

Rothamsted Repository Download

A - Papers appearing in refereed journals

James, L., Davies, T. G. E., Lim, K. S. and Reynolds, A. M. 2020. Do bumblebees have signatures? Demonstrating the existence of a speed-curvature power law in *Bombus terrestris* locomotion patterns. *PLOS ONE*. 15 (1), p. e0226393.

The publisher's version can be accessed at:

- <https://dx.doi.org/10.1371/journal.pone.0226393>
- <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0226393>

The output can be accessed at: <https://repository.rothamsted.ac.uk/item/96zq0/do-bumblebees-have-signatures-demonstrating-the-existence-of-a-speed-curvature-power-law-in-bombus-terrestris-locomotion-patterns>.

© 15 January 2020, Please contact library@rothamsted.ac.uk for copyright queries.

1
2
3
4
5
6
7
8
9
10
11
12
13
14

Do bumblebees have signatures?

Demonstrating the existence of a speed-curvature power law in *Bombus terrestris* locomotion patterns.

Laura James^{1*}, T. G. Emyr Davies¹, Ka S. Lim¹, Andrew Reynolds¹

¹ Rothamsted Research, West Common, Harpenden, Hertfordshire, UK.

*Corresponding author:

Laura James

Laura.james@rothamsted.ac.uk

15 **Abstract**

16 We report the discovery that *Bombus terrestris audax* (Buff-tailed bumblebee) locomotor trajectories
17 adhere to a speed-curvature power law relationship which has previously been found in humans, non-
18 human primates and *Drosophila* larval trajectories. No previous study has reported such a finding in
19 adult insect locomotion. We used behavioural tracking to study walking *Bombus terrestris* in an arena
20 under different training environments. Trajectories analysed from this tracking show the speed-
21 curvature power law holds robustly at the population level, displaying an exponent close to two-thirds.
22 This exponent corroborates previous findings in human movement patterns, but differs from the
23 three-quarter exponent reported for *Drosophila* larval locomotion. There are conflicting hypotheses
24 for the principal origin of these speed-curvature laws, ranging from the role of central planning to
25 kinematic and muscular skeletal constraints. Our findings substantiate the latter idea that dynamic
26 power-law effects are robust, differing only through kinematic constraints due to locomotive method.
27 Our research supports the notion that these laws are present in a greater range of species than
28 previously thought, even in the bumblebee. Such power laws may provide optimal behavioural
29 templates for organisms, delivering a potential analytical tool to study deviations from this template.
30 Our results suggest that curvature and angular speed are constrained geometrically, and
31 independently of the muscles and nerves of the performing body.

32

33

34 1. Introduction

35 At any point along a curve there is a unique circle or line which most closely approximates the curve
36 near that location. The radius of that circle defines the 'radius of curvature', R, whilst curvature, C, is
37 defined to be its reciprocal, 1/R. According to this definition, it can be expected that straight lines will
38 have zero curvature, and for a given observer at a fixed scale large circles will have small curvature
39 and small circles will have high curvature. Curvature along with angular speed, A, has been used to
40 quantify human writing signatures[1].

41 Remarkably the human signature, a powerful individual identifier, adheres to a speed-curvature
42 power law[1]. The speed-curvature, or two-thirds, power law dictates that the instantaneous angular
43 speed of movements vary proportionally to two-thirds power of their curvature[1]. According to the
44 law, movements under high curvature tend to slow down, whereas movements under low curvature

$$A = kC^{2/3} \quad (1)$$

where k is a constant of proportionality.

45 speed up[2]. The law is given by

$$A \equiv kC^{2/3} \quad (1)$$

where k is a constant of proportionality.

49
50 Maximally-smooth movements, which minimize rates of change of acceleration (i.e., jerks and jolts),
51 are generated under the two-thirds power law[3-5], which holds true across a range of voluntary
52 human movements, including drawing, walking and pursuit eye movements[1,3,6,7]. The law also
53 holds true across a diverse range of taxa. The law has been observed in the motor cortical control of
54 Rhesus monkey hand movements whilst drawing [8], and even in the larval movement of the fruit fly
55 (*Drosophila melanogaster*)[5] albeit with a marginally different power-law exponent, three quarters
56 rather than two thirds.

57 The principal origins of this speed-curvature power law are contentious. One hypothesis suggests that
58 the law results from central planning constraints imposed by the nervous system[8,9]. Another, that
59 the law arises due to physiological constraints conferred by muscular properties and
60 kinematics[2,5,10]. A further view, that the law exists to maximize movement smoothness and
61 minimize jerk[3,9]. Identifying the generative mechanism holds the key to understanding the
62 statistical law, the occurrence of which is remarkable given that behaviours are shaped by individual
63 psyches and by complex social and environmental interactions. It's identification may help to
64 elucidate how other statistical regularities can occur within the complex movement patterns that arise
65 in nature[11-16]. Progress towards identifying the underlying mechanism can be made by
66 determining the pervasiveness of the two-thirds law, and by establishing whether or not it occurs in
67 other modes of locomotion.

68 Given that the locomotive patterns of *Bombus terrestris*, and indeed animal organisms, are probably
69 shaped by their motivational states and by environmental factors, a seemingly natural null hypothesis
70 would be that individuals have unique locomotive patterns and that statistical regularities are absent
71 or trivial (for example, a tendency to move forwards with near constant speed). Therefore, to
72 determine the pervasiveness of the law, we must first determine whether the speed-curvature power
73 law persists in the walking trajectories of the bumblebee at all and, if it does, whether the law differs
74 depending on a bee's environment. We must then determine whether the exponent of the law
75 adheres closely to the two thirds exponent. Finally, it is necessary to also assess whether the power
76 law is the best mathematical descriptor of walking bumblebee trajectories or whether an alternative
77 better describes the relationship.

