



Josef Bertrand Catches Some Ants: Unbiased Random Trajectories for the Simulation of Position Effects in Groups

MITCHELL B. BAKER*†‡ AND AMOS ZEMEL§

**Entomology-Fernald Hall, University of Massachusetts, Amherst, Amherst MA 01003, U.S.A.,*

‡*Mitrani Department for Desert Ecology, The Jacob Blaustein Institute for Desert Research, Ben Gurion*

University of the Negev, Sde Boker Campus 84990, Israel and §Department of Energy and

Environmental Physics, The Jacob Blaustein Institute for Desert Research,

Ben Gurion University of the Negev, Sede Boker Campus 84990, Israel

(Received on 5 January 2000, Accepted on 31 March 2000)

Quantifying the costs and benefits of group formation is central to understanding animal social organization. Group members may experience different fitness consequences depending upon their position within a group (Hamilton, 1971; Eggers, 1976; Krause, 1994). Individuals closer to the edges of groups may experience higher predation risk, or higher foraging success, or a combination of both effects (Rayor & Uetz, 1990, 1993). Because of this tradeoff, the quantitative effects of position on foraging and predation risk will determine the positions conferring highest fitness to individuals within groups.

Interactions among group members, or between group members and predators or prey, can qualitatively or quantitatively affect the fitness due to position. For example, incomplete capture efficiency reduces the foraging costs for central group members (unpublished data). A “ricochet” effect has been observed in colonial *Metepeira* spiders (Uetz, 1997), where flying prey are slowed down by flying through or bouncing off of the first web encountered. A positive effect

of aggregation on foraging success in antlions has been suggested by laboratory experiments showing high rates of escape from antlion pits by ants, which are less likely to escape if they encounter a second antlion pit (Dickey, 1998). These interactions should lead to complex position effects on foraging success, suggesting that simulation models that can include those interactions will aid in understanding the costs and benefits of group formation and structure. In designing these simulations, the algorithm used to simulate the entry of individuals into an area occupied by a group must not bias the encounter rates with group members residing in different parts of the area.

In an interesting combination of simulation modeling and laboratory experiments on antlions, Linton *et al.* (1991) examined the behavioral response of antlions to “shadow competition” (Wilson, 1974). Shadow competition occurs when sedentary foragers closer to the source of mobile prey reduce the foraging success of those further from the prey source. Originally used to describe site selection in clusters of antlions, the same dynamics should also affect prey-capture rates, predator or parasite avoidance, and other situations where the differential interception of highly mobile objects from outside

† Author to whom correspondence should be addressed.
E-mail: mbbaker@ent.umass.edu

a group affects the fitness of relatively sedentary group members. Linton *et al.* (1991) showed that antlions relocate in response to feeding rates and that if an advantage accrues to group members closer to the periphery, individual antlions will move outwards from the centers of groups. They demonstrated this by simulating the entry of ants into a circular arena containing various numbers of antlion larvae, each with a satisficing movement rule: remain when well fed, relocate when hungry. They then tested the effect of feeding rate on movement by feeding antlion larvae in laboratory arenas on a schedule determined by the simulation model, and observed pit relocation. However, we show below that the algorithm used to generate the ant paths was inadvertently biased to reduce the simulated capture rates of antlion pits closer to the center. Therefore, the simulations predicted an advantage for positions near the periphery, even in the absence of shadow competition. The difficulty in identifying an appropriate algorithm for the simulation of straight line paths of entrants into a circular arena illustrates the challenge of defining randomness.

The question of how to generate the paths taken by entrants into a circular arena is not trivial. The ambiguity of the term “random” was first illustrated by Josef Bertrand, who published a collection of paradoxes in 1889 [reviewed in Marinoff (1994); see also Parzen (1960, pp. 302–304) and references therein]. Bertrand asked the following question: “If a chord is drawn randomly in a circle, what is the probability that it is longer than the chords formed by an equilateral triangle inscribed in that circle?” Bertrand provided three different yet equally valid answers to the question as it was worded. Others have been suggested since, and the paradox stands as an example of the difficulty in unambiguously interpreting randomness in geometric problems. Marinoff (1994) shows that Bertrand’s paradox results from his providing answers to three different questions which clearly specify where the randomization takes place. Two of Bertrand’s answers are relevant to the simulation of entrants into an arena.

