Intro to Neuroscience: Behavioral Neuroscience

Animal Navigation: Behavioral strategies, sensory cues, and brain mechanisms

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Intro to Neuroscience: Behavioral Neuroscience

Animal Navigation I (*today*):

Behavioral strategies, sensory cues

Animal Navigation II (*next week*):

Brain mechanisms

Why study the neurobiology of animal navigation & the neural basis of space representation ?

- **Navigation is a behavior that is:**
  - **Important for the animal's survival (behaviorally relevant)**
  - **Quantifiable** (spatial accuracy, straightness, time…)
  - **Closely related to learning and memory (spatial memory)**
- **Space is:**
  - **Basic for human thought (Kant)**
  - **Euclidean** (notion of distance: allows mathematical modeling)
- **Simple neural representations in high brain areas**

→ For these reasons, many neuroscientists who are interested more generally in (i) behavior, (ii) higher brain functions, or (iii) learning & memory – study the case of navigation and spatial memory.

- **Meeting place of neuroethological & neuropsychological approaches.**

Outline of today's lecture

- **Introduction: Feats of animal navigation**
- **Navigational strategies:**
  - **Beaconing**
  - **Route following**
  - **Path integration**
  - **Map and Compass / Cognitive Map**
- **Sensory cues for navigation:**
  - **Compass mechanisms**
  - **Map mechanisms**

Next Week:

- **Brain mechanisms of Navigation (brief introduction)**
- **Summary**

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- **Brain mechanisms of Navigation (brief introduction)**
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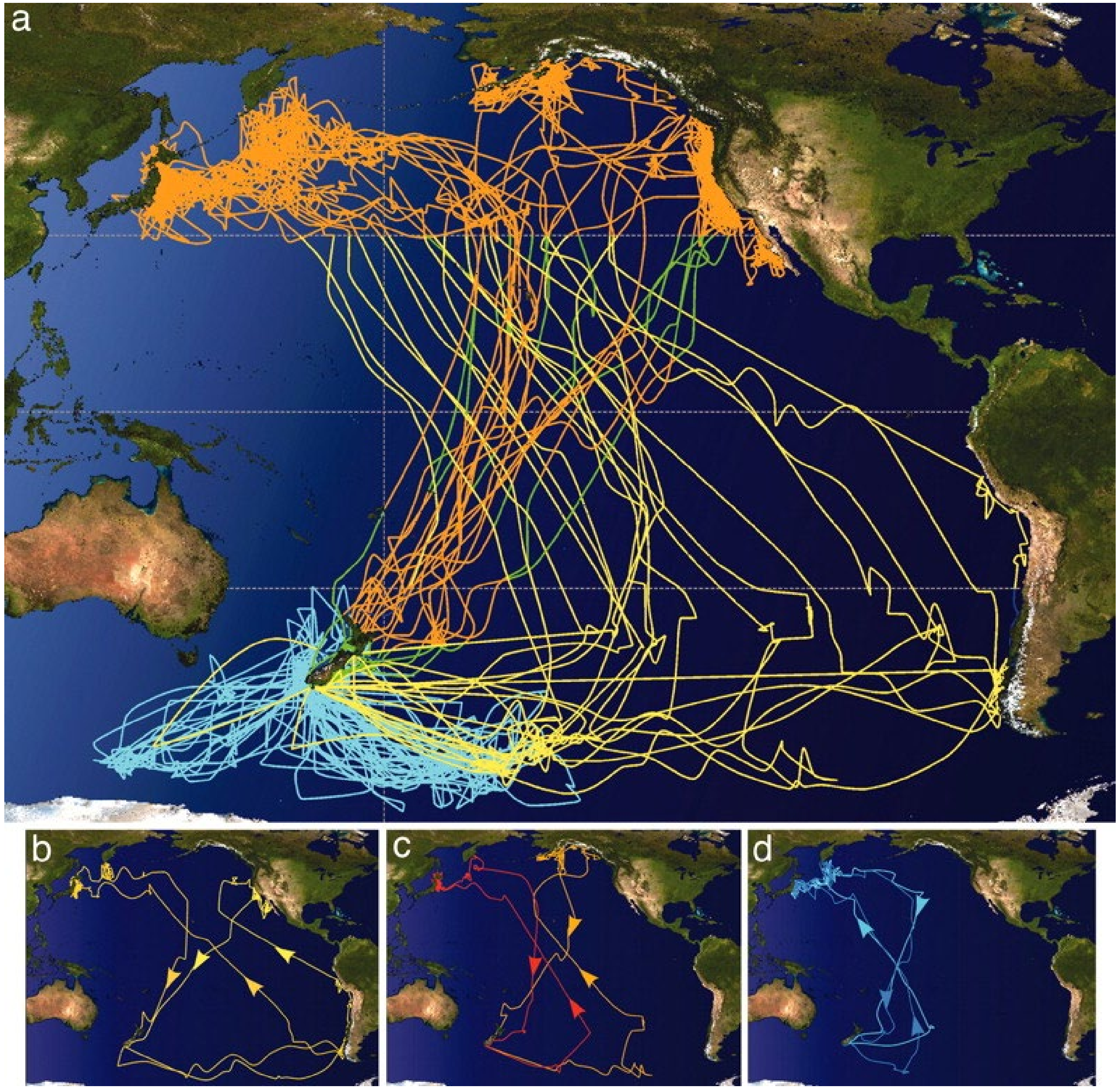
Shearwater migration across the pacific



Shaffer et al. *PNAS* 103:12799-12802 (2006)

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Population data from 19 birds

←3 pairs of birds

Recaptured at their breeding grounds in New Zealand

Some other famous examples

- **Wandering Albatross:** finding a tiny island in the vast ocean
- **Salmon:** returning to the river of birth after years in the ocean
- **Sea Turtles**
- **Monarch Butterflies**
- **Spiny Lobsters**
- **… And many other examples (some of them we will see later)**

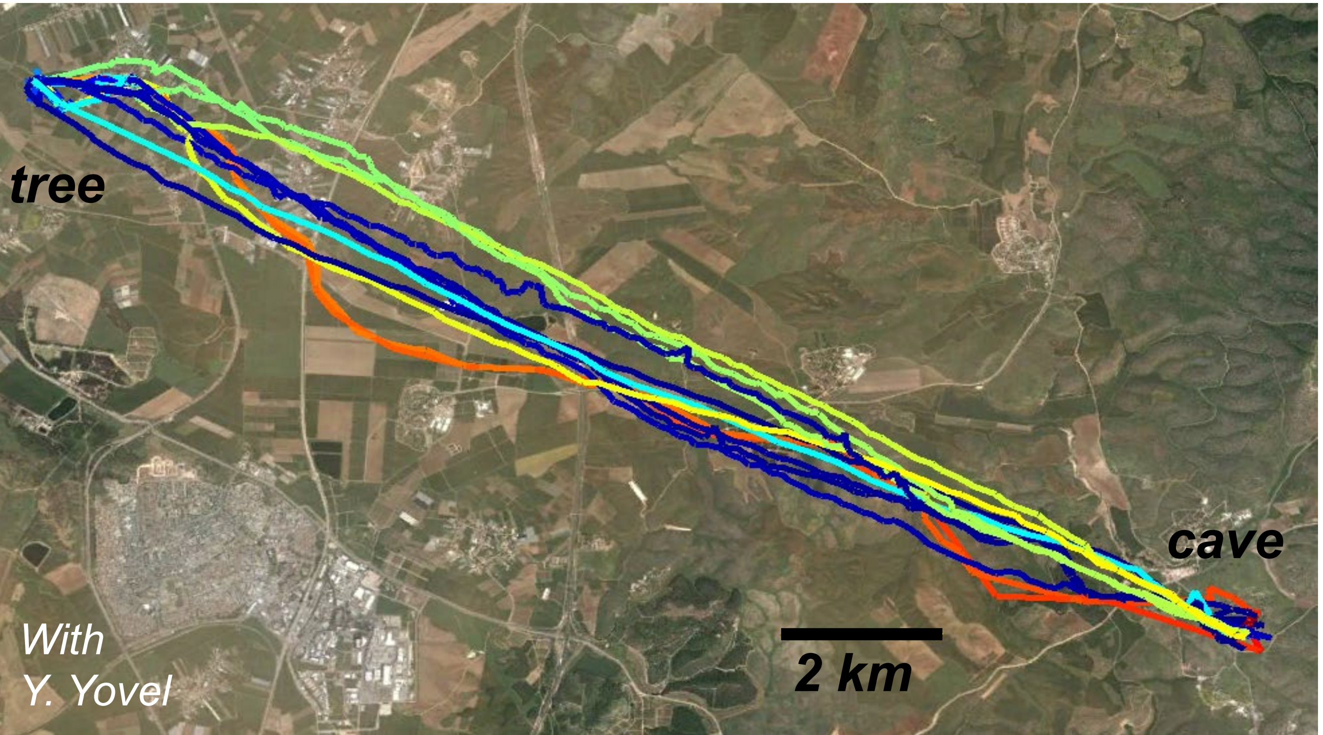
Mammals can also do it… Medium-scale navigation: Egyptian fruit bats navigating to an individual tree

