Physical Principles in Biology
Biology 3550
Fall 2017

Lecture 12

More on Two-dimensional Random Walks

and

The Gaussian Probability Distribution Function

Monday, 18 September

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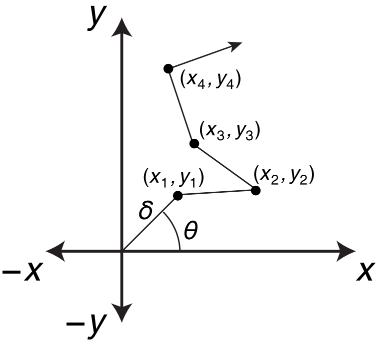
A Random Walk in Two Dimensions



1. Start at (x, y) coordinates (0,0).
2. Choose a random direction, defined by the angle θ from the x-axis.
3. Move distance δ in the chosen direction.
4. Repeat 2 and 3 another $(n - 1)$ times.

Major Results for a Two-Dimensional Random Walk

For n steps of length δ:

- Displacement along the x- and y-axes (or any other direction):
  - Mean displacement: $\langle x_n \rangle = \langle y_n \rangle = 0$.
  - Mean-square displacement: $\langle x_n^2 \rangle = \langle y_n^2 \rangle = n\langle \delta_{x,y}^2 \rangle = n\delta^2/2$
  - RMS displacement: $\mathrm{RMS}(x_n) = \mathrm{RMS}(y_n) = \sqrt{(n/2)}\delta$
- Distance from starting point, r:
  - Mean-square displacement: $\langle r_n^2 \rangle = 2n\langle \delta_{x,y}^2 \rangle = n\delta^2$
  - RMS displacement: $\mathrm{RMS}(r_n) = \sqrt{n}\delta$
  - Just like the one-dimensional random walk!
  - Mean displacement: ?

An Implication

- Number of steps = n.
- Length of steps = δ
- Total distance: $D_t = n\delta$.
- If total distance is fixed and δ is changed:

$$n = D_t/\delta$$

$$\begin{aligned} \mathrm{RMS}(r) &= \sqrt{n}\delta \\ &= \sqrt{(D_t/\delta)} \cdot \delta \\ &= \sqrt{D_t}\sqrt{\delta} \end{aligned}$$

Average distance from start to end increases with step length.

Clicker Question #1

For a 2-dimensional random walk of a total distance of 100 m and a step length of 5 m, which (if any) of the following are correct?

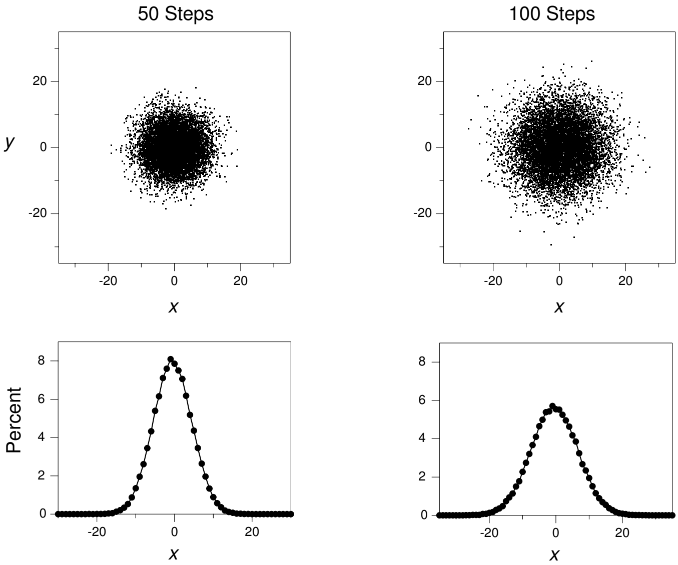
Choose up to 2.