The algorithm used in Linton *et al.* (1991) is essentially similar to Bertrand’s first algorithm. A point is first selected on the periphery of the arena (by sampling an angle α between 0 and 2π

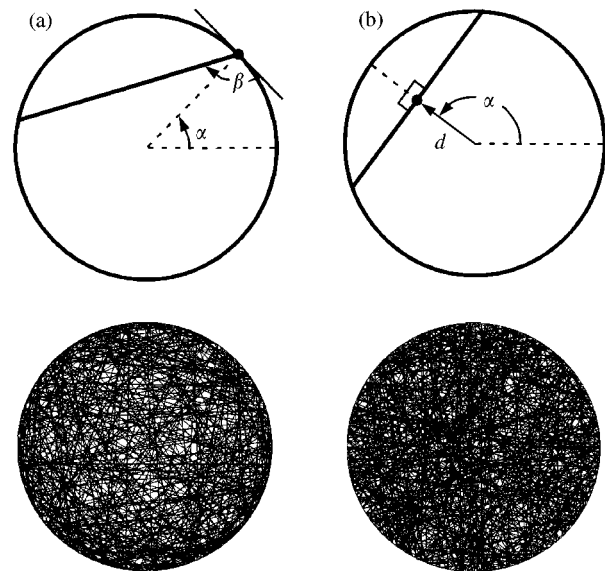


FIG. 1. Two methods of drawing random chords in a circle of radius R . Above are diagrams defining each algorithm, below are 500 chords drawn with each algorithm. The first method (a) chooses a point on the circumference by sampling the angle α , and then samples the angle β from the tangent at that point. In the second method (b) the orientation α of a radius is sampled, then the random distance d defines a point on that radius and the chord is the perpendicular segment drawn through that point. All random quantities are sampled from independent uniform distributions.

from a uniform distribution). From that point an angle β from the tangent is independently selected from a uniform distribution as the direction of the entrant into the arena [Fig. 1(a)]. An alternative method is to select first the angle α from 0 to 2π from a uniform distribution as before, but this time to interpret the angle as the orientation of a certain radius. Then, one selects independently a distance d from a uniform distribution between 0 and the radius R of the arena. Measured from the center, this length defines a point on the selected radius. The chord perpendicular to the radius at that point is the simulated path [Fig. 1(b)]. This algorithm is in fact the same as Bertrand’s second answer.

Though both algorithms draw “random” chords, the distributions of chord lengths, and therefore of the trajectories of ants entering the arena, are not identical. At this point, however, our interest diverges somewhat from Bertrand’s considerations, since the chord lengths are not our direct concern. Rather, we wish to ensure

that any two infinitesimal equal-area segments of the arena will have equal probabilities of being intercepted by the chord. An arena in this type of model is an artificial construct, an imaginary boundary around the foraging antlion group. In the absence of shadow competition, there should be no difference in interception rate depending on position within the arena. Differences should only arise from interactions among group members. It is apparent (Figs 1 and 2) that the Linton *et al.* (1991) algorithm results in a lower chance of a point intersecting a chord in the center of the arena. Indeed, for small circular targets of radius ε located at a distance r away from the center of the arena of radius R , we establish (in Appendix A) that this algorithm yields intercept probabilities given by $P(r) = (4\varepsilon/R\pi^2)K(r^2/R^2)$ where K is the complete elliptic integral [see Abramowitz & Stegun, 1965, eqn (17.3.1)]. In contrast, the second algorithm results in the capture probability $P(r) = \varepsilon/R$, independently of the position r within the arena (see Fig. 2). In the example shown in Fig. 2, interception rates produced by the biased algorithm near the periphery (with $r/R = 0.99$) are more than twice those at the center. (On the periphery itself the elliptic integral diverges, but edge effects must then be accounted for.) Any simulation using the biased algorithm would predict a greater number of interceptions for individuals occupying positions near the periphery separate from any group effects.

It is possible that use of a satisficing strategy for antlions in the Linton *et al.* (1991) foraging model prevented discovery of the bias in chord generation. In the model antlions stopped moving when their feeding rate exceeded a certain threshold. Though satisficing may be more biologically appropriate for modeling antlions, an optimizing model would have shown an effect of position separate from density, and led to a relocation of pits towards the periphery at all densities. The laboratory experiment on antlion movement did not reveal the algorithm bias because the algorithm itself was used to schedule feeding rates for experimental subjects.