GPS movie: Bat 079

A typical example of a full night flight of an individual bat released @ cave

Characteristics of the bats' commuting flights:

- Long-distance flights (often > 15 km one-way)
- Very straight flights (straightness index > 0.9 for almost all bats)
- Very fast (typically 30–40 km/hr, and up to 63 km/hr)
- Very high (typically 100–200 meters, and up to 643 m)
- Bats returned to the same individual tree night after night, for many nights



Tsoar, Nathan, Bartan, Vyssotski, Dell'Omo & Ulanovsky (PNAS, 2011)

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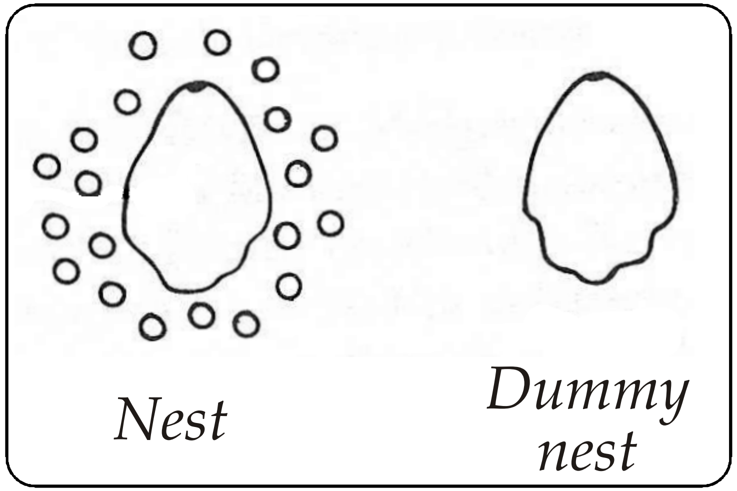
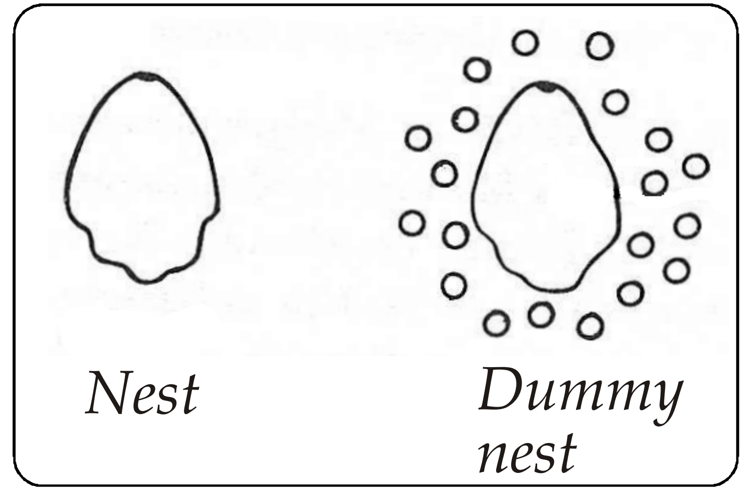
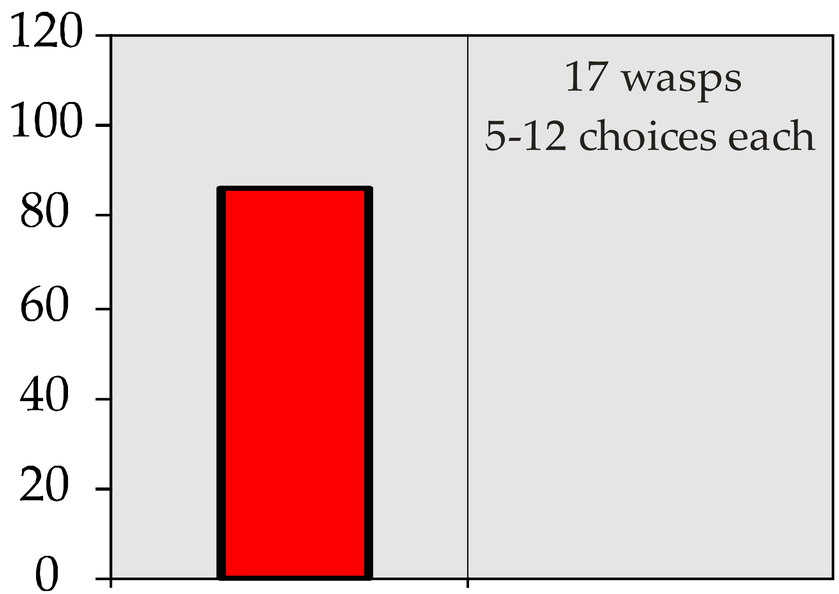
Visual Beaconing in Wasps (Tinbergen)

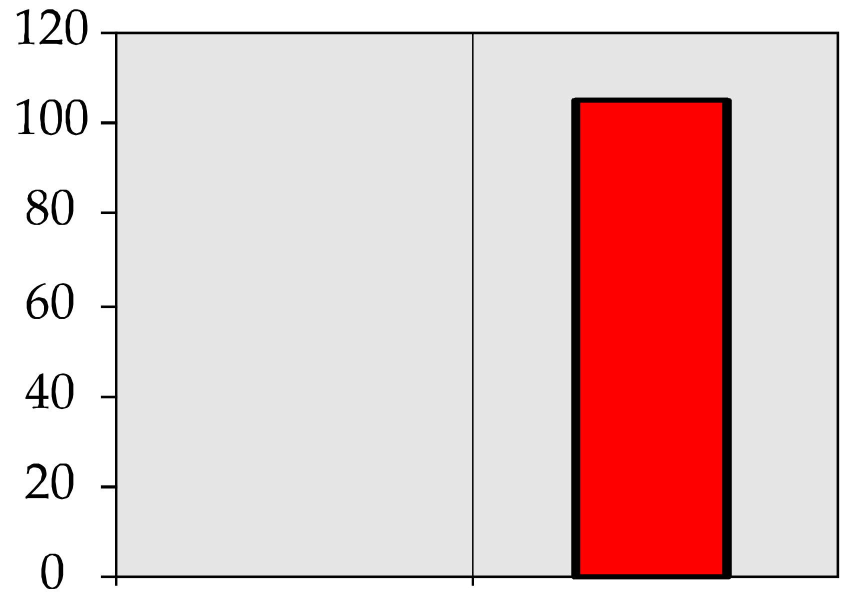
Beaconing: Navigation towards a directly-perceptible sensory cue.