1. $\mathrm{RMS}(r) \approx 50\,\mathrm{m}$
2. $\langle r^2 \rangle \approx 500\,\mathrm{m}^2$
3. $\langle r^2 \rangle \approx 250\,\mathrm{m}^2$
4. $\mathrm{RMS}(r) \approx 22\,\mathrm{m}$
5. None of the above

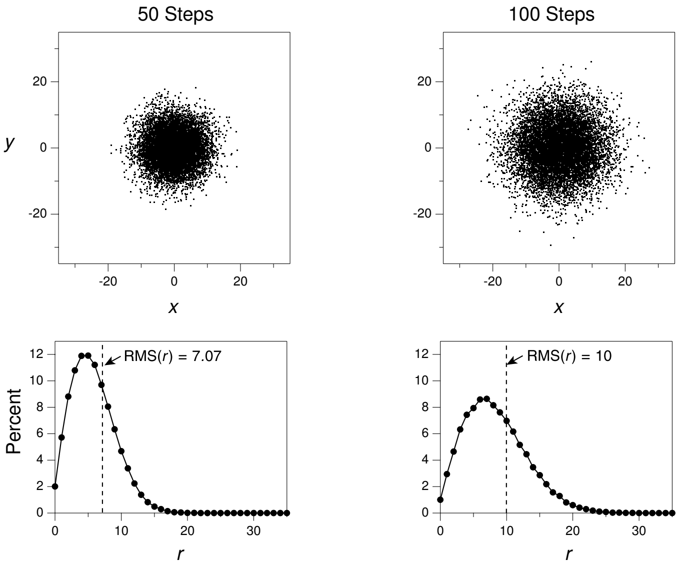
$$n = 100\,\mathrm{m}/5\,\mathrm{m} = 20$$

$$\langle r^2 \rangle = n\delta^2 = 20 \times (5\,\mathrm{m}^2) = 500\,\mathrm{m}^2$$

Final *x*-Coordinate for 2-d Random Walks



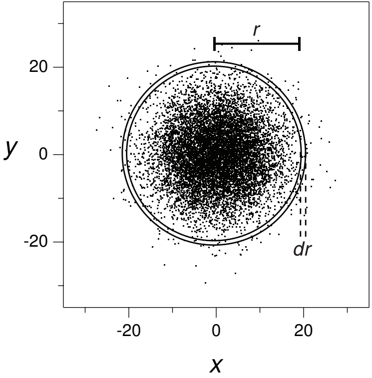
Final Distance from Origin for 2-d Random Walks

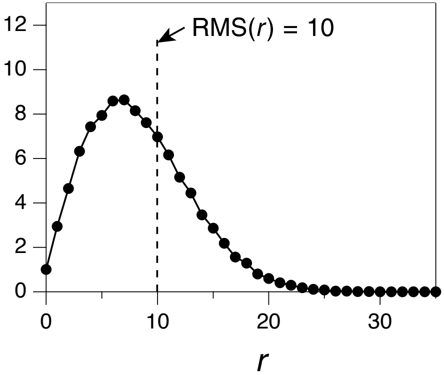


- Why isn't the peak at $r = 0$?

Why Isn't the Peak at $r = 0$

- $\int_{r_a}^{r_b} p(r)dr =$ probability that the walk endpoint lies between r_a and r_b.

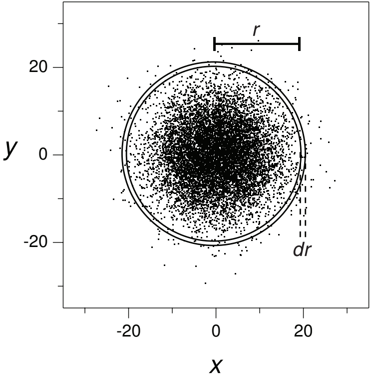




- $p(r)dr =$ probability that the endpoint lies in the annulus (ring) dr thick.

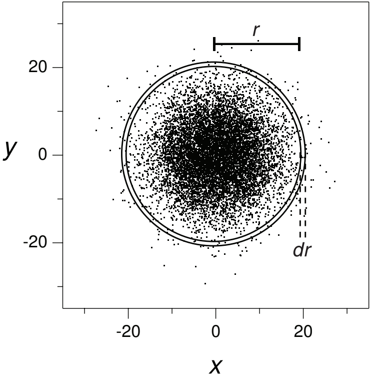
Clicker Question #2

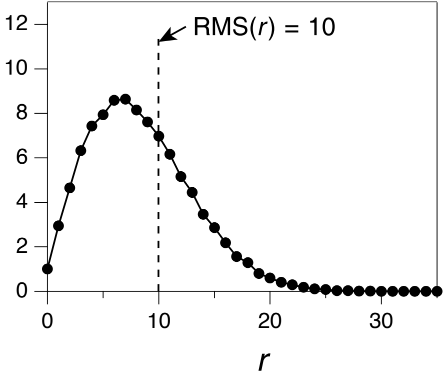
What is the area of the annulus?