78 Walking is distinctly different from the crawling movements made by limbless larvae[17]. Therefore,
79 we might predict that walking bee trajectories would adhere more closely to the two-thirds power law
80 exponent reported for unconstrained movements such as human drawing and walking[1,6], than the
81 three-quarters exponent reported for the mechanically constrained movements of larvae[5].

82 To the best of our knowledge the speed-curvature power law has not been studied in any other
83 invertebrate other than *Drosophila melanogaster* larvae[5] and never in the final, adult stage of an
84 insect. Here, we report that *Bombus terrestris audax*, a social bumblebee species with a complex
85 behavioural repertoire, displays a two-thirds speed-curvature power law whilst walking in an arena,
86 under differing environments.

87

88

89

90 **2. Methods**

91 **Bee subjects**

92 All subjects were *Bombus terrestris audax* from research hives obtained from Biobest Belgium NV
93 (Westerlo, Belgium). Colonies were settled in wooden nest boxes (29 x 21 x 16 cm) and provided with
94 biogluc (Biobest Belgium NV, Westerlo, Belgium) in two gravity feeders in a Perspex foraging tunnel
95 (26 x 4 x 4 cm) connected to the nest box. Pollen was also provided in baskets in the Perspex tunnel.
96 Gravity feeders and pollen were replenished, as necessary, to ensure a consistent supply of food to
97 the colony. Newly emerged individuals were marked in colour groups by age cohort with coloured
98 plastic bee marking tags (EH Thorne Ltd, Market Rasen, UK) superglued to the top of the thorax. This
99 allows tracking of an individual's age. All individuals used in a single trial were one-week post-
100 emergence (to allow bees to begin foraging and to be monitored) and of the same age cohort. The
101 hive was observed each day and foragers of each age cohort were identified in the foraging tube by
102 their colour and number. From the foragers recorded in each age cohort ten individuals were
103 randomly selected to be tested per trial. The selected individuals are then randomly allocated to either
104 the treatment or control groups for each trial. Trials were replicated 3 times; all treatments replicated
105 3 times across 3 different hives.

106 **The experimental arena**

107 Experiments were conducted within a thermal-visual arena (Fig.1-a-d), similar to a platform previously
108 used for *Drosophila* tracking[18]. The arena enables the creation of controlled, but naturalistic,
109 environments. A Peltier array of 64 2.5x2.5 cm individually controllable thermoelectric Peltier
110 elements, arranged in an 8x8 grid, facilitates control of the arena's floor temperature. The arena's
111 floor is covered in white masking tape to create an inconspicuous, featureless surface which can be
112 easily cleaned and replaced between trials to prevent the use of scent marks by foragers to locate
113 arena rewards. In the training trials, visual patterns were adhered to the surface of the arena's walls
114 to create a visual landscape consisting of repeating patterns of stars, dots, horizontal and vertical
115 bars, denoting the four quadrants of the arena's circumference. Light-emitting diodes (LEDs) (colour
116 temperature 6500K) around the top edge of the arena were used to light the arena consistently above
117 the bee flicker fusion frequency [19] (Fig.1-c). The arena was kept in a controlled environment room
118 at 22° C with a day: night cycle of 16:8 hr.

119 **Training environments**

120 The task required forager bees to use visual landscape patterns to locate a reward zone within the
121 arena, in response to four training environments: 1) control environment with no reward or
122 punishment, 2) appetitive reward environment (0.1ml 50% sucrose solution in reward zone), 3)
123 aversive punishment environment (heated arena floor (45°C), cool (25°C) reward zone) and 4)
124 combined aversive and appetitive environment (heated arena floor (45°C), 0.1ml 50% sucrose
125 solution in cool (25°C) reward zone). All rewards (cool zone or sucrose) were inconspicuous and not
126 visually distinguishable from any other tiles on the arena floor.

127 **Training regime**

128 None of the test subjects had experience of the thermal-visual arena prior to the training trials. Each
129 bee was given ten trials in the arena (each trial was of three minutes duration) spaced across three
130 days. Spaced conditioning, in which temporal spacing exists between successive conditioning trials,

131 has been shown to lead to higher memory consolidation in bees, especially at long intervals [20].
132 When placed into the thermal visual arena, bees were confined under a clear plastic tube for one
133 minute prior to the trial start, to allow orientation within the arena. The tube was then removed, and
134 the three-minute trial started. All bees were starved for one hour prior to trial start to motivate
135 individuals in the appetitive condition and to remove starvation as a confounding variable between
136 treatments. Bees were confined to individual cages in-between trials to prevent further foraging
137 experience not in the arena and standardise the amount of foraging experience in the arena each
138 bee received. Cages were placed next to each other and adjacent to the hive to allow visual and
139 olfactory communication between hive members.

140 **Trajectory tracking**

141 To facilitate 2D trajectory tracking, foragers were confined to walking on the test platform by wing
142 clipping. Selected foragers' wings were clipped using a queen marking cage and dissection scissors
143 (EH Thorne Ltd, Market Rasen, UK).

144 Individual bee trajectories were filmed using a camera (FLIR C2 Infrared Camera) attached to a tripod
145 above the arena (Fig.1-b). Video recording was at four frames per second for ten, three-minute trials
146 per bee. Video files were tracked using CTRAX: the Caltech Multiple Walking Fly Tracker software[21].
147 The raw centroid tracking data files outputted by CTRAX were then used for speed-curvature power
148 law calculation.