Training

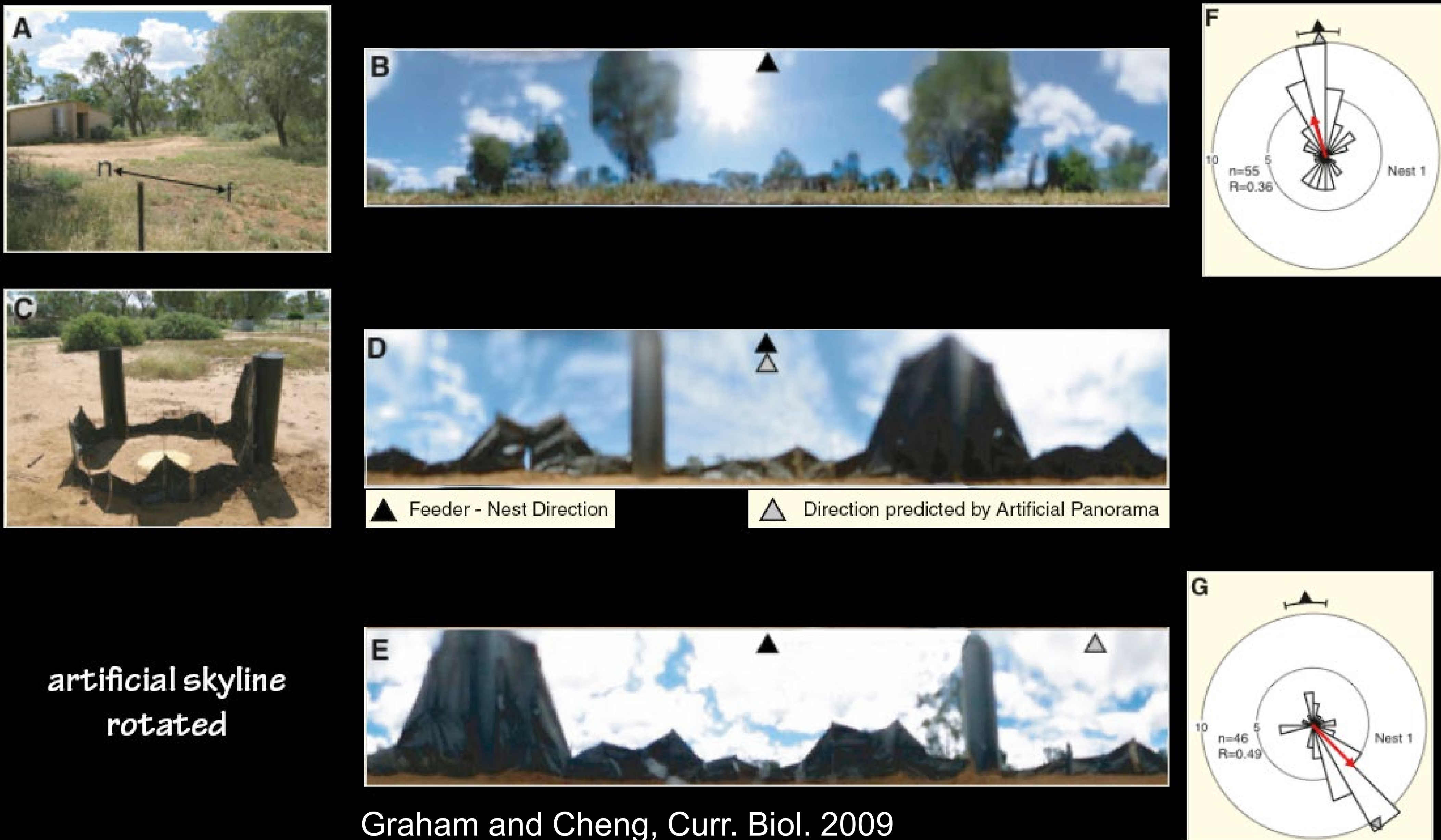








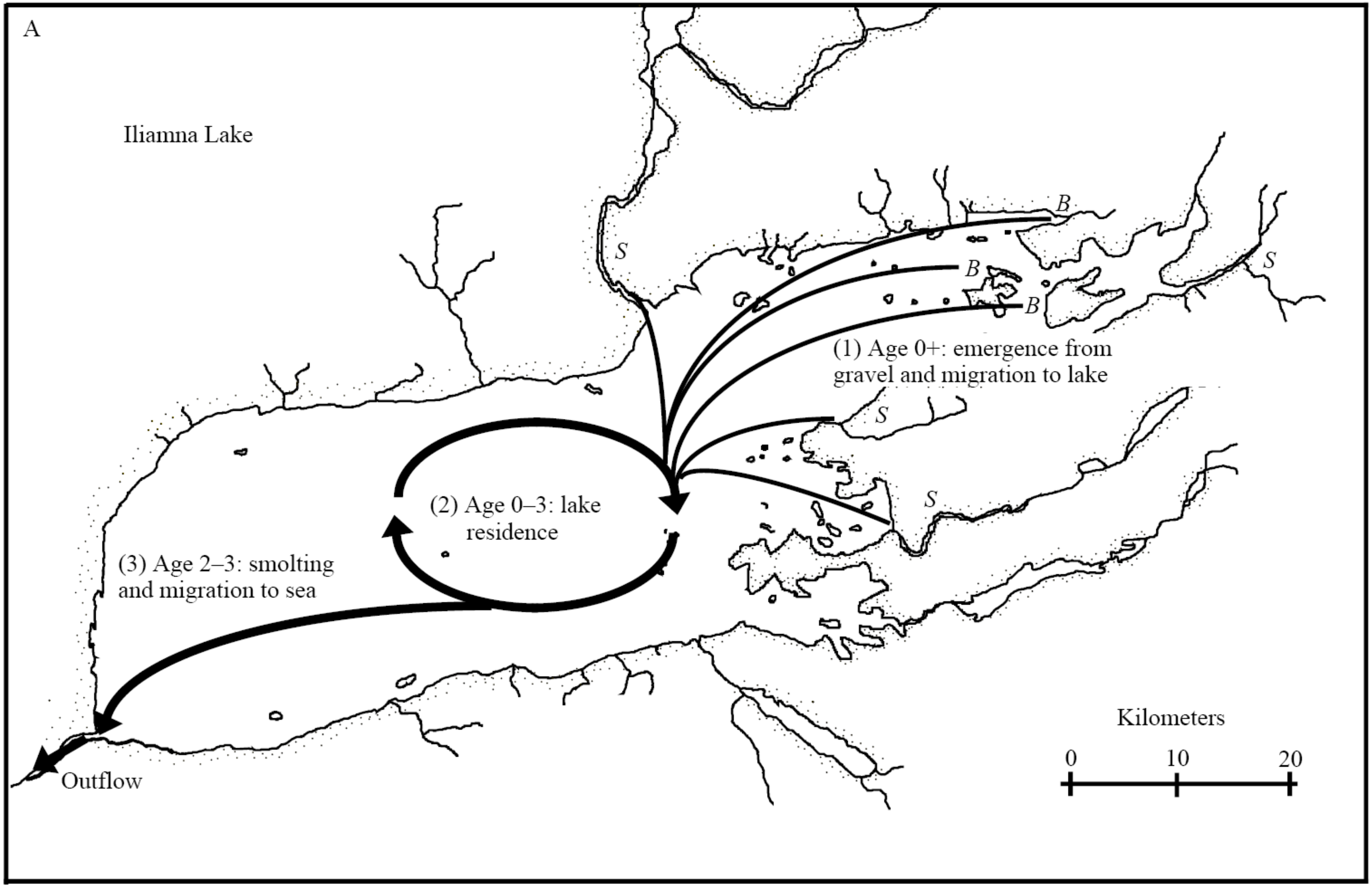
Visual Beaconing in Ants that inhabit cluttered environments