1. πr^2
2. πdr^2
3. $2\pi r$
4. $2\pi dr$
5. $2\pi r dr$

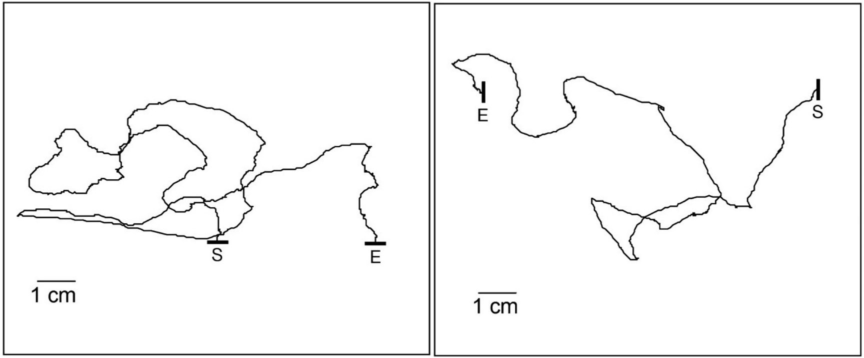
Why isn't the Peak at $r = 0$





- The probability, $p(r)dr$, is proportional to the area of the annulus.
- The area increases with r: $A = 2\pi r dr$.
- The density of endpoints decreases with r.
- The two effects balance at the peak of the distribution.

Ants on a Walk for Food



Brachymyrmex depilis
(25 s)

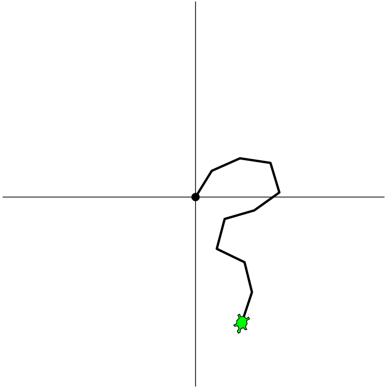
Dorymyrmex insanus
(21 s)

- Do either look like a random walk?

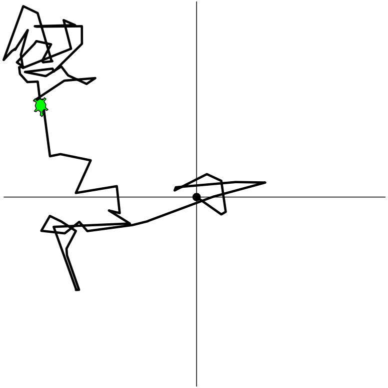
Pearce-Duvet, J. M. C., Elemens, C. P. H. & Feener, D. H. (2011). Walking the line: search behavior and foraging success in ant species. *Behavioral Ecology*, 22, 501–509. http://dx.doi.org/10.1093/beheco/arr001

Simple Variations on the Two-dimensional Random Walk

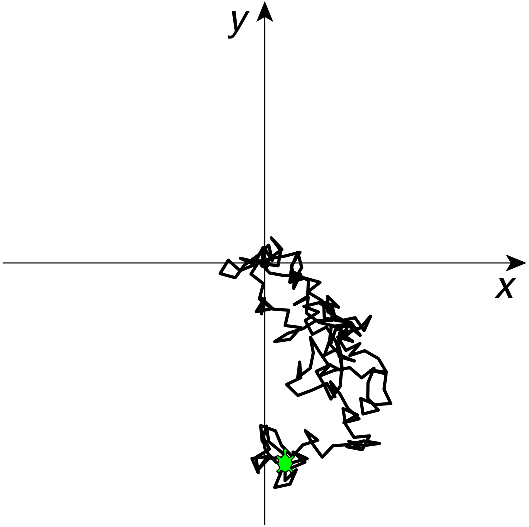
- Constrain change in direction.



- Introduce variation in step length.