149 **Speed-curvature power law calculation**

150 For the data analysis, the x, y coordinates and corresponding timestamps for whole trajectories, for
151 individual bees, from the centroid tracking were used to compute angular speed $A(t)$ and curvature
152 $C(t)$ using standard differential geometry[22]. Velocities were calculated from consecutive, regularly
153 timed, positional fixes, $\bar{x} = \frac{x(t + \Delta t) - x(t)}{\Delta t}$ and $\bar{y} = \frac{y(t + \Delta t) - y(t)}{\Delta t}$ where $\Delta t = 0.2$ s is the time
154 interval between consecutive recordings. Accelerations \ddot{x} and \ddot{y} were calculated in a directly

155 analogous way from consecutive velocities. Together these quantities determine the 'radius of
156 curvature'³⁶,

$$157 \quad R = \left| \frac{(\dot{x}^2 + \dot{y}^2)^{3/2}}{\dot{x}\ddot{y} - \dot{y}\ddot{x}} \right| \quad (2)$$

158 which in turn gives the angular speed,

$$159 \quad A = (\dot{x}^2 + \dot{y}^2)^{1/2} / R \quad (3)$$

160 and the curvature,

$$161 \quad C = 1 / R \quad (4)$$

162 **Data selection**

163 Whole trajectories were analysed, with data selected so that only individual bee tracks which had
164 greater than 50 data points ($n > 50$) were used for analyses (for all other tracks $n =$ between 66 and
165 1047). Excluded bees: $n = 14$. Bees used for analysis, $n = 45$. When we removed all bees with under
166 100 data points the outcomes of our analyses did not change and therefore we can consider selection
167 at 50 data points to be robust and there was no need to exclude further bees. Data were not filtered
168 (smoothed) prior to processing. Filtering does not affect the outcomes of our analyses (see [S2 Figs](#)
169 [A, B and C supporting information](#)).

170 **Statistical analysis**

171 The hallmark of a power-law relationship between curvature, C , and angular speed, A , is a straight-
172 line relationship between $\log(C)$ and $\log(A)$. Taking the logarithm of both sides of the two-thirds
173 power-law rule gives the linear relationship $\log A = \log K + \beta \log C$, with $\beta = 2/3$. Here, following
174 Zago et al.[5] we looked for such relationships by least squares linear regression of $\log(C)$ and $\log(A)$.
175 Using this method, we estimated the exponent, β , and the variance, r^2 , accounted for by the power-
176 law.

177 The power-law scaling demonstrated by our analysis extends over two or more scales of magnitude.
178 This fulfils Stumpf and Porter's[23] 'rule of thumb'; after critically appraising power laws identified in
179 biological systems, they suggested that a candidate power law probability frequency distribution
180 should apply over at least two orders of magnitude along both axes and should be explainable by a
181 viable mechanism.

182 We then went beyond previous analyses[5,24] by comparing our observations with strongly
183 competing functions that resemble power-laws but are not underpinned mechanistically. The power-
184 law relationship between curvature and angular speed cannot, of course, extend to arbitrarily large
185 curvatures and angular speeds because of physiological constraints that place limits on the tightness
186 of turning and on the speed that can be attained by an individual. Departures from power-law are
187 expected when the maximum curvatures and speeds are approached by an individual. Here we
188 examine this by fitting our data to two functions that resemble power-laws over a range of scales, but
189 which depart from power-laws when curvatures and speeds are sufficiently high. These functions are
190 stretched exponentials (which include exponentials as a special case),

$$191 \quad A = a \cdot \exp(bC^p)$$

192 and log-normal like functions,

$$193 \quad A = a \cdot \exp(b(\ln C - \ln d)^2)$$

194 where a, b, p and d are free parameters that are determined by fitting the functions to our data. The
195 relative merits of the power-law, stretched exponential and log-normal functions as representations
196 of our data were determined using the Akaike information criterion[25].

197 The stretched exponential and the log-normal like functions can be considered as strongly competing
198 descriptions of our data that contain three rather than two free parameters. This extra flexibility could
199 result in better fits to our data. Functions were fitted to individuals' movement patterns, rather than
200 to pooled data as we sought to capture an individual's constraints. We then compared the pooled
201 data with functions parameterized in terms of the average best fit parameters.

202 Stretched exponentials (typically with $p \sim 0.007$) provided good fits to our data, but better fits are
203 obtained with power-laws. Even better fits were obtained with the log-normal like functions which is
204 not surprising given that they are more flexible than simple power-laws (Fig3 a-d). In all cases, the
205 Akaike weights for the log-normal like functions are 1.00 which indicates that the log-normal like
206 functions are convincingly favoured over the power-law and stretched exponential functions.
207 However, as is often the case, the better fit of the complex model (the log-normal like function) trades
208 off with the elegance and clarity of the simpler model (the power-law function). The log-normal
209 functions are, however, convex with maxima at $\ln C = \ln d$. Such maxima are not evident in our
210 observations and consequently the estimates for $\ln d$ (approximately 35) were much larger than $\ln C_{\max}$
211 (approximately ten). This implies that the fitted log-normal like functions are effectively fits to power-
212 laws because when $\ln d$ are much larger than $\ln C_{\max}$

$$213 \quad A \approx a \cdot \exp(-2b \ln(d) \ln(C) + b \ln(d)^2) \\ = kC^\beta$$

214 where $k = a \cdot \exp(b \ln(d)^2)$ and $\beta = -2b \ln(d)$.

215 Our mean estimates for the power-law exponents; 0.59 (controls, $n = 14$, range 0.42 - 0.87), 0.61
216 (appetitive + aversive, $n = 12$, range 0.43 - 0.87), 0.60 (aversive, $n = 7$, range 0.49 - 0.94) and 0.57
217 (appetitive, $n = 12$, range 0.44 - 0.8) are broadly consistent with the two-thirds power-law rule. We
218 have therefore arrived at this law using two different approaches; by fitting our data to power-laws
219 and by fitting our data to log-normal functions.

220 Statistically significant differences between the power exponents (β) of treatment groups and
221 expected exponent values of two thirds (0.66) and three quarters (0.75) were calculated using non-
222 parametric tests (Kruskal-Wallis ANOVA by ranks), as data were not normally distributed (Shapiro-
223 Wilk test, p value = 0.000587518***). Kruskal-Wallis tests were conducted in RStudio (Version 1.0.44
224 - © 2009-2016 RStudio, Inc.). Summary boxplot, Fig 4 was produced in RStudio using the 'ggplot'
225 package.