The use of an unbiased algorithm removes any effect of position not due to interactions among group members. It does not rely on the geometry of a circular arena, and will work with any group arrangement or shape. The biological scenario it

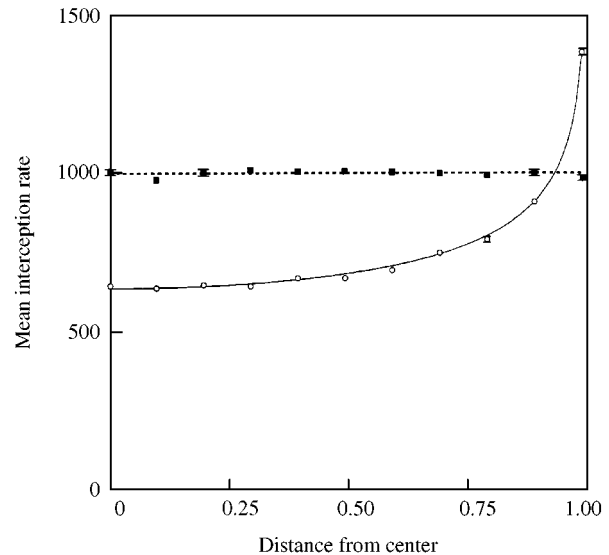


FIG. 2. Theoretical and simulated capture rates at different relative distances r/R from the arena center. The simulated points represent the number of chords intercepted by a circular target of radius $\varepsilon/R = 0.001$ in a run of a million entrants into the arena. The error bars (visible if they extend beyond the plot symbols) indicate the standard errors of the means estimated from 16 replicates of each run. The solid squares were generated by simulations using the unbiased algorithm. The open circles were generated by simulations using the biased algorithm. The curves follow the theoretical expressions given in the text.

best approximates is that of ants originating from remote random colonies whose trajectories do not change when they cross the imaginary boundary of an arena surrounding the aggregation. If there was a major effect of the arena boundary on movement (e.g. due to a change in habitat), then the shape of the arena and the effect on movement would need to be explicitly modeled.

Simulation modeling offers great potential to understand the observed consequences of aggregation (Krause, 1994), and to incorporate realistic interactions among group members and intercepted outsiders (Dickey, 1998; Uetz, 1997; Rayor & Uetz, 1990, 1993). Simulations can build greater realism into aggregation models than earlier geometric approaches (Hamilton, 1971; Morton *et al.*, 1994). The algorithms used to generate randomized inputs into simulations can have subtle yet significant effects on observed results. Bertrand's paradox vividly demonstrates the care needed in implementing such simulations, and its resolution points at the way to

identify the unbiased algorithm relevant to each application.

The authors would like to thank Sharon Lawlor and Marcel Holyoak for helpful comments on an early draft, and three anonymous reviewers for their suggestions. This is publication no. 291 of the Mitrani Department of Desert Ecology, Ben Gurion University.

REFERENCES

- ABRAMOWITZ, M. & STEGUN, I. A. (1965). *Handbook of Mathematical Functions*. New York: Dover.
- DICKEY, B. F. (1998). The insider-trading theory of antlion foraging. *ESA abstracts* 51.
- EGGERS, D. M. (1976). Theoretical effects of schooling by planktivorous fish predators on rate of prey consumption. *J. Fish. Res. (B) Can.* **33**, 1964–1971.
- HAMILTON, W. D. (1971). Geometry for the selfish herd. *J. theor. Biol.* **31**, 295–311.
- KRAUSE, J. (1994). Differential fitness returns in relation to spatial position in groups. *Biol. Rev. Cam. Philos. Soc.* **69**, 187–206.
- LINTON, M. C., CROWLEY, P. H., WILLIAMS, J. T., DILLON, P. M., ARAL, H., STROHMEIER, K. L. & WOOD, C. (1991). Pit relocation by antlion larvae: a simple model and laboratory test. *Evol. Ecol.* **5**, 93–104.
- MARINOFF, L. (1994). A resolution of Bertrand's paradox. *Philos. Sci.* **61**, 1–24.
- MORTON, T. L., HAEFNER, J. W., NUGALA, V., DECINO, R. D. & MENDES, L. (1994). The selfish herd revisited: do simple movement rules reduce relative predation risk? *J. theor. Biol.* **167**, 73–79.
- PARZEN, E. (1960). *Modern Probability Theory and its Applications*. New York: Wiley.
- RAYOR, L. S. & UETZ, G. W. (1990). Trade-offs in foraging success and predation risk with spatial position in colonial spiders. *Behav. Ecol. Sociobiol.* **27**, 77–85.
- RAYOR, L. S. & UETZ, G. W. (1993). Ontogenetic shifts within the selfish herd: predation risk and foraging trade-offs change with age in colonial web-building spiders. *Oecologia* **95**, 1–8.
- UETZ, G. W. (1997). Colonial web-building spiders: balancing the costs and benefits of group-living. In: *The Evolution of Social Behavior in Insects and Arachnids* (Choe, J. C & Crespi, B. J., eds), pp. 458–475. New York: Cambridge University Press.
- WILSON, D. S. (1974). Prey capture and competition in the antlion. *Biotropica* **6**, 187–193.