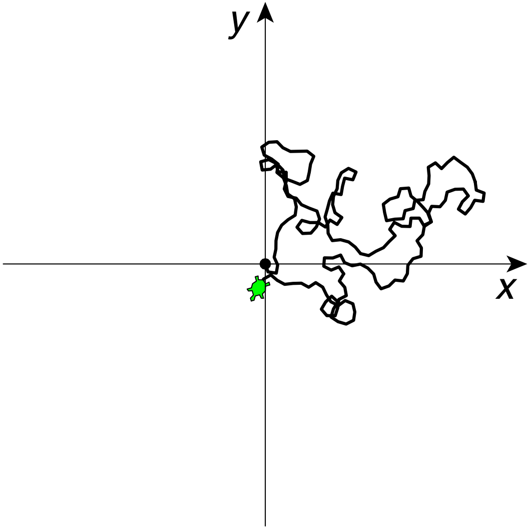


A ‘Plain’ Random Walk



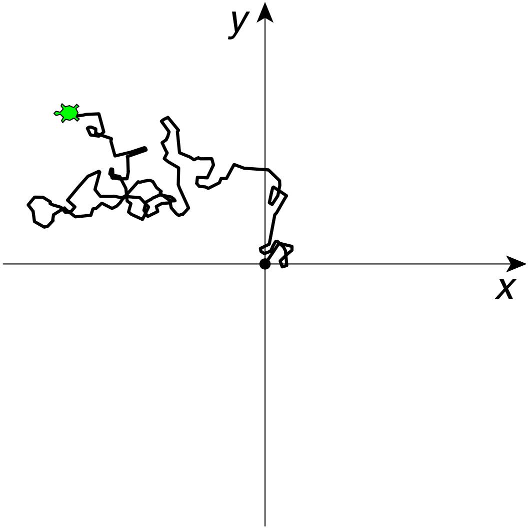
- Step length = 20
- No. steps = 200

A “Correlated” Random Walk



- Turn angle restricted to -90° to 90°
- Step length = 8
- No. steps = 200

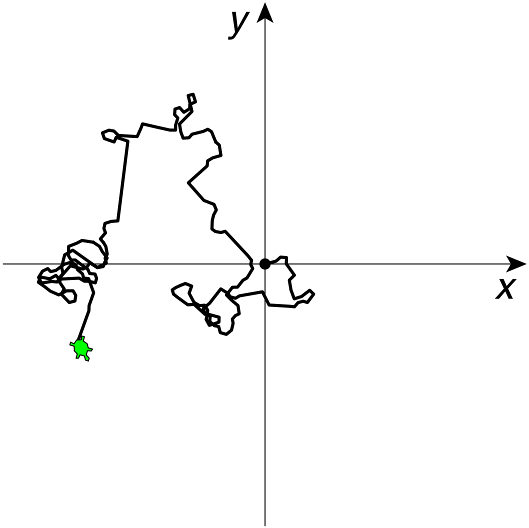
A Random Walk With a Distribution of Step Lengths



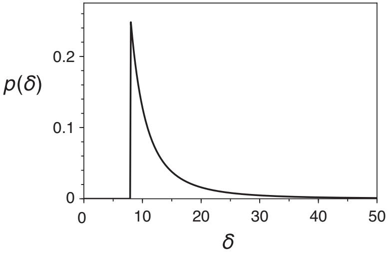
- Turn angle restricted to -90° to 90°
- Half-Gaussian (bell curve) distribution of step lengths
- No. steps = 200

A “Lévy Flight”

A random walk with a “heavy-tailed” distribution of step lengths



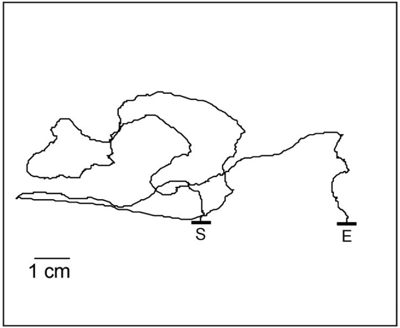
- Turn angle restricted to -90° to 90°
- Pareto distribution of step lengths



- No. steps = 200

Clicker Question #3

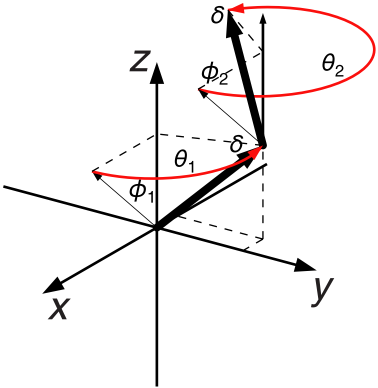
What does the ant walk most resemble?