226 3. Results

227 Varying exploratory strategies

228 To facilitate the creation of different walking trajectories, bees were tested across differing training
229 environments within a thermal-visual arena (Fig 1). Training environments differed in the reward or
230 incentive provided to foragers, providing either no reward or punishment (control), an appetitive
231 sucrose reward, an aversive punishment (heated arena floor) or a combined aversive punishment
232 and appetitive reward environment. Each bee was given ten training trials, experiencing only one of
233 the training environments across all ten trials. In each training trial bees were required to use visual
234 landscape patterns, around the circumference of the arena, to locate the appropriate reward zone
235 (refer to 'training environments' in methods section for further details).

~~Figure 1 (a-d) The thermal-visual arena. (a) Diagrammatic representation of the thermal-visual arena. (b) The arena *in-situ* in the lab. (c) A birds-eye view of the arena with an example *Bombus terrestris* forager completing a training trial. (d) A thermal camera being used pre-training trial to confirm the location of the inconspicuous cool reward zone within the arena.~~

236 Figure 1 (a-d) The thermal-visual arena. (a) Diagrammatic representation of the thermal-visual arena. (b) The arena *in-situ* in
237 the lab. (c) A birds-eye view of the arena with an example *Bombus terrestris* forager completing a training trial. (d) A thermal
238 camera being used pre-training trial to confirm the location of the inconspicuous cool reward zone within the arena.

239

240 In all environmental conditions, bees traced complex trajectories (Fig 2 panels a, b, c, d). In each case
241 curvature is seen to occur across a broad range of scales, as evidenced by the presence of nearly
242 straight-line movements with low curvature and the presence of tight turns with high curvature.
243 Across differing environments bees appeared to display varying exploratory trajectories. Individuals
244 tested in the control condition often traced concentric paths, delineating the boundary of the arena
245 (Fig 2). Individuals in the aversive condition located and remained in the cool reward zone for
246 extended periods, making directed exploratory trajectories to a section of the arena's edge (Fig 2b).
247 Similar trajectories were seen for individuals in the combined aversive and appetitive environment
248 where both a sucrose and cool zone reward were given in the same location (Fig 2c). In the appetitive
249 reward environment individual's trajectories were more varied, not being constrained to particular
250 routes (Fig 2d).

251 Individual bees' trajectories may be governed in part by differing motivations in response to differing
252 training stimuli. When provided with no training stimuli there is no motivation for foragers to complete
253 any task other than escape, resulting in delineating pathways (control group, Fig 2a). Training appears
254 to be most effective in the aversive (Fig 2b) and combined aversive and appetitive (Fig 2c) conditions
255 as foragers are increasingly motivated to take direct paths to and from the reward zone. Nonetheless,
256 these complex, highly unique pathways all have statistical regularities characterised by a simple
257 power law, which holds true irrespective of motivational environment or training regime.

258 Figure 2 (a-d). Trajectories of representative bees from the control (a), aversive (b), appetitive (c) and combined aversive and
259 appetitive conditions (d). The blue squares indicate the location of the reward zone (specific to condition) in the arena
260 environment. Bees appear to implement differing exploratory strategies, dependent on the reward or punishment environment
261 they are in. In the control condition (a), individuals often trace concentric paths which delineate the arena boundary. In the
262 aversive condition (b), with a heated floor, individuals were motivated to locate and remain in the cool reward zone. Therefore,
263 trajectories often showed directed exploratory paths out from the reward zone to a facet of the arena. Similar directed trajectories
264 are seen for individuals in the combined aversive and appetitive condition (d). This is not surprising as this is the condition which
265 should provide foragers with the most motivation to remain in the reward zone, with two rewards (sucrose and cool zone) and a
266 punishment in the form of the heated arena floor. Individuals in the appetitive reward environment (c) often tracked more varied
267 paths, not constrained to set routes or areas of the arena.

268

~~Figure 2 (a-d). Trajectories of representative bees from the control (a), aversive (b), appetitive (c) and combined
aversive and appetitive conditions (d). The blue squares indicate the location of the reward zone (specific to condition)
in the arena environment. Bees appear to implement differing exploratory strategies, dependent on the reward or
punishment environment they are in. In the control condition (a), individuals often trace concentric paths which delineate
the arena boundary. In the aversive condition (b), with a heated floor, individuals were motivated to locate and remain
in the cool reward zone. Therefore, trajectories often showed directed exploratory paths out from the reward zone to a
facet of the arena. Similar directed trajectories are seen for individuals in the combined aversive and appetitive condition
(d). This is not surprising as this is the condition which should provide foragers with the most motivation to remain in the
reward zone, with two rewards (sucrose and cool zone) and a punishment in the form of the heated arena floor.
Individuals in the appetitive reward environment (c) often tracked more varied paths, not constrained to set routes or
areas of the arena.~~

269

270 The speed-curvature relationship

271 A power-law relationship between curvature, C , and angular speed, S , ($C = aS^b$) will manifest itself
272 as a straight-line ($\log A = \log K + \beta \log C$) on a log-log plot. We tested for such a straight-line
273 relationship by linearly regressing $\log C$ on $\log S$ for each bee within each environmental condition
274 (Fig 3 a, b, c, d). The average (mean) estimates for the power-law exponents are 0.59 (controls, $n =$

275 14, range 0.42 - 0.87), 0.61 (appetitive + aversive, n = 12, range 0.43 - 0.87), 0.60 (aversive, n = 7,
276 range 0.49 - 0.94) and 0.57 (appetitive, n = 12, range 0.44 - 0.8).

277 The suitability of the power law to describe our data was tested against two competing statistical
278 relationships; stretched exponentials and log-normal like functions (Fig 3 a, b, c, d) (see 'statistical
279 analysis' methods section for further details). Power laws provide better fits than stretched
280 exponentials, and although good fits are obtained with log-normal functions, they are consistent with
281 the two-thirds power law rule, making the simpler, more elegant power law model the best choice.

