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SHREEJATA GUPTA^{1,*}
ANINDYA SINHA^{1,2,3}

¹*National Institute of Advanced Studies, Indian Institute of Science Campus, Bangalore 560 012, India*

²*Nature Conservation Foundation, Mysore 571 126, India*

³*Dhole's Den Research Foundation, Bandipur National Park, Chamarajnagar District, India*

*For correspondence.

e-mail: shreejata@gmail.com

Ant runners: an analysis of running speed of *Leptogenys processionalis* (Hymenoptera: Formicidae: Ponerinae)

Leptogenys processionalis are shiny and slender ants commonly found in India. They nest on ground and feed mainly on termites, cockroaches and other insects. They are nomadic and for these predatory ants, searching for food is an important activity. Coordination and speed could play a key role in hunting prey. Running speed in trail can affect flow of traffic, search distances and thus their foraging efficiency. These ants maximize their foraging efficiency by forming trails such that the area covered to distance travelled ratio is maximum¹. They actively clear obstacles to form physical paths, more often seen near the nest than away from it¹. This may increase their foraging efficiency as the paths are used frequently. Like many other trail-forming ants, these ants deposit pheromones along their trail.

The literature on running speed of ants has focused mainly on how temperature, body mass or morphology affects speed^{2,3}. What are the other main variables that affect their speed significantly? Here I report the variations in running speed of *L. processionalis* under different natural conditions.

The study was carried out in Bangalore (12.97°N, 77.56°E) during June and July 2013. Data were collected from four different colonies (two in IISc, one each in GKVK and NCBS campus). The distance between the two colonies selected in IISc was at least 150 m apart, and thus they could be considered two distinct colonies. The study sites selected were

reasonably faraway from buildings and thus had less human intervention. Time taken to travel 30 cm of a fixed position in the trail was measured for randomly chosen ants, for 30 min. A total of 16 such 30-min readings (16 replicates) were taken from the 4 colonies. For a given colony, the fixed positions of observation in the trail were chosen at different distances from the nest to check whether distance from the nest affects running speed. The speed was not measured where the hunting (for insects) takes place – at the terminal search field (TSF)¹. TSF is the leading front of a trail where ants fan out from the trail resulting in a triangular field of ants searching for prey¹. Sometimes these ants form multiple lanes side by side, similar to roads with multiple traffic lanes. For simplicity in observation, all the readings were taken only in cases where the ants formed a single lane. Information about the other possible variables – temperature, direction of ant (towards or away from nest), terrain, slope of the fixed position, whether the ant is laden with food or not, and number of interactions made by the ant under observation with other ants running in opposite direction was collected. Terrain was classified into three categories: soil, leaf litter and grass lawn. Any brief antennal contact or head-on collision between the test ant and another ant was considered to be an interaction. Since there are no morphological differences between foragers and soldiers in *L. processionalis*, the body

weight and length of all individuals were assumed to be similar. If an ant was crippled with one or two amputated legs, a note was taken, to avoid any bias in measurements. All the observations were made between 10:00 and 17:00 h.

The data from different replicates were pooled and speed of the ants was calculated for each variable separately. The analysis was done using trial version of StatistiXL and SPSS statistical package.

It was found that the mean \pm SD running speed from pooled data ($n = 913$) was 4.24 ± 1.90 cm/s (0.15 ± 0.07 km/h) and median was 4.02 cm/s. Mean speed in the different categories is listed in Table 1. The distribution of speed was non-normal and skewed to the right ($\chi^2 = 46.98$, $df = 3$, $n = 913$, $P < 0.001$). The mean running speed and median after removing data points from crippled ants (38 out of 913) were 4.28 ± 1.90 cm/s and 4.04 respectively.

According to the literature², at 28°C, desert ants like *Cataglyphis bicolor* (13.71 cm/s) and *Ocymyrmex barbiger* (8.81 cm/s) run faster than *L. processionalis* (4.22 cm/s, from my data), whereas ants like *Solenopsis invicta* (1.67 cm/s) and *Pogonomyrmex desertorum* (1.62 cm/s) run slower. These interspecific variations could arise mainly due to differences in body mass, leg allometry, foraging temperature range and lifestyle (e.g. nomadic predatory ants run faster)².

As reported in previous studies on different species^{2,4}, running speed increased

Table 1. Mean \pm SD running speeds of foraging *Leptogenys processionalis*

Variable	Category	Speed (mean \pm SD; cm/s)	Number of ants
Terrain	Soil	4.83 \pm 2.03	485
	Leaf litter	2.31 \pm 0.52	149
	Ant trail on grass lawn	4.24 \pm 1.37	279
Direction	Towards nest	4.47 \pm 1.93	422
	Away from nest	4.31 \pm 1.90	390
Food laden/unladen	Laden	4.09 \pm 2.20	120
	Unladen	4.26 \pm 1.85	788
Slope	Upward slope	3.47 \pm 1.14	46
	Downward slope	4.21 \pm 1.01	45

