed by the higher light levels under orange filters. This suggests that they are using light levels to determine the abundance of nest entrances.

The third set of results (III) shows that the ants do not discriminate between nests with one or two entrances, even under red filters (see experiments 9 and 10). This adds to the evidence that the ants are not counting (*sensu stricto*), since distinguishing between 1 and 2 is a prerequisite for counting.

The fourth set of results (IV) shows that they do not distinguish between two or more and any greater number of nest entrances (under red or orange filters; see experiments 11–16). This is also consistent with the ants not being able to count.

The fifth set of results (V) shows that the ants prefer nests with narrow entrances under red, orange or black filters (experiments 17–20). This suggests that the ants are using an additional metric to light levels to measure the width of entrances.

The sixth set of results (VI) shows that in the spring, colonies split much more often between nests that, in the autumn, they would discriminate between by rejecting one of the alternatives (compare the results of experiment 21 with 4 and experiment 22 with 2). Nevertheless, their aversion to wide entrances overcomes their tendency to split in spring (compare the results of experiments 19 and 20 with experiments 21 and 22).

The ants do not discriminate between bright nests (i.e. those with orange filters) with different numbers of nest entrances, suggesting that light plays a role in assessing entrance number. Nevertheless, under either red or orange filters the majority of colonies do significantly prefer nests with fewer entrances. This can be shown by a meta-analysis of which type of nest the majority of colonies chose in all of the experiments that compared nests with different numbers of entrances of the same width. The majority choices in these experiments are indicated in bold in table 1. In 13 of these experiments, the majority of colonies chose the option with fewer entrances. In three of the experiments, the majority of colonies chose the option with more entrances. This is a significant difference (two-tailed binomial test, $p=0.0212$). This meta-analysis combines results for the different filter types. It suggests that, overall, the ants have a tendency to choose nests, all else being equal, with fewer entrances. When only experiments with orange or no filters were considered, colonies still chose nests with fewer entrances more often (Wilcoxon test, $p=0.035$, $n=7$). Thus, orange filters probably cut out enough light to enable the ants to discriminate weakly between numbers of entrances.

4. DISCUSSION

Earlier work has shown that *Temnothorax* ants are exceptionally discriminating with regard to nest attributes, including the width of nest entrances (Franks *et al.* 2003*b*). Hence, we wished to determine if these ants show any choices that may be associated with an ability to count nest entrances. They do not. For example, they seem incapable of discriminating between nests with one and two narrow entrances. Instead of counting *per se* they seem to use a much simpler method of assessing the abundance of entrances.

Our results suggest strongly that the ants use light levels within the nest cavity to assess the abundance of nest entrances. This explains why they are more discriminating over entrance numbers in dark (red filtered) nests compared to bright nests (i.e. those with orange filters, in which the light from the entrances is likely to be less distinguishable because of the high light levels within the nest that enter through its roof). Of course, it could be argued that the ant might be counting entrances (*sensu stricto*) in dark nests but that they cannot do so in light nests. We can count stars in the inky firmament of the sky at night, but we cannot see such stars to enumerate them by the light of day. However, since the ants do not distinguish between one entrance and two, even in dark nests, this strongly suggests that they are not using vision to count. Of course, it could be argued that they might equally prefer nests with one or two entrances but this is, in turn, inconsistent with them liking nests that have narrow entrances, i.e. nest walls that are breached minimally (Franks *et al.* 2003*b*).

Our results also show that the ants use some other measure of entrance widths to discriminate against nests with wide entrances, because colonies chose narrower entrances even when the alternative had the same, or even a smaller, total gap in the wall. Such a metric for directly measuring nest entrance width might be a 'mechanical' measurement, such as a rule of thumb 'if both sides of an entrance cannot be simultaneously touched with outstretched antennae, it is too wide'.