~~Figure 3 (a-d). The relationship between angular speed and curvature of path in walking bee trajectories. The two-thirds power law holds true in walking bees across differing environments (control (a), aversive (b), appetitive (c) and combined aversive+ appetitive (d)). (a) Scatter plot of instantaneous angular speed plotted against local path curvature at a population level on a log-log scale, for all individuals in the control group. All data points (n = 12224) were sampled at equal time intervals along the trajectories of 14 individual bees. Data was fitted to the power function $A(t) = kC(t)^{2/3}$ (red line), to stretched exponentials (green line) and log-normal (blue line) functions. Stretched exponentials and log-normals can resemble power-laws and are strongly competing models of the data. (b) Log-log plot of angular speed versus curvature for 7 bees in the aversive group (n = 1081). (c) Log-log plot of angular speed versus curvature for 12 bees in the appetitive group (n = 1835). (d) Log-log plot of angular speed versus curvature for 12 bees in the combined aversive + appetitive group (n = 2309).~~

282 Figure 3 (a-d). The relationship between angular speed and curvature of path in walking bee trajectories. The two-thirds power
283 law holds true in walking bees across differing environments (control (a), aversive (b), appetitive (c) and combined aversive+
284 appetitive (d)). (a) Scatter plot of instantaneous angular speed plotted against local path curvature at a population level on a log-
285 log scale, for all individuals in the control group. All data points (n = 12224) were sampled at equal time intervals along the
286 trajectories of 14 individual bees. Data was fitted to the power function $A(t) = kC(t)^{2/3}$ (red line), to stretched exponentials (green
287 line) and log-normal (blue line) functions. Stretched exponentials and log-normals can resemble power-laws and are strongly
288 competing models of the data. (b) Log-log plot of angular speed versus curvature for 7 bees in the aversive group (n = 1081).
289 (c) Log-log plot of angular speed versus curvature for 12 bees in the appetitive group (n = 1835). (d) Log-log plot of angular speed
290 versus curvature for 12 bees in the combined aversive + appetitive group (n = 2309).

291

292 **Adherence to a power law across environments**

293 Adherence to the law did not depend on the environment an individual forager was exposed to (see
294 Fig 3 a-d) and the distribution of power exponents did not differ significantly between treatments
295 (including controls) (Kruskal-Wallis ANOVA by ranks, chi-squared = 0.62489, df = 3, p-value = 0.8907
296 (>0.05)). As would be expected, all treatment exponents were significantly different from zero
297 (Kruskal-Wallis ANOVA by ranks, chi-squared = 32.321, df = 4, p = 1.645e-06**** (<0.00001)).

298 **Two-thirds or three-quarters?**

299 To determine whether bees' trajectories adhered more closely to the two-thirds or the three-quarters
300 power law exponent, treatments were tested for significance against populations with assumed
301 power exponents of 0.66 and 0.75.

302 Treatment populations were highly significantly different from the three-quarters power law exponent
303 (0.75) (Kruskal-Wallis ANOVA by ranks, chi-squared = 17.79, df = 4, p-value = 0.001356** (<0.05)).

304 However, treatment populations were not found to be significantly different from the two-thirds power
305 law (0.66) (Kruskal-Wallis ANOVA by ranks, chi-squared = 6.0816, df = 4, p-value = 0.1931 (>0.05)).

306 However, Fig 4 shows that although treatment groups did not differ significantly from 0.66, the
307 medians of treatment groups vary around a 0.55 power exponent line. Populations were found to not
308 significantly differ from this 0.55 power exponent either (Kruskal-Wallis ANOVA by ranks, chi-squared
309 = 1.7447, df = 4, p-value = 0.7826 (>0.7826)).

~~Figure 4. Summary boxplot statistics for the β -exponent of bees in the four conditions: control (n=14), aversive (n=7), appetitive (n=12) and aversive + appetitive (n=12 (post data filtering) and individuals from all conditions combined. 99% of all data lies within the boxplot whiskers (outliers represented as dots). The two-thirds power exponent (0.66) is represented by the red line. The three-quarters exponent (0.75) by the blue line and a new predicted exponent of 0.55 by the green line. Although treatment groups did not differ significantly from the two-thirds exponent (Kruskal-Wallis analysis), when visualised, it is clear that median β -exponent values vary around a 0.55 power exponent value, suggesting that an exponent range of 0.5 to 0.66 best describes the exponents of our walking bees.~~

310 Figure 4. Summary boxplot statistics for the β -exponent of bees in the four conditions: control (n=14), aversive (n=7), appetitive
311 (n=12) and aversive + appetitive (n=12 (post data filtering) and individuals from all conditions combined. 99% of all data lies within
312 the boxplot whiskers (outliers represented as dots). The two-thirds power exponent (0.66) is represented by the red line. The
313 three-quarters exponent (0.75) by the blue line and a new predicted exponent of 0.55 by the green line. Although treatment
314 groups did not differ significantly from the two thirds exponent (Kruskal-Wallis analysis), when visualised, it is clear that median
315 β -exponent values vary around a 0.55 power exponent value, suggesting that an exponent range of 0.5 to 0.66 best describes
316 the exponents of our walking bees.

317

318 4. Discussion

319 Locomotive patterns are frequently complex but do, nonetheless, have surprising regularities
320 (primitives) that may provide insights into the underlying generative mechanisms for movement and

321 into motor planning. These regularities take the form of power-laws that have been shown to
322 characterise not only curvature[1], but also the duration of movement bouts and pauses[26].

323 Our work in *Bombus terrestris* supports previous findings in *Drosophila* larvae[5] that the power laws
324 which govern voluntary human behaviours[1,3,4,6] also govern the behaviours of less complex
325 organisms. Remarkably, this law holds, not just across vastly different locomotive methods and
326 speeds (walking[6], drawing[1], crawling[5]), but also across greatly differing organisms
327 (human[1,3,4,6] and non-human primates[8], Diptera[5], and now Hymenoptera).