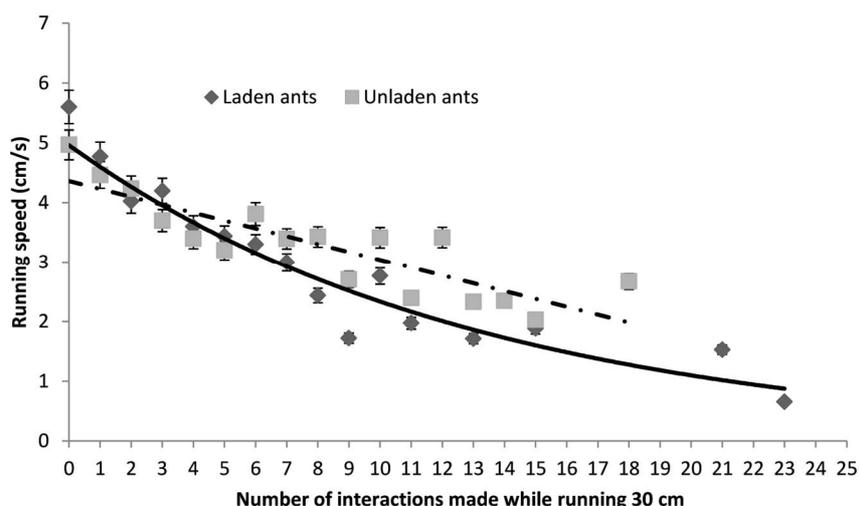


Figure 1. Mean running speeds with different numbers of interaction (95% CI error bars).

with temperature. Ants were seen foraging when temperature of substrate was in the 23–30°C range. Regression analysis revealed that speed and temperature (range 23–30°C) are related by an inverse function with a negative coefficient (speed = $(-275.733)/T$ (°C) + 14.073, $R^2 = 0.723$, $P < 0.05$). In this study, terrain, slope of substrate and number of interactions were also found to significantly affect running speed of *L. processionalis* during foraging.

For ants, leaf litter and grass lawn are complex terrains than soil. It was observed that the ants had trodden path on grass lawn. The order of mean speed on different terrains was: soil > grass lawn > leaf litter ($P < 0.001$, Table 1). It suggests that by running in trodden paths in complex terrains like grass lawn, the running speed of ants improves.

Ants ran significantly faster down a naturally inclined substrate (whose slope was not measured) than up the slope (Mann–Whitney $U = 1478$, $df_1 = 45$,

$df_2 = 46$, $P < 0.0010$). The observed trend could be attributed mainly to the slope of the substrate as the readings were taken at different temperatures and terrains. More controlled laboratory experiments with slope measurements are needed in this regard to give a quantitative comparison.

It is interesting that the way speed changed with increasing number of interactions was different for food-laden (size of the food could not be noted as they usually carried different parts of insects) and unladen ants (Figure 1). It is an exponential function ($P < 0.01$) for food-laden ants and a linear function ($P < 0.01$) for unladen ants. Speed of laden ants was less than that of unladen ants when the number of interactions was more than four (Figure 1). Since the interactions have the potential to communicate, difference in running speed could emerge as a result of change in the number of interactions or flux of ants in any direction. This could be useful while

hunting in TSF. It needs to be checked how flux of ants in a given direction and number of interactions made in a trail are related. In *L. processionalis*, it was observed that, at any time, the flux of ants was more in one direction than the other. This could possibly be explained by noting that these ants hunt in TSF, which is the front and widest portion of the foraging trail. Since more ants are required there while they hunt insects, initially most ants are seen going towards TSF. Once the ants have successfully obtained food, most ants are seen running towards the nest. But this observation remains to be re-confirmed.

Speed was not significantly different, whether an ant was laden or unladen with food (Mann–Whitney $U = 51674.5$, $P = 0.101$). But, this could be because of large difference in sample size in each category ($n = 120$ for food-laden and $n = 788$ for unladen ants). It was noticed that many ants returned towards the nest without food even while hunting at TSF

was rampant. At any given place, ants were seen carrying food only in one direction. The direction in which ants were carrying food was considered to be towards the nest. The speed of the ants running towards or away from the nest was not significantly different (Mann-Whitney $U = 86708$, $df_1 = 422$, $df_2 = 390$, $P = 0.186$). Since a species of fly was found to attack and steal food (kleptoparasitism) from the nest-bound ants, running towards food was as important as running towards the nest with food.

Whether an ant ran in a group or alone (no individuals behind or ahead of it for at least 5 cm in the trail), its speed was not significantly different (Mann-Whitney $U = 671$, $df_1 = 32$, $df_2 = 38$, $P = 0.464$). This suggests that the speed of all ants in one direction was maintained even when density was changed. However, it was observed that a few food-laden ants overtook the unladen ants ahead of them, when the unladen ant interacted more with the ants in opposite direction. It should be noted that the food-laden ant in this case was not speeding up actively to overtake the ant ahead of it, unlike vehicles in traffic.

Although such differences exist, ants have inspired humans in assessing different vehicle traffic flow management systems⁵.

In summary, running speed in *L. processionalis* is affected not only by temperature, but also by the terrain, slope of substrate and number of interactions. This study raises a few further questions about the running speed of ants. Does their running speed change in TSF and during migration? In other species with morphological differences between soldiers and foragers, does the speed differ according to their caste? Further computational studies related to how fast one can reach a point in a complex environment (with factors analogous to terrain, number of interactions, etc.) might be useful in finding optimum path in travelling salesman problem.

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P. N. RAVINDRA

*Department of Biology,
Indian Institute of Science Education and
Research,
Pune 411 008, India
e-mail: rvndrpn@gmail.com*