The ants in our experiments were not exhibiting Weber's Law. For example, Weber's Law would predict that if the ants can discriminate between one and three entrances, based on light levels, they should also be able to discriminate between two and six entrances or three and nine entrances. This they do not do (compare the results of experiment 4 with experiments 12 and 14). Moreover, they do not even discriminate between 2 and 10 entrances (experiment 13), or under orange filters even between 4 and 24 entrances (experiment 15). Their abilities to determine light levels and hence the relative abundances of narrow entrances of the same width seems rather poor. This is very intriguing given that their eyesight is sufficiently good that they can use small landmarks during nest emigrations (Mcleman *et al.* 2002).

It seems likely that the ants always measure the width of entrances, given their extremely high aversion to wide ones. We suspect that they might measure them from inside the nest, because after entering a nest they survey it with great care and patrol its inside walls (Mallon & Franks 2000).

The ants are probably using light levels within a nest to determine the total abundance of its entrances. Indeed, individual *T. albipennis* workers might learn the light level in one nest and compare it with the light level in the other. Alternatively, different ants might rate the nests on some intrinsic scale of desirability based in part on ambient light. Both are possible because individual ants can make direct comparisons, even though these do not appear always to be necessary (Pratt *et al.* 2002).

Temnothorax albipennis colonies are seasonally polydomous. That is, in the spring, colonies tend to split into two nest sites (Partridge *et al.* 1997). This accounts for differences in the results of otherwise identical experiments in the autumn and spring. Colonies are very prone to splitting in the spring even when the numbers of nest entrances in the two nests differ by a factor of 10 (experiment 22). Nevertheless, such is their apparent aversion to wide entrances that, even in the spring, all of the colony will occupy a single nest with many entrances in preference to one with a single wide entrance. This is all the more remarkable because in one of our designs the multiple-entrance nest had a greater total entrance gap width and hence much more light ingress than the nest with a single wide entrance (experiment 20).

It is, thus, clear that the ants are using two different metrics, overall light ingress and the width of individual entrances to assess the suitability of potential dwellings. Given that they also assess floor area (Mallon & Franks 2000), headroom (Franks *et al.* 2003*b*) and even issues associated with nest hygiene (Franks *et al.* 2005) when assessing nests, they have a lot of separate factors to consider and compare. Indeed, earlier work suggests they use one of the most comprehensive strategies for evaluating alternatives, the weighted additive strategy (Franks *et al.* 2003*b*).

We suspect that in general these ants prefer nests with fewer and narrower entrances because these are easier to defend (Franks & Partridge 1993). Indeed, they are influenced by the proximity of hostile conspecific colonies when they emigrate and may even drive out smaller conspecific colonies from desirable nests (Franks *et al.* submitted). It is remarkable that these ants pay so much attention to fixed entrance sizes when they can easily encircle themselves with a complete wall of debris in an empty cavity (Franks *et al.* 1992). This suggests that fixed, immutable, entrances are more important than easily built ones that can be demolished just as readily by their natural enemies.

In general, we advise caution over current claims that insects might be able to count (*sensu stricto*). Much simpler rules of thumb are likely often to suffice. Not everything that counts, and might be counted, needs to be counted.

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REFERENCES

Briscoe, A. D. & Chittka, L. 2001 The ecology of color vision in insects. *Annu. Rev. Entomol.* **46**, 471–510. (doi:10.1146/annurev.ento.46.1.471)

Chittka, L. & Geiger, K. 1995 Can honey bees count landmarks? *Anim. Behav.* **49**, 159–164. (doi:10.1016/0003-3472(95)80163-4)

Church, R. M. & Meck, W. H. 1984 The numerical attribute of stimuli. In *Animal cognition* (ed. H. L. Roitblat, T. G. Bever & H. S. Terrace), pp. 445–464. Hillsdale, NJ: Erlbaum.

Davis, H. & Pérusse, R. 1988 Numerical competence in animals: definitional issues, current evidence, and a new research agenda. *Behav. Brain Sci.* **11**, 561–615.

Dehaene, S. 1999 *The number sense: how the mind creates mathematics*. Oxford, UK: Oxford University Press.