328 The explanations for these power laws within movement patterns are contentious with contrasting
329 hypotheses for their existence. Originally ascribed to central motion planning by the nervous
330 system[8,9] it was thought that the existence of the relationship between speed and curvature could
331 not be a result of muscular properties and limb dynamics[10]. This is supported by the observation
332 that the law holds true for human drawing under isometric conditions[27]. Notably, the speed-
333 curvature power law is also corroborated across widely diverse taxa. Evidence that the law originates
334 as a result of decoding complex cortical processes is apparent in the motor cortical control of Rhesus
335 monkey hand movements, as population vectors in the motor cortex obey the power law during
336 drawing[8], adding weight to the central planning origin hypothesis.

337 *Drosophila* Larval locomotion power exponents have been recorded to deviate from the two-thirds
338 exponent reported for human voluntary movements[1,3,4,6], at closer to three-quarters[5]. The
339 researchers suggest that these findings prove a role for dynamic effects adding on purely kinematic
340 constraints[5]. In support of this notion, the power exponent recorded for human drawing shifts closer
341 to this value of three-quarters (0.73) when drawing underwater[28], suggesting that power laws can
342 indeed be governed by kinematic constraints. Our analyses suggest that, in walking bumblebees, a
343 power law exponent between 0.55 and 0.66 (two-thirds) better defines movements than the near
344 0.75 exponents previously reported for *Drosophila*[5] and constrained human movements[28]. Our
345 evidence further supports the idea that exponents are forced closer to the three-quarters value when

346 kinematic constraints are present, as our constraint-free bees have a generally much lower exponent
347 at closer to two thirds.

348 However, other studies take a less definitive approach, suggesting that biomechanical factors and
349 central planning may interact to constrain kinematic movement aspects, limiting the degrees of
350 freedom which they can take[29]. An extension of this, the minimum jerk hypothesis[3,9] states that
351 the law exists to maximize smoothness, selecting for jerk-free, stable, controllable movements. The
352 occurrence of these laws across organisms could be seen to support a convergent evolution theory
353 of a jerk-free movement mode which remains behaviourally efficient across organisms of different
354 size, complexity, and phyla. Maximally smooth movements may seem to be without biological
355 significance for grounded invertebrates, like crawling *Drosophila* larvae[5] and walking bumblebees.
356 However, they could, nonetheless, be adaptive for airborne invertebrates, allowing for downwind
357 flights in the absence of visual cues for orientation. Such common orientation has been widely
358 documented since the advent of entomological radar, and allows noctuid fliers to add their flight
359 speed to the wind speed, so maximizing their dispersal[30]. Our analysis suggests that this ability is
360 a spandrel that predates flight, lying dormant in terrestrial movements.

361 Contrarily, the pervasiveness of the law may be an inconsequential by-product of the noise inherent
362 to central pattern generators (CPGs)[31]. Or more positively, an accidentally advantageous property
363 of noise, as somewhat paradoxically, noise may result in maximally smooth, controllable movement.
364 Possibly, the law may stem from simple harmonic motions[32], such as those outputted by CPGs
365 when combined with muscular viscoelastic properties[2]. However, this hypothesis seems unrealistic
366 when considering the power law in walking bees as we report here.

367 Our findings, together with those of Gomez-Marin et al.[5] for *Drosophila* larvae, are suggestive of
368 common mechanics of model switching in the locomotion of limbless and legged animals. As first
369 suggested by Kuroda et al.[33] who noted similarities between leg-density waves of centipedes and
370 millipedes and the locomotive waves of limbless animals. Our findings hint at a deeper analogy.
371 Marken & Shaffer[34] have argued that these power laws are artefacts of the calculations themselves.

372 However, this seems improbable, as the law is shown to persist regardless of its calculation
373 methodology[35].

374 Any tendency to walk around the perimeter of the circular arena (of radius $r=10$ cm) either in part or
375 wholly will be associated with a curvature of radius $R = r$. Our data for this curvature is consistent with
376 the overall power-law scaling seen across all radii and is not anomalous. This suggests that the circular
377 geometry of the arena is not impacting on the speed-curvature power law. This may not be true of
378 other geometries, such as squares, whose corners might be associated with high curvatures.

379 In our analyses, individual bee's tracking data were pooled within each learning environment. This
380 allowed us to collectively compare each training group to differing statistical models and to examine
381 a potential training environment impact on power law exponents. We acknowledge that this approach
382 minimises the role of intra-individual behavioural variation often seen in bees[36]. Although we have
383 not examined it here, future studies could examine the impact of this intra-individual variation on
384 power law exponents between bees and across learning experience.

385 The multitude of evidence for varying originating mechanisms suggests that the origins of such power
386 laws are most likely pluralistic in nature and potentially constraints vary across organisms.
387 Nonetheless, the pervasiveness of these multiple scaling laws, across both taxa and locomotive mode,
388 could imply an underlying driver. The notion that scale-free movements are intrinsic[11] suggests
389 universal scaling laws could present an optimal behavioural template which may then be favoured
390 by natural selection.

391 Nonetheless, this might be overemphasizing the role of evolution as the fundamental determinate of
392 behaviour, and underemphasizing the role of physical laws and mechanical limitations, as exemplified
393 by the minimum jerk hypothesis[3,9]. As animals, may simply be predisposed to have jerk-free
394 movements due to physical constraints. The argument for process structuralism[37], in which
395 mathematical laws supersede natural selection as a "shaping agency"[38] may therefore be more
396 applicable. This resonates with the occurrence of Levy walks; movement patterns that are

397 characterised by power-laws and seen across taxa from single cells to humans. In many cases these
398 appear to be shaped by physical constraints rather than by natural selection[39].