Brachymyrmex depilis
(25 s)

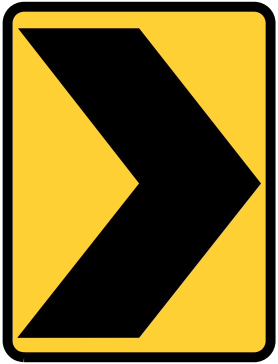
1. A plain random walk
2. A correlated random walk
3. A Lévy Flight

Description of a Three-dimensional Random Walk



- Each step is defined by a tilt from the local z-axis (ϕ_i) and a rotation around the z-axis (θ_i).
- The end of each step lies on a sphere of radius δ.
- $\langle r^2 \rangle = n\delta^2$, and $\mathrm{RMS}(r) = \sqrt{n}\delta$, just like in one and two dimensions.

Warning!



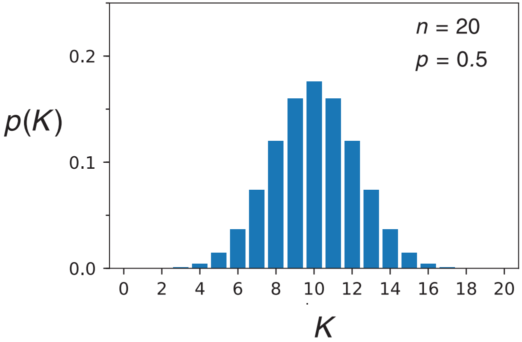
Direction Change

The Gaussian Probability Distribution Function

The Binomial Distribution Revisited

- The probability of k successes in n successive binary (yes/no) trials when the probability of success in each trial is p.

$$p(k; n, p) = \frac{n!}{k!(n-k)!} p^k (1-p)^{(n-k)}$$



Two Important Parameters for any Probability Distribution Function

- Mean (μ)
  - For a discrete probability distribution ($\mu = \langle k \rangle = E(k)$):

$$\mu = \sum_{k=1}^{n} kp(k)$$

  - For a continuous probability distribution ($\mu = \langle x \rangle = E(x)$):

$$\mu = \int_{x_{min}}^{x_{max}} xp(x)dx$$

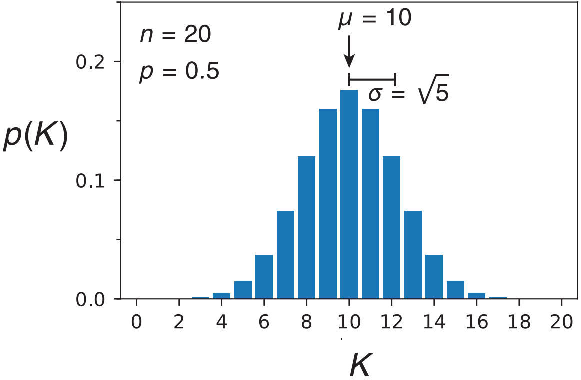
- Variance (σ^2)
  - For a discrete probability distribution:

$$\sigma^2 = \sum_{k=1}^{n} p(k)(k - \mu)^2$$

  - For a continuous probability distribution:

$$\mu = \int_{x_{min}}^{x_{max}} p(x)(x - \mu)^2 dx$$

Mean, Variance and Standard Deviation for The Binomial Distribution



- Mean

  $\mu = np$

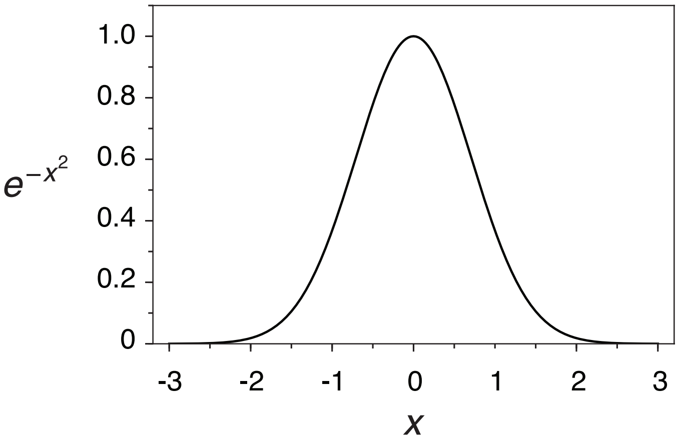
- Variance

  $\sigma^2 = np(1-p)$

- Standard deviation

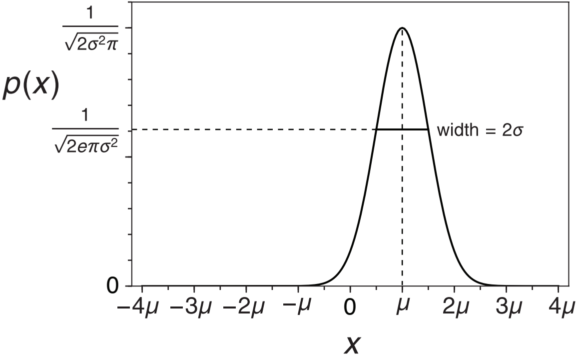
  $\sigma = \sqrt{\sigma^2} = \sqrt{np(1-p)}$