artificial skyline rotated

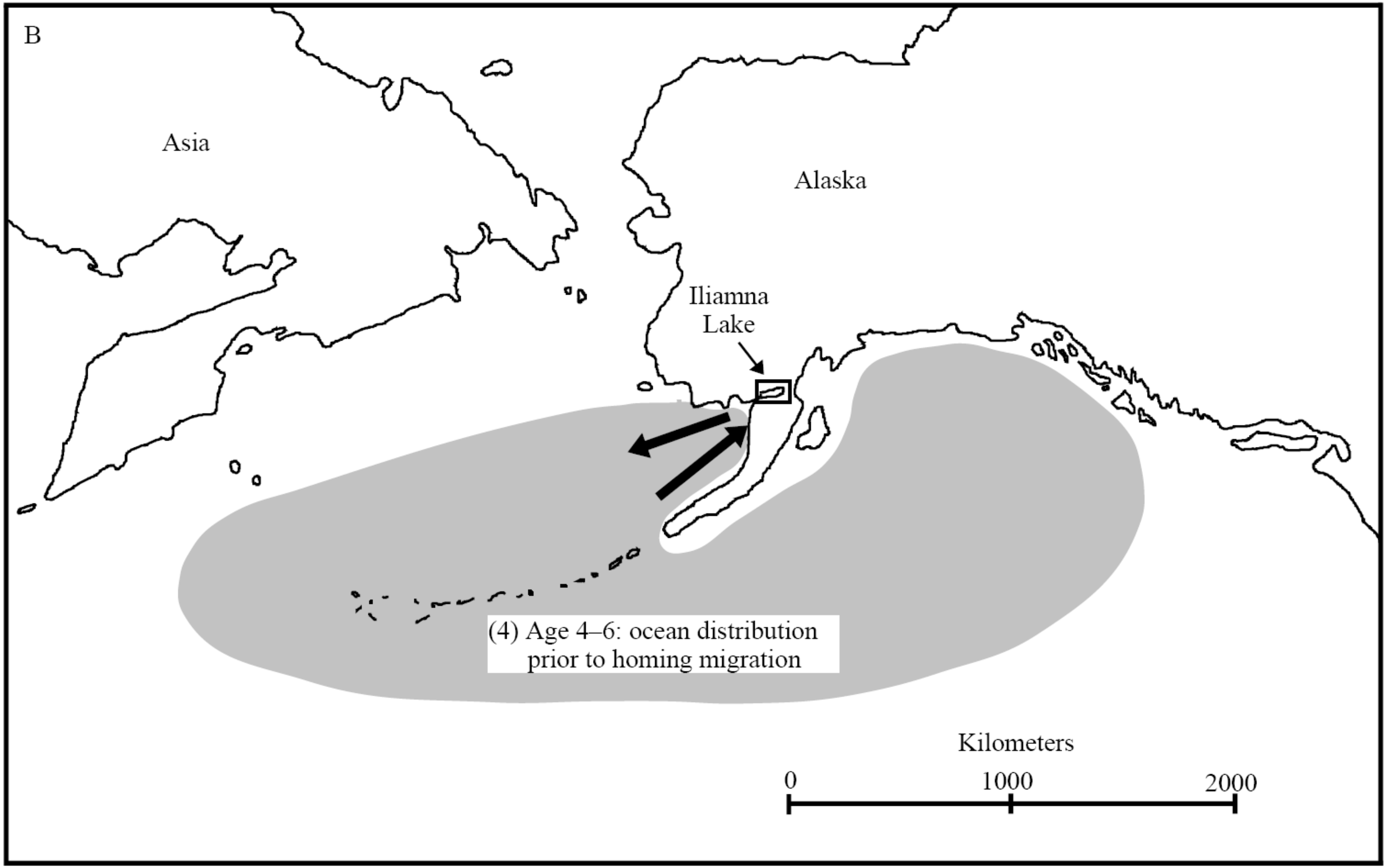
Graham and Cheng, Curr. Biol. 2009

Olfactory Beaconing in Pacific Salmon

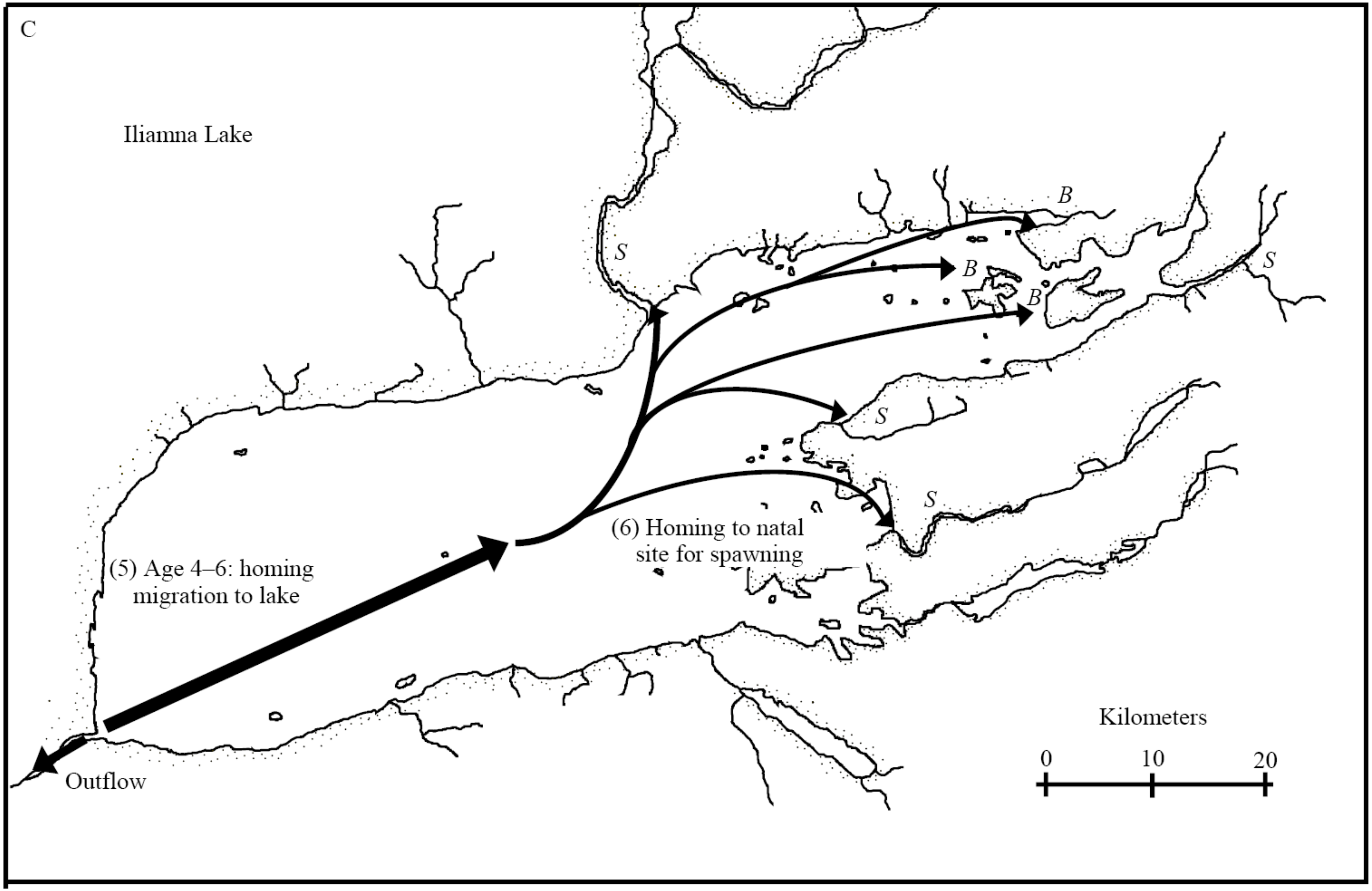


Dittman and Quinn, JEB 1996

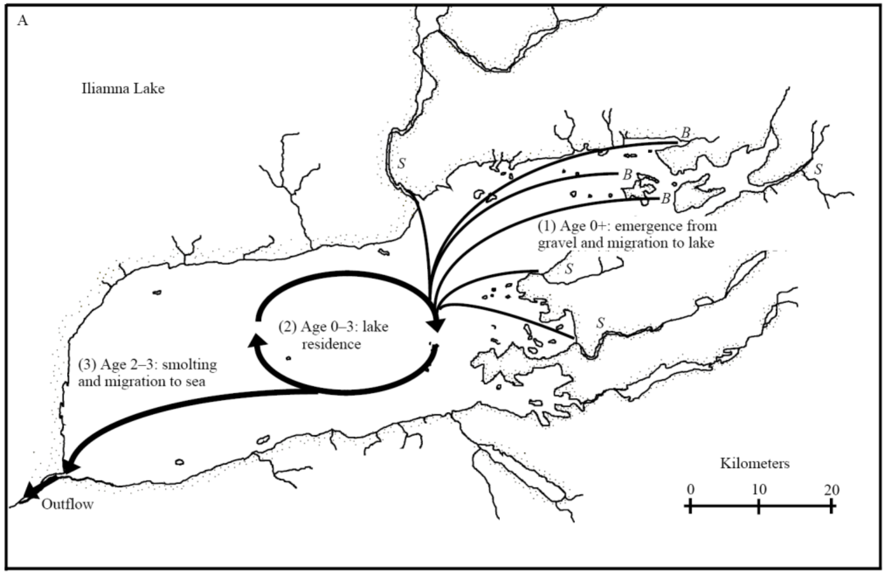
Olfactory Beaconing in Pacific Salmon

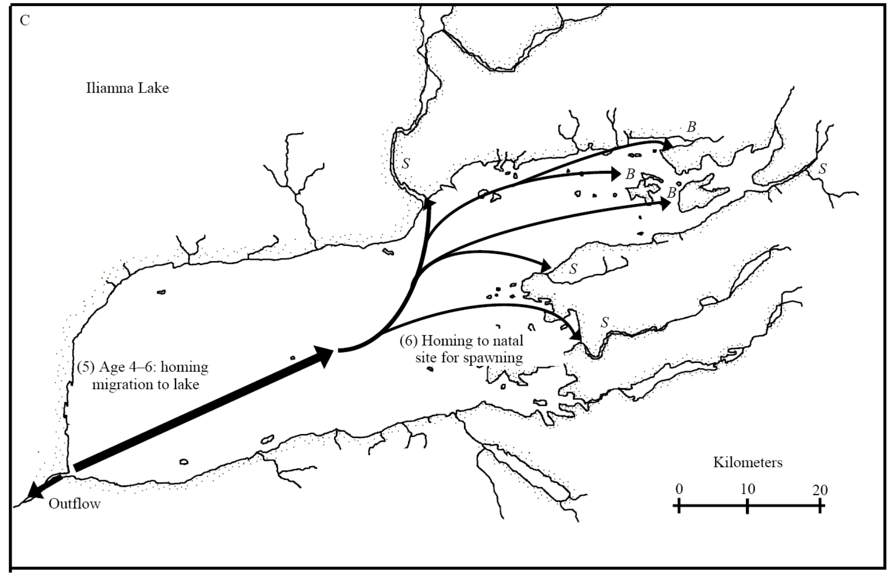


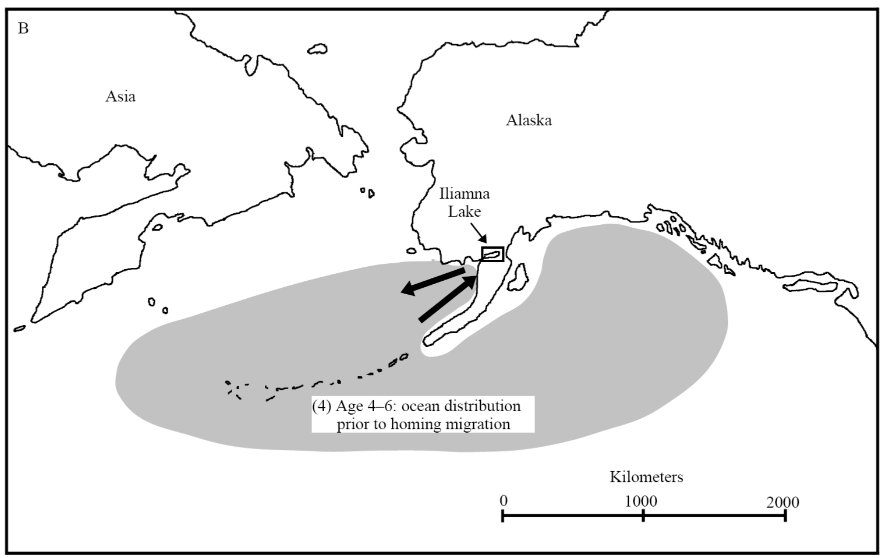
Olfactory Beaconing in Pacific Salmon