399 Understanding the basal behavioural templates behind organisms' locomotive trajectories may
400 provide a tool for behavioural study. Biological stressors, such as disease, have been shown to cause
401 deviations from this optimal behavioural template[40]. Power laws may therefore provide a diagnostic
402 tool for the sub-lethal impact of such stressors at a finer scale.

403 Our work with *Bombus terrestris* is one of the few examples of the speed curvature power law outside
404 human movements. Supporting the notion of an optimal behavioural template which is pervasive
405 across movement modes and organisms as a result of kinematic constraints. The discovery of this
406 null template in *Bombus terrestris* may add a tool to the arsenal of scientists, allowing us to better
407 study potential sublethal disruptors of optimal behaviour.

408 **Data availability**

409 The datasets generated and analysed during the current study are available as supporting files [S1
410 [fileTable](#): Raw centroid tracking data] with this submission.

411 **Acknowledgements**

412 We wish to thank Rebecca Reid for advice and assistance with experimental design and testing.

413 **Contributions**

414 ~~E.D. and K.S.L. co-conceived and co-designed the study. K.S.L. designed and built the experimental~~
415 ~~arena. L.J. designed and carried out all experimental procedures, processed all data and wrote the~~
416 ~~draft manuscript. A.R. analysed and interpreted data and assisted with manuscript writing. All~~
417 ~~authors gave approval for final publication.~~

418

419 **References**

- 420 1. Lacquaniti F, Terzuolo C, Viviani P. The law relating the kinematic and figural
421 aspects of drawing movements. *Acta Psychol (Amst)*. 1983;54: 115–130.
422 doi:10.1016/0001-6918(83)90027-6
- 423 2. Gribble PL, Ostry DJ. Origins of the Power Law Relation Between Movement Velocity
424 and Curvature: Modeling; the Effects of Muscle Mechanics and Limb Dynamics.
425 *JOURNAL OF Neurophysiol*. 1996;76. Available:
426 <https://www.physiology.org/doi/pdf/10.1152/jn.1996.76.5.2853>
- 427 3. Wann J, Nimmo-Smith I, Wing AM. Relation between velocity and curvature in
428 movement: Equivalence and divergence between a power law and a minimum-jerk
429 model. *J Exp Psychol Hum Percept Perform*. 1988;14: 622–637. doi:10.1037/0096-
430 1523.14.4.622
- 431 4. Flash T, Hochner B. Motor primitives in vertebrates and invertebrates. *Curr Opin*
432 *Neurobiol*. 2005;15: 660–666. doi:10.1016/j.conb.2005.10.011
- 433 5. Gomez-Marin A, Zago M, Lacquaniti F. The speed- curvature power law in
434 *Drosophila* larval locomotion. *Biol Lett*. 2016;12. Available:
435 <http://dx.doi.org/10.1098/rsbl.2016.0597>
- 436 6. Ivanenko YP, Grasso R, Macellari V, Lacquaniti F. Two-thirds power law in human
437 locomotion: role of ground contact forces. *Neuroreport*. 2002;13: 1171–1174.
438 doi:10.1097/00001756-200207020-00020
- 439 7. de'Sperati C, Viviani P. The Relationship between Curvature and Velocity in Two-
440 Dimensional Smooth Pursuit Eye Movements. *J Neurosci*. 1997;17: 3931–3945.
441 Available: <http://www.jneurosci.org/content/jneuro/17/10/3932.full.pdf>
- 442 8. Schwartz AB. Direct Cortical Representation of Drawing. *Science (80-)*. 1994;265:
443 540–542. Available: <http://science.sciencemag.org/content/sci/265/5171/540.full.pdf>
- 444 9. Viviani P, Flash T. Minimum-jerk, two-thirds power law, and isochrony: converging
445 approaches to movement planning. *J Exp Psychol Hum Percept Perform*. 1995;21:

- 446 32–53. doi:10.1037/0096-1523.21.1.32
- 447 10. Viviani P, Cenzato M. Segmentation and coupling in complex movements. *J Exp*
448 *Psychol Hum Percept Perform.* 1985;11: 828–845. doi:10.1037/0096-1523.11.6.828
- 449 11. Barabasi A-L. The origin of bursts and heavy tails in human dynamics. *Nature.*
450 2005;435: 207–211. doi:10.1038/nature03526
- 451 12. González MC, Hidalgo CA, Barabási A-L. Understanding individual human mobility
452 patterns. *Nature.* 2008;453: 779–782. doi:10.1038/nature06958
- 453 13. Nakamura T, Kiyono K, Yoshiuchi K, Nakahara R, Struzik ZR, Yamamoto Y. Universal
454 Scaling Law in Human Behavioral Organization. *Phys Rev Lett.* 2007;99: 138103.
455 doi:10.1103/PhysRevLett.99.138103
- 456 14. Song C, Koren T, Wang P, Barabási A-L. Modelling the scaling properties of human
457 mobility. *Nat Phys.* 2010;6: 818–823. doi:10.1038/nphys1760
- 458 15. Viswanathan GM. *The physics of foraging : an introduction to random searches and*
459 *biological encounters.* Cambridge University Press; 2011.
- 460 16. Proekt A, Banavar JR, Maritan A, Pfaff DW. Scale invariance in the dynamics of
461 spontaneous behavior. *Proc Natl Acad Sci U S A.* 2012;109: 10564–9.
462 doi:10.1073/pnas.1206894109
- 463 17. Tanaka Y, Ito K, Nakagaki T, Kobayashi R. Mechanics of peristaltic locomotion and
464 role of anchoring. *J R Soc Interface.* 2012;9: 222–33. doi:10.1098/rsif.2011.0339
- 465 18. Ofstad TA, Zuker CS, Reiser MB. Visual place learning in *Drosophila melanogaster.*
466 *Nature.* 2011;474: 204–7. doi:10.1038/nature10131
- 467 19. Inger R, Bennie J, Davies TW, Gaston KJ. Potential biological and ecological effects
468 of flickering artificial light. *PLoS One.* 2014;9: e98631.
469 doi:10.1371/journal.pone.0098631
- 470 20. Menzel R, Manz G, Menzel R, Greggers U. Massed and spaced learning in
471 honeybees: the role of CS, US, the intertrial interval, and the test interval. *Learn*
472 *Mem.* 2001;8: 198–208. doi:10.1101/lm.40001
- 473 21. Branson K, Robie AA, Bender J, Perona P, Dickinson MH. High-throughput ethomics