APPENDIX A

Derivation of the Theoretical Distributions

Consider a small circular target of radius ε located on the vertical axis at a distance r from the arena center, so that the coordinates of the target center are $(0, r)$. Recalling that the square of the distance of any arbitrary point (x_0, y_0) from the line defined by the equation

$Ax + By + C = 0$ is given by $(Ax_0 + By_0 + C)^2 / (A^2 + B^2)$, and denoting $E = \{\text{the line passes through the target}\}$ we find for the probability of the event E :

$$P(E) = \text{Prob}\{(Br + C)^2 / (A^2 + B^2) \leq \varepsilon^2\}.$$

The two algorithms differ in the choice of the random coefficients (A, B, C) .

A.1. THE UNBIASED ALGORITHM

Considering Fig. 1(b), we see that the required chord passes at a distance d from the origin and is perpendicular to the radius of slope angle α . One can verify that the equation

$$\cos(\alpha)x + \sin(\alpha)y - d = 0$$

meets these requirements. Thus,

$$\begin{aligned} P(E) &= \text{Prob}\{(r \sin(\alpha) - d)^2 \leq \varepsilon^2\} \\ &= \text{Prob}\{r \sin(\alpha) - \varepsilon \leq d \leq r \sin(\alpha) + \varepsilon\}. \end{aligned}$$

Neglecting edge effects (when $|r \sin \alpha| < \varepsilon$ or when the target extends out of the arena) and recalling that d is uniformly distributed over $[0, R]$, we see that the required probability is simply $2\varepsilon/R$ when $\sin \alpha \geq 0$, and zero otherwise. Since the event $\{\sin \alpha \geq 0\}$ is independent of d and bears the probability of $1/2$, we finally obtain

$$P(E) = \varepsilon/R,$$

which is *independent* of r , and shown by the dotted line of Fig. 2.

A.2. THE BIASED ALGORITHM

Considering Fig. 1(a), we verify that the chord equation is $\cos(\alpha - \beta)x + \sin(\alpha - \beta)y - R \cos \beta = 0$. Following the arguments above, we find

$$\begin{aligned} P(E) &= \text{Prob}\{r \sin(\alpha - \beta) - \varepsilon \leq R \cos \beta \\ &\leq r \sin(\alpha - \beta) + \varepsilon\}. \end{aligned}$$

It is expedient at this point to introduce the angle $\gamma = \alpha - \beta$, noting that although this angle

depends on β , the distribution of $\sin \gamma$ is independent of the latter, since α is uniformly distributed over the full period $[0, 2\pi]$. Thus,

$$P(E) = \text{Prob}\{\arccos[(r \sin(\gamma) + \varepsilon)/R] \leq \beta \\ \leq \arccos[(r \sin(\gamma) - \varepsilon)/R]\}.$$

Restricting attention to infinitesimally small targets, we expand the *arccos* function to first order in ε/R and find that in order to ensure that the event E occurs, β must be restricted to a small interval of size $(2\varepsilon/R)(1 - r^2 \sin^2(\gamma)/R^2)^{-1/2}$, hence the probability of E , for a given angle γ , is

given by this size divided by π . Averaging over the uniform distribution of γ , it is clear that it suffices to consider only the interval $[0, \pi/2]$, yielding

$$P(E) = (4\varepsilon/R\pi^2) \int_0^{\pi/2} (1 - r^2 \sin^2(\gamma)/R^2)^{-1/2} d\gamma \\ = (4\varepsilon/R\pi^2)K(r^2/R^2),$$

where the latter equation follows from the definition of the complete elliptic integral [Abramowitz & Stegun, 1965, eqn (17.3.1)]. This function is plotted as the solid line of Fig. 2.