Olfactory Beaconing in Pacific Salmon







Olfactory Imprinting: experimental manipulations of artificial odorants using laboratory- or hatchery-reared salmon have shown that the fish navigate up-gradient towards the <u>odor</u> with which they were imprinted (in the wild: the odor of their stream).

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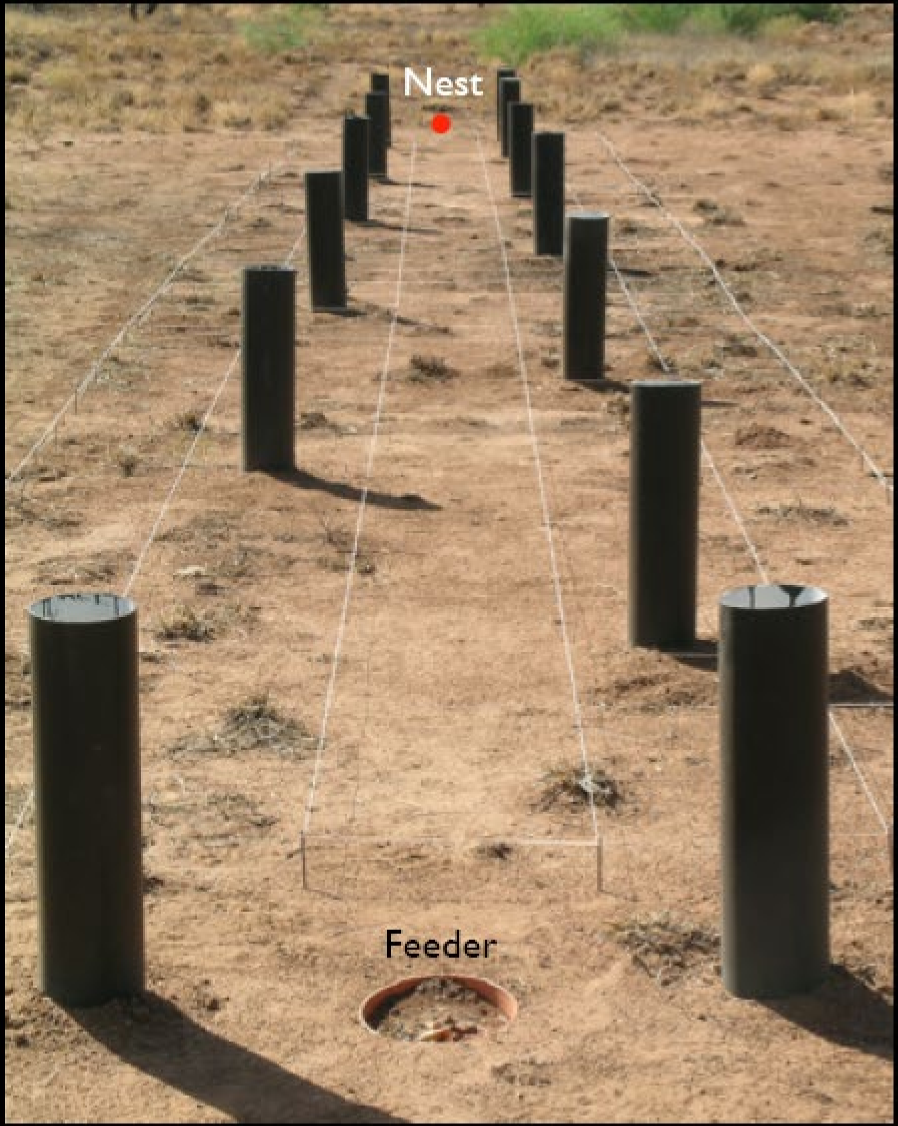
Route following (route guidance) in ants