Dornhaus, A., Franks, N. R., Hawkins, R. M. & Shere, H. N. S. 2004 Ants move to improve—colonies of *Leptothorax albipennis* emigrate whenever they find a superior nest site. *Anim. Behav.* **67**, 959–963. (doi:10.1016/j.anbehav.2003.09.004)

Esch, H. & Burns, J. E. 1995 Honeybees use optic flow to measure the distance to a food source. *Naturwissenschaften* **82**, 38–40.

Franks, N. R. & Partridge, L. W. 1993 Lanchester battles and the evolution of combat in ants. *Anim. Behav.* **45**, 197–199. (doi:10.1006/anbe.1993.1021)

Franks, N. R., Wilby, A., Silverman, B. W. & Tofts, C. 1992 Self-organizing nest construction in ants: sophisticated building by blind bulldozing. *Anim. Behav.* **44**, 357–375. (doi:10.1016/0003-3472(92)90041-7)

Franks, N. R., Pratt, S. C., Mallon, E. B., Britton, N. F. & Sumpter, D. J. T. 2002 Information flow, opinion-polling and collective intelligence in house-hunting social insects. *Phil. Trans. R. Soc. B* **357**, 1567–1583. (doi:10.1098/rstb.2002.1066)

Franks, N. R., Dornhaus, A., Fitzsimmons, J. P. & Stevens, M. 2003*a* Speed versus accuracy in collective decision-making. *Proc. R. Soc. B* **270**, 2457–2463. (doi:10.1098/rspb.2003.2527)

Franks, N. R., Mallon, E. B., Bray, H. E., Hamilton, M. J. & Mischler, T. C. 2003*b* Strategies for choosing among alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* **65**, 215–223. (doi:10.1006/anbe.2002.2032)

Franks, N. R., Hooper, J., Webb, C. & Dornhaus, A. 2005 Tomb evaders: house-hunting hygiene in ants. *Biol. Lett.* **1**, 190–192. (doi:10.1098/rspb.2005.0302)

Franks, N. R., Dornhaus, A., Hitchcock, G., Guillem, R., Hooper, J. & Webb, C. Submitted. Avoidance of conspecific colonies during nest choice by ants. *Anim. Behav.*

Karban, R., Black, C. A. & Weinbaum, S. A. 2000 How 17-year cicadas keep track of time. *Ecol. Lett.* **3**, 253–256. (doi:10.1046/j.1461-0248.2000.00164.x)

Mallon, E. & Franks, N. R. 2000 Ants estimate area using Buffon's needle. *Proc. R. Soc. B* **267**, 765–770. (doi:10.1098/rspb.2000.1069)

Mcleman, M. A., Pratt, S. C. & Franks, N. R. 2002 Navigation using visual landmarks by the ant *Leptothorax albipennis*. *Insect. Soc.* **49**, 203–208. (doi:10.1007/s00040-002-8302-2)

Meck, W. H. & Church, R. M. 1983 A mode control model of counting and timing processes. *J. Exp. Psychol.: Anim. Behav. Processes* **9**, 320–334. (doi:10.1037//0097-7403.9.3.320)

Partridge, L. W., Partridge, K. & Franks, N. R. 1997 Field survey of a monogynous leptothoracine ant (Hymenoptera: Formicidae): evidence of seasonal polydomy? *Insect. Soc.* **44**, 75–83. (doi:10.1007/s000400050031)

Pratt, S. C., Mallon, E. B., Sumpter, D. J. T. & Franks, N. R. 2002 Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* **52**, 117–127. (doi:10.1007/s00265-002-0487-x)

Shettleworth, S. J. 1998 *Cognition, evolution and behaviour*. Oxford, UK: Oxford University Press.

Shorter Oxford English Dictionary 2002. Oxford, UK: Oxford University Press.

Tautz, J., Zhang, S., Spaethe, J., Brockman, A., Si, A. & Srinivasan, M. 2004 Honeybee odometry: performance in varying natural terrain. *PLOS Biol.* **2**, 915–923. (doi:10.1371/journal.pbio.0020211)