The Simplest Form of a Gaussian Function



$$f(x) = e^{-x^2}$$

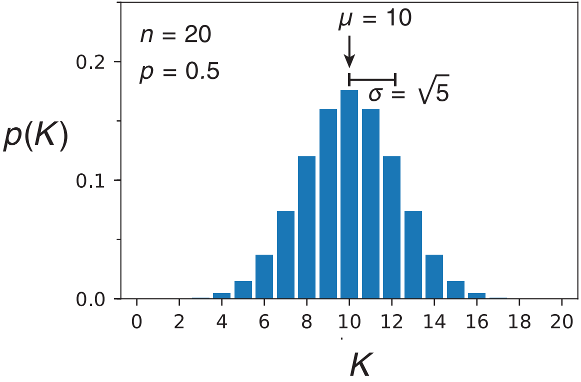
The Gaussian Probability Distribution Function



$$p(x) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$

- Mean $= \mu$
- Variance $= \sigma^2$
- Standard deviation $= \sigma$

Mean and Variance for The Binomial Distribution



- Mean

  $\mu = np$

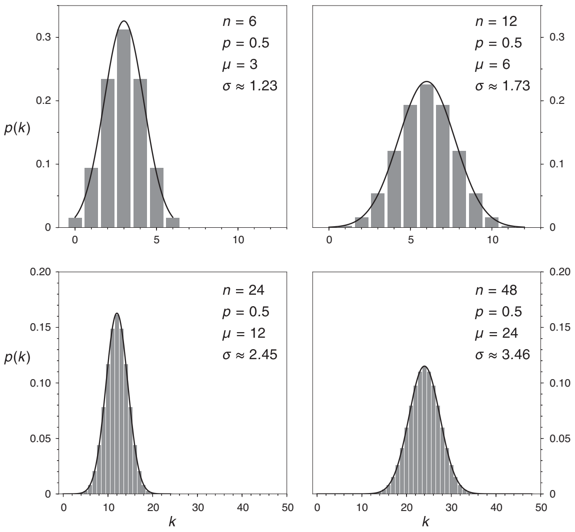
- Variance

  $\sigma^2 = np(1-p)$

- Gaussian probability function to approximate the binomial distribution function:

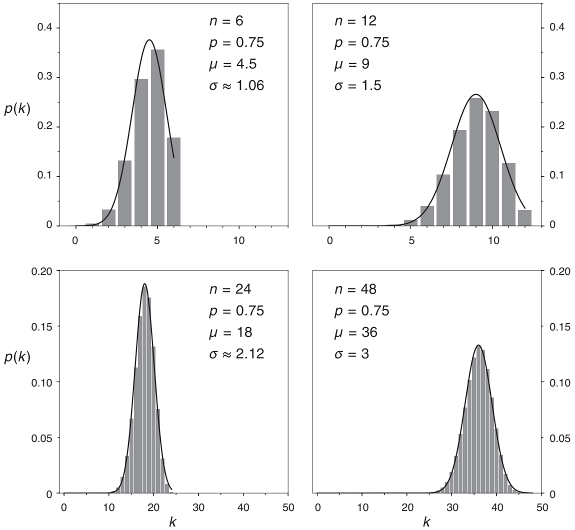
$$p(k) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(k-\mu)^2}{2\sigma^2}} = \frac{1}{\sqrt{2\pi np(1-p)}} e^{-\frac{(k-np)^2}{2np(1-p)}}$$

Approximation of Binomial Distributions by Gaussian Distributions



- *n* doesn't have to be very large for a pretty good approximation!

Approximation of Binomial Distributions by Gaussian Distributions



- It doesn't work so well if the binomial distribution is biased, with $n \neq 0.5$.
- The Gaussian distribution is inherently symmetrical; the binomial distribution isn't.
- If n is large enough, the Gaussian distribution is a good approximation, even if $n \neq 0.5$.
- A general rule of thumb: The Gaussian distribution is a good approximation if:

$$n > 9\frac{1-p}{p} \text{ and } n > 9\frac{p}{1-p}$$