20 m long corridor of 1-m wide with cues at every 2 m interval

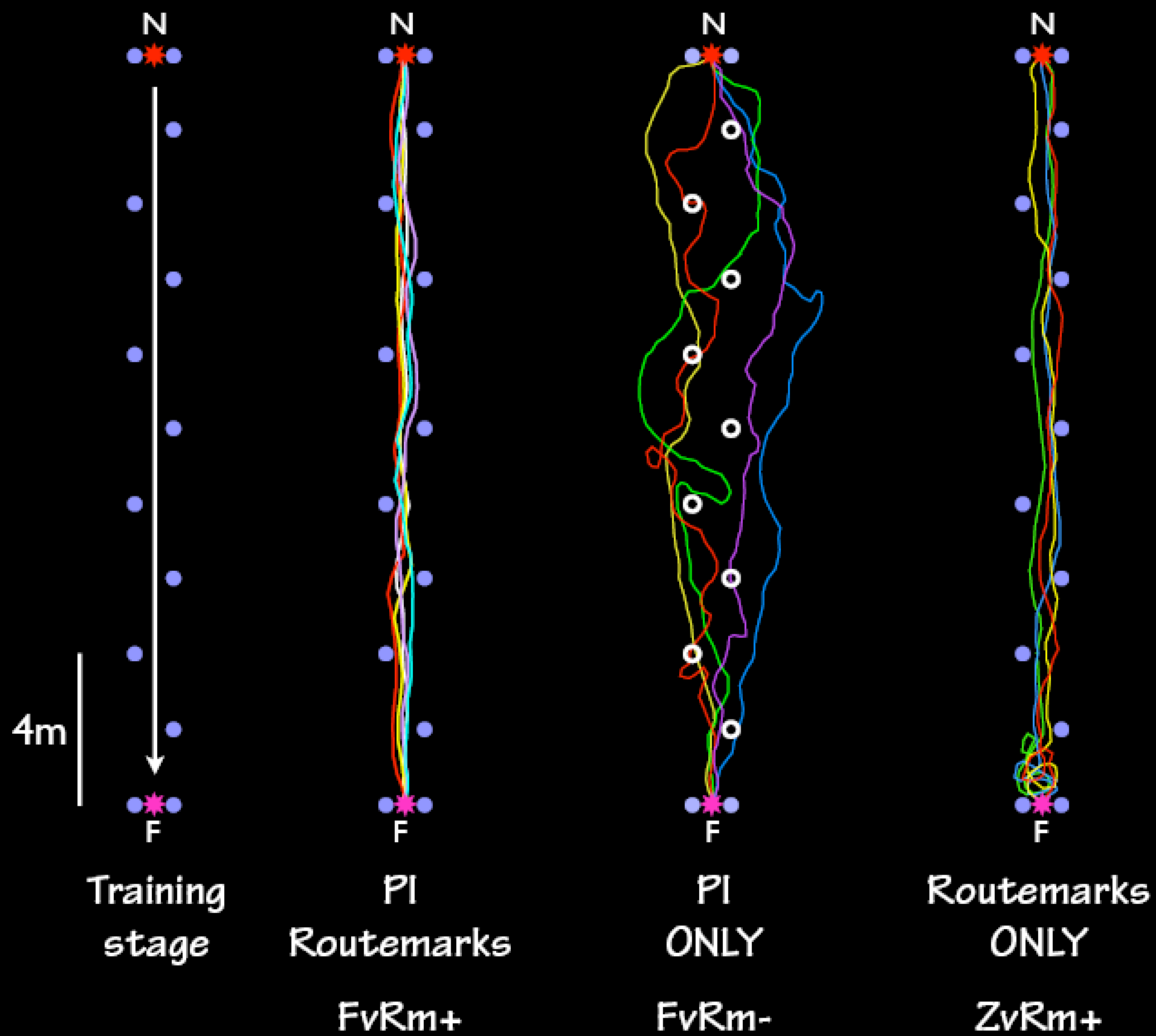
cylinder: 60 cm height
:16 cm diameter

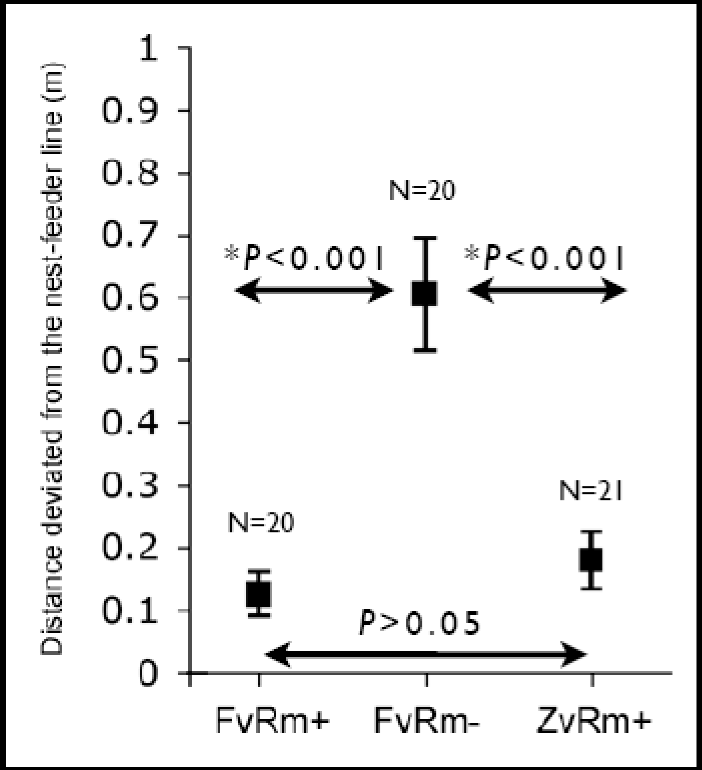
Ants trained for 14 days (~300 trials)



Narendra 2007. Journal of Experimental Biology 210: 1804-1812

Route following (route guidance) in ants





Information from path integrator is used, but it is not essential!

Narendra 2007. Journal of Experimental Biology 210: 1804-1812

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Path integration

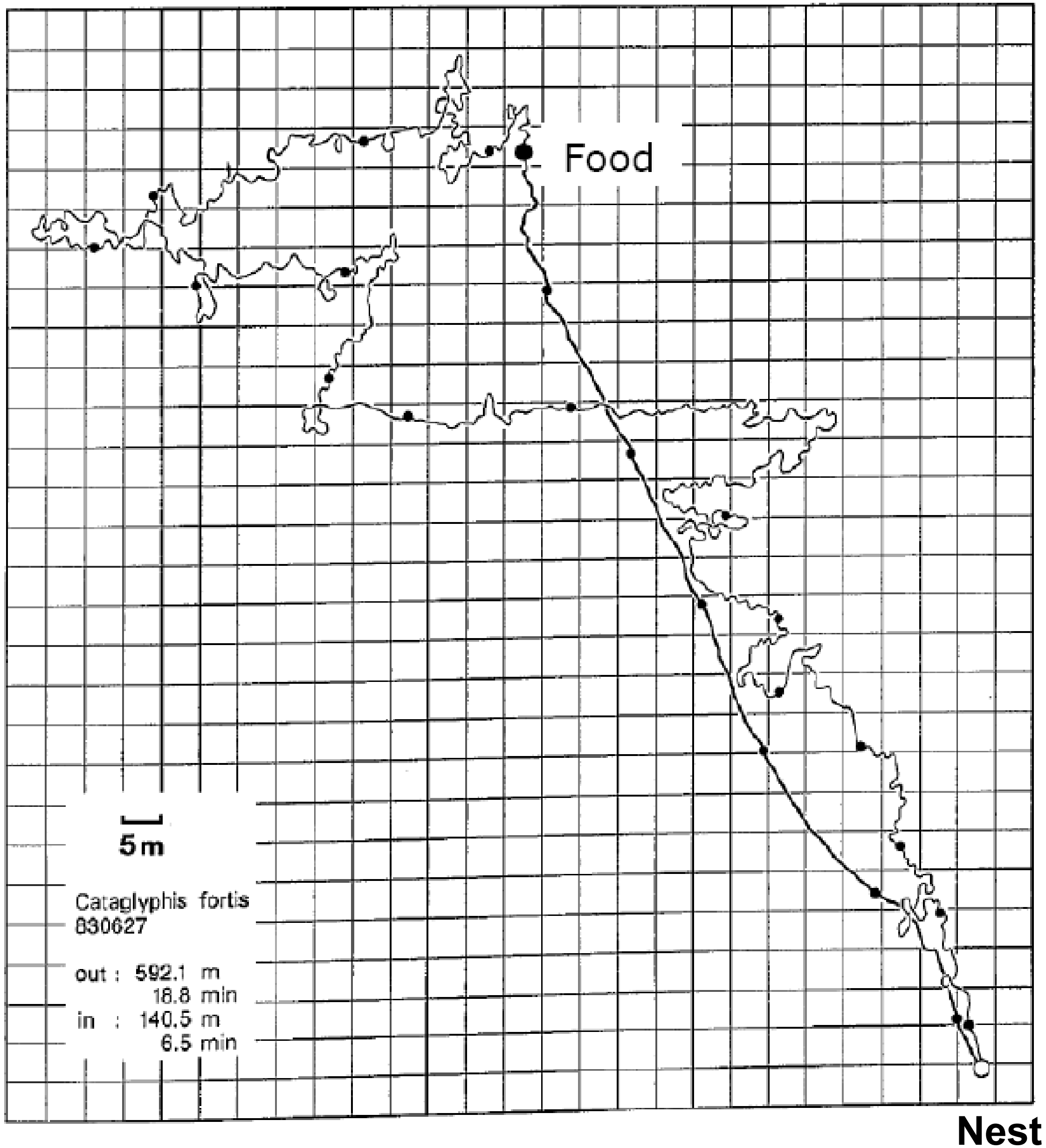
Definition of Path Integration:

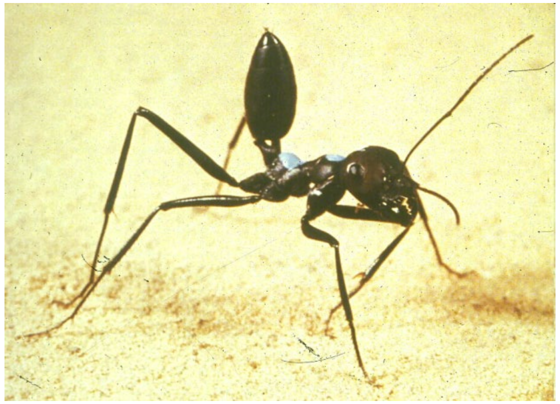
"…a running computation of the present location from the past trajectory"

(term coined by Horst Mittelstaedt)

- A continuous process of computation/integration
- Provides an estimate of present location
- Trajectory/motion cues are required
- Landmarks or trails are *not* required

Most famous path-integrator: The desert ant, *Cataglyphis fortis*

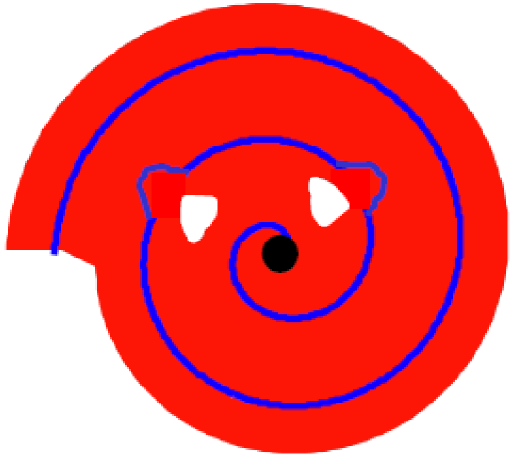


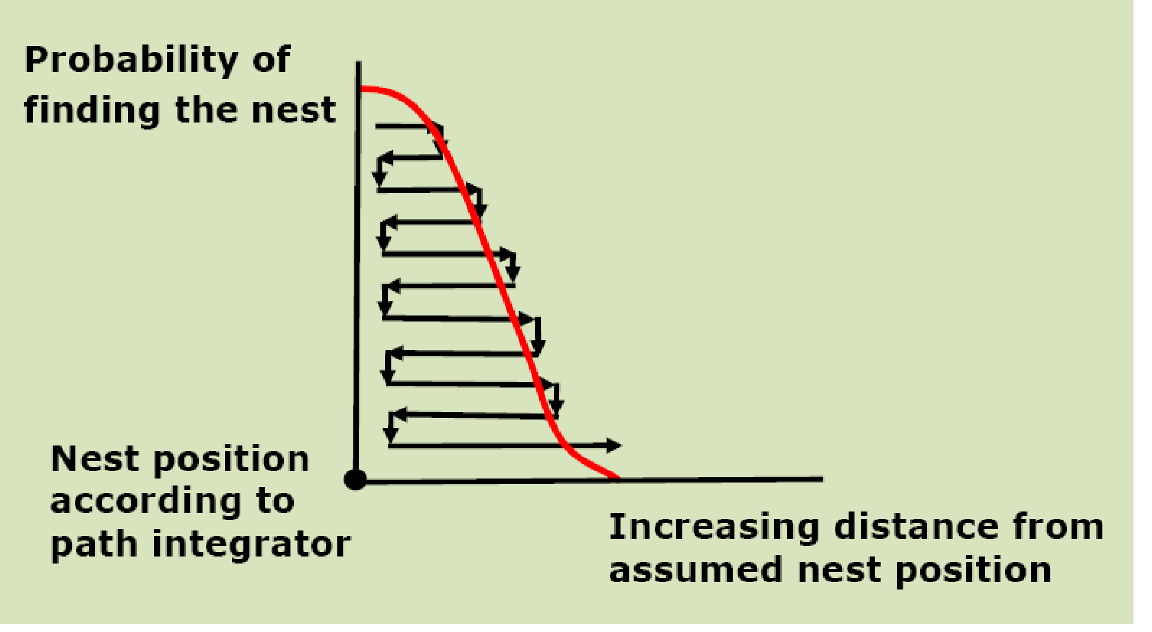


Lives in extremely flat and featureless salt planes in the Sahara

Rudiger Wehner

Backup strategy in the desert ant: Systematic Search





Outline of a Path Integration system

Distance:
per unit time

Direction
Rotation per
unit time

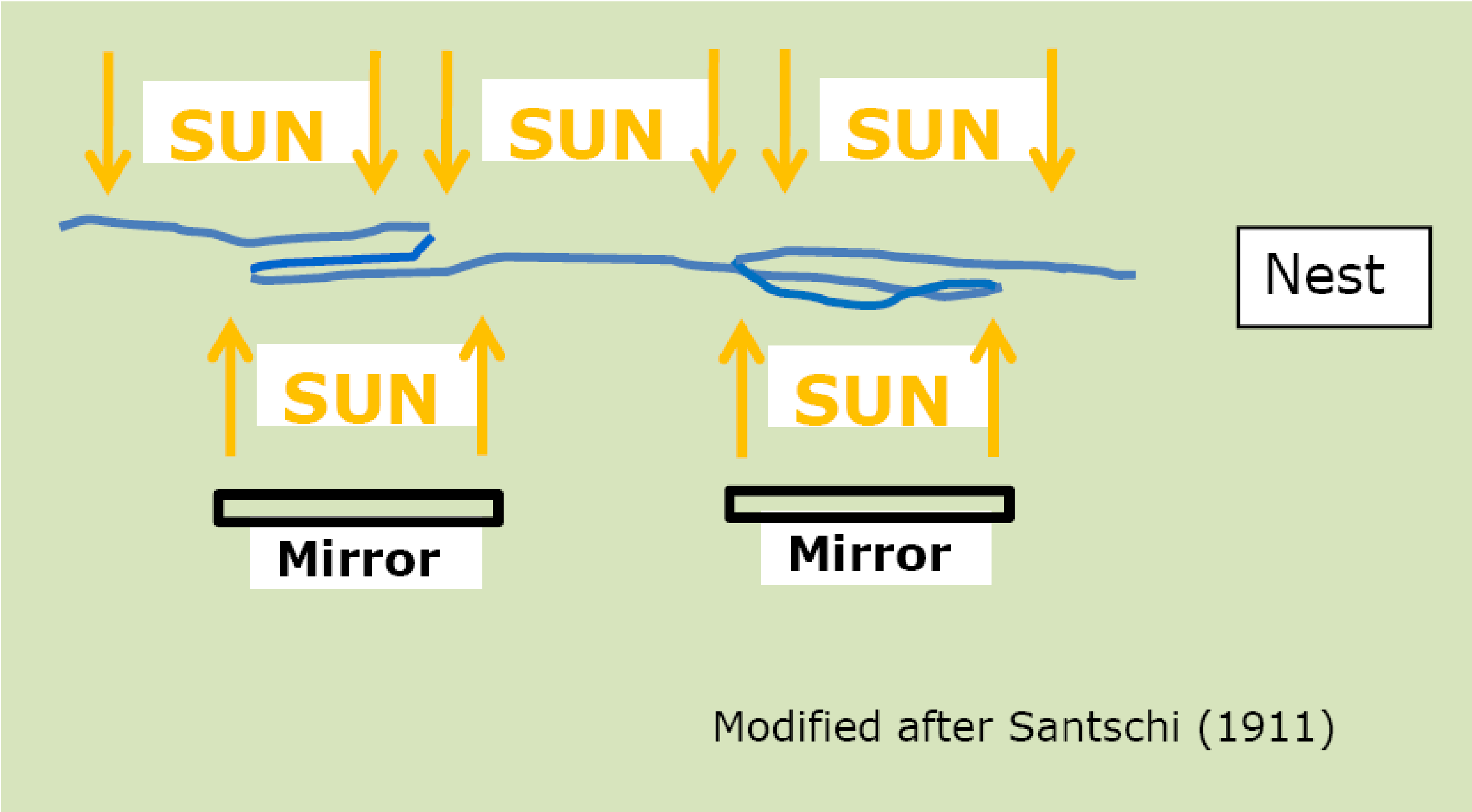
→ **Path Integration system** →

"Home vector"
(estimates the vector
pointing towards home)

Need mechanisms for:

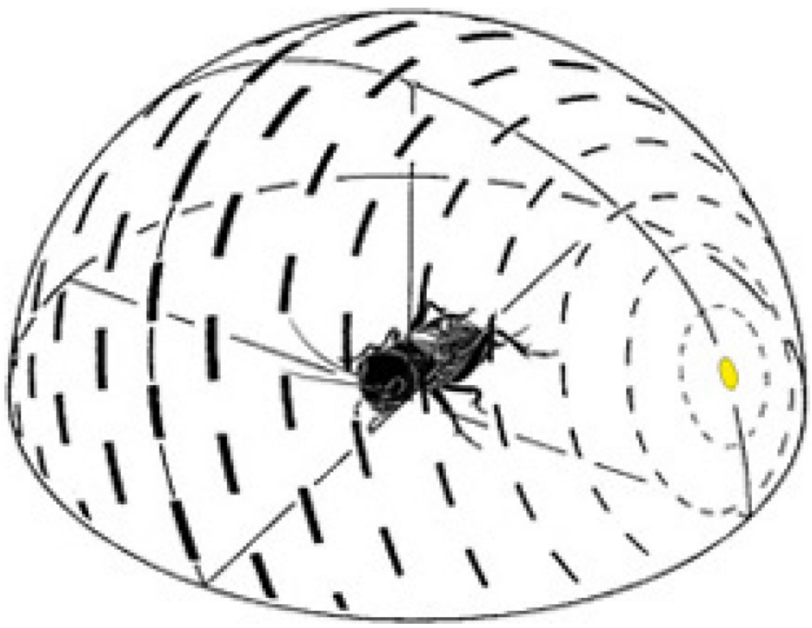
- **Measuring <u>distance</u> (per unit time)**
- **Measuring <u>direction</u> (per unit time)**

Direction cues in desert ants I: Sun Compass



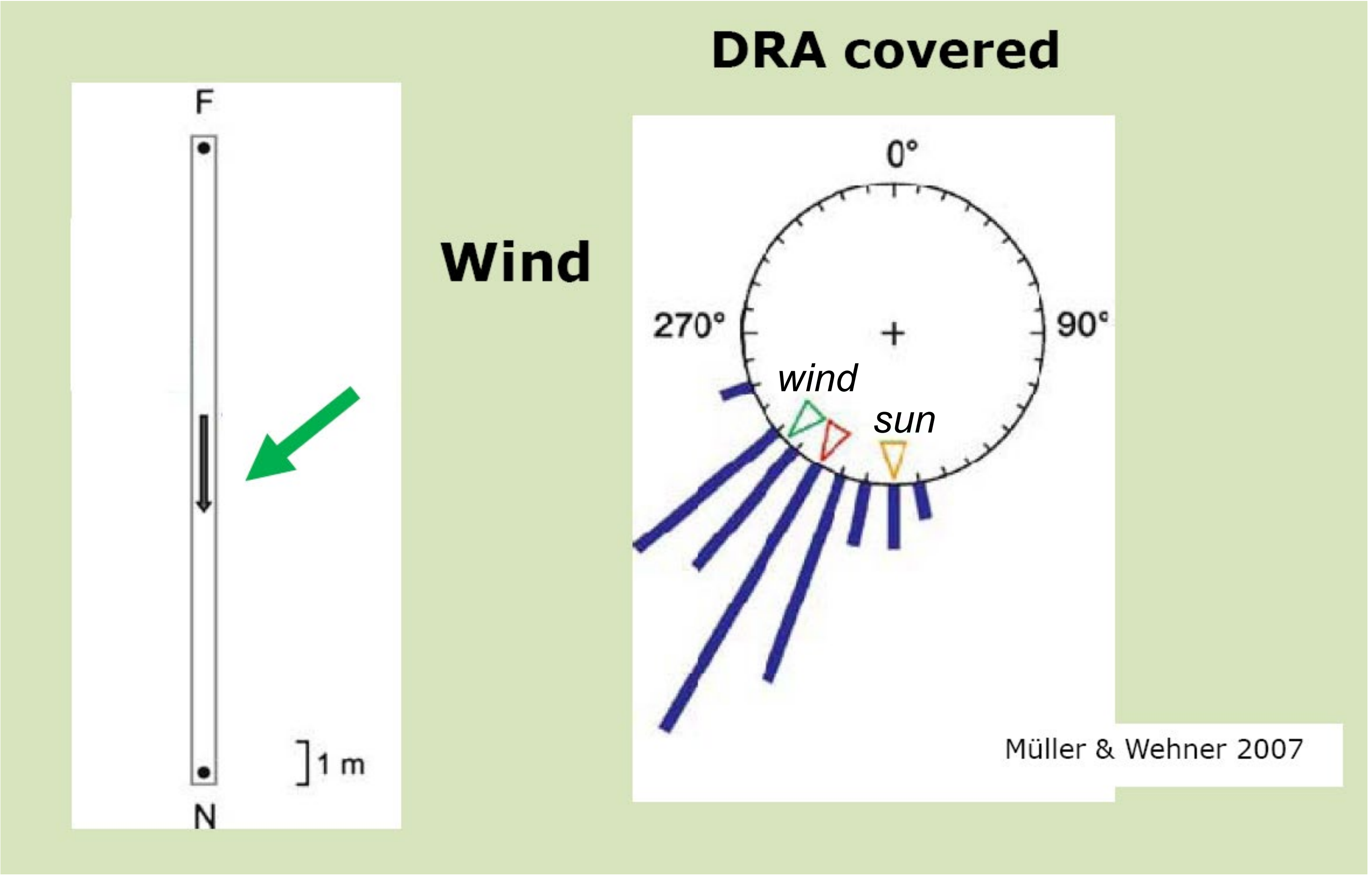
Manipulating the Sun's direction by using a mirror showed that ants use a sun compass.

Direction cues in desert ants II : Polarization Compass



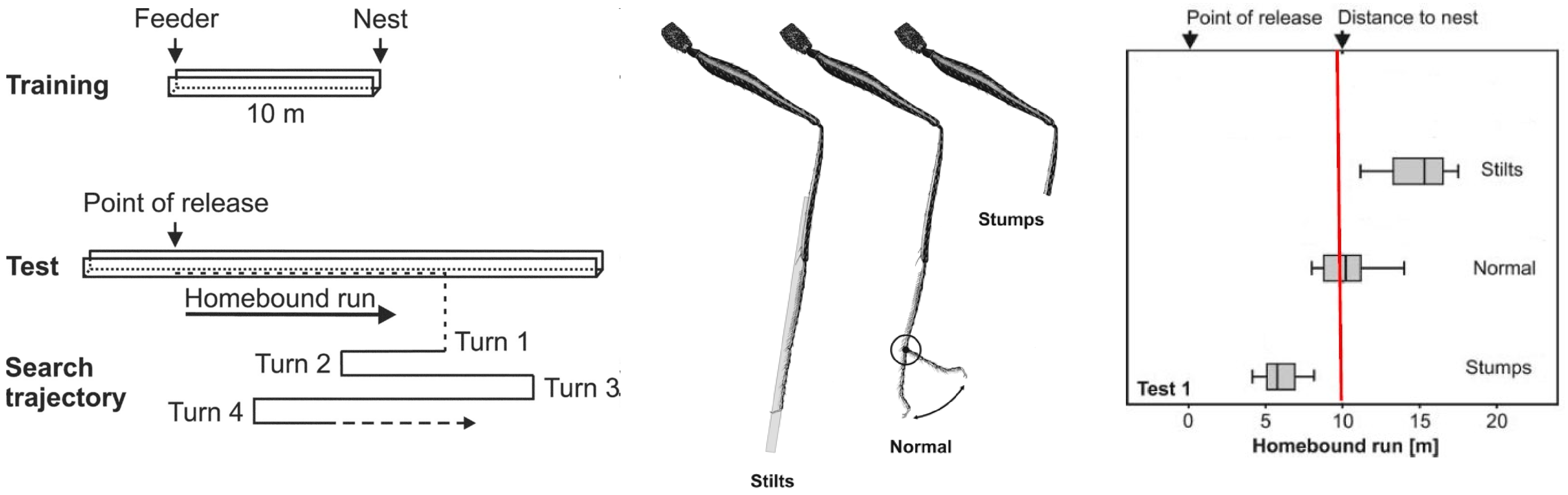
Insects can see the polarization pattern of the sky in the Dorsal Rim Area of their compound eyes. Experiments with rotating polarization filters have shown that desert ants indeed functionally use a polarization compass.

Direction cues in desert ants III : Wind



When sun and polarization directional cues are unavailable, the desert ant uses a wind compass.

Distance measurement (odometer) in desert ants: Step Counter