- 474 in large groups of *Drosophila*. *Nat Methods*. 2009;6: 451–7.
475 doi:10.1038/nmeth.1328
- 476 22. Wikipedia. Radius of curvature [Internet]. [cited 5 Feb 2018]. Available:
477 https://en.wikipedia.org/wiki/Radius_of_curvature
- 478 23. Stumpf MPH, Porter MA. Critical truths about power laws. *www.sciencemag.org Sci*.
479 2012;335. doi:10.1126/science.1218171
- 480 24. Huh D, Sejnowski TJ. Spectrum of power laws for curved hand movements. *Proc Natl*
481 *Acad Sci U S A*. 2015;112: E3950-8. doi:10.1073/pnas.1510208112
- 482 25. Spanos A. Curve Fitting, the Reliability of Inductive Inference, and the
483 Error-Statistical Approach. *Philos Sci*. 2007;74: 1046–1066. doi:10.1086/525643
- 484 26. Reynolds AM, Jones HBC, Hill JK, Pearson AJ, Wilson K, Wolf S, et al. Evidence for a
485 pervasive template in flying and pedestrian insects. *R Soc open sci*. 2015;2.
- 486 27. Massey JT, Lurito JT, Pellizzer G, Georgopoulos AP. Three-dimensional drawings in
487 isometric conditions: relation between geometry and kinematics. *Exp Brain Res*.
488 1992;88: 685–690. Available: <http://brain.umn.edu/pdfs/JM054.pdf>
- 489 28. Catavittello G, Ivanenko YP, Lacquaniti F, Viviani P. Drawing ellipses in water:
490 evidence for dynamic constraints in the relation between velocity and path
491 curvature. *Exp Brain Res*. 2016;234: 1649– 1657.
- 492 29. Gribble PL, Ostry DJ. Origins of the power law relation between movement velocity
493 and curvature: modeling the effects of muscle mechanics and limb dynamics. *J*
494 *Neurophysiol*. 1996;76: 2853–2860. doi:10.1152/jn.1996.76.5.2853
- 495 30. Reynolds AM, Reynolds DR, Sane SP, Hu G, Chapman JW. Orientation in high-flying
496 migrant insects in relation to flows: mechanisms and strategies. *Philos Trans R Soc*
497 *Lond B Biol Sci*. 2016;371. doi:10.1098/rstb.2015.0392
- 498 31. Maoz U, Portugaly E, Flash T, Weiss Y. Noise and the two-thirds power law. *Adv*
499 *Neural Inf Process Syst*. 2006; 851–858. Available:
500 <https://papers.nips.cc/paper/2874-noise-and-the-two-thirds-power-law.pdf>
- 501 32. Schaal S, Sternad D. Origins and violations of the 2/3 power law in rhythmic three-

- 502 dimensional arm movements. *Exp brain Res.* 2001;136: 60–72. Available:
503 <http://www.ncbi.nlm.nih.gov/pubmed/11204414>
- 504 33. Kuroda S, Kunita I, Tanaka Y, Ishiguro A, Kobayashi R, Nakagaki T. Common
505 mechanics of mode switching in locomotion of limbless and legged animals. *J R Soc*
506 *Interface.* 2014;11: 20140205. doi:10.1098/rsif.2014.0205
- 507 34. Marken RS, Shaffer DM. The power law of movement: an example of a behavioral
508 illusion. *Exp Brain Res.* 2017;235: 1835–1842. doi:10.1007/s00221-017-4939-y
- 509 35. Zago M, Matic A, Flash T, Gomez-Marin A, Lacquaniti F. The speed-curvature power
510 law of movements: a reappraisal. *Exp Brain Res.* 2017; 1–14. doi:10.1007/s00221-
511 017-5108-z
- 512 36. Muller H, Chittka L. Consistent Interindividual Differences in Discrimination
513 Performance by Bumblebees in Colour, Shape and Odour Learning Tasks
514 (Hymenoptera: Apidae: *Bombus terrestris*). *Entomol Gen.* 2012;34. Available:
515 http://chittkalab.sbcs.qmul.ac.uk/2012/Muller_Chittka_12.pdf
- 516 37. Thompson DaW. *On Growth and Form* [Internet]. Bonner JT, editor. Cambridge:
517 Cambridge University Press; 1992. doi:10.1017/CBO9781107325852
- 518 38. Ball P. In retrospect: *On Growth and Form*. *Nature.* 2013;494: 32–33.
519 doi:10.1038/494032a
- 520 39. Reynolds A. Liberating Lévy walk research from the shackles of optimal foraging.
521 *Phys Life Rev.* 2015;14: 59–83. doi:10.1016/j.PLREV.2015.03.002
- 522 40. Viswanathan GM, Peng CK, Stanley HE, Goldberger AL. Deviations from uniform
523 power law scaling in nonstationary time series. *Phys Rev E - Stat Physics, Plasmas,*
524 *Fluids, Relat Interdiscip Top.* 1997;55: 845–849. doi:10.1103/PhysRevE.55.845

525

526 **Supporting information**

527 **S1 Table: Raw centroid tracking data:** this data was used to calculate speed-curvature power
528 laws from bee trajectories.

529 **S2: Data filtering and pre-processing:** additional information is provided on the processing and
530 filtering of the raw centroid tracking data prior to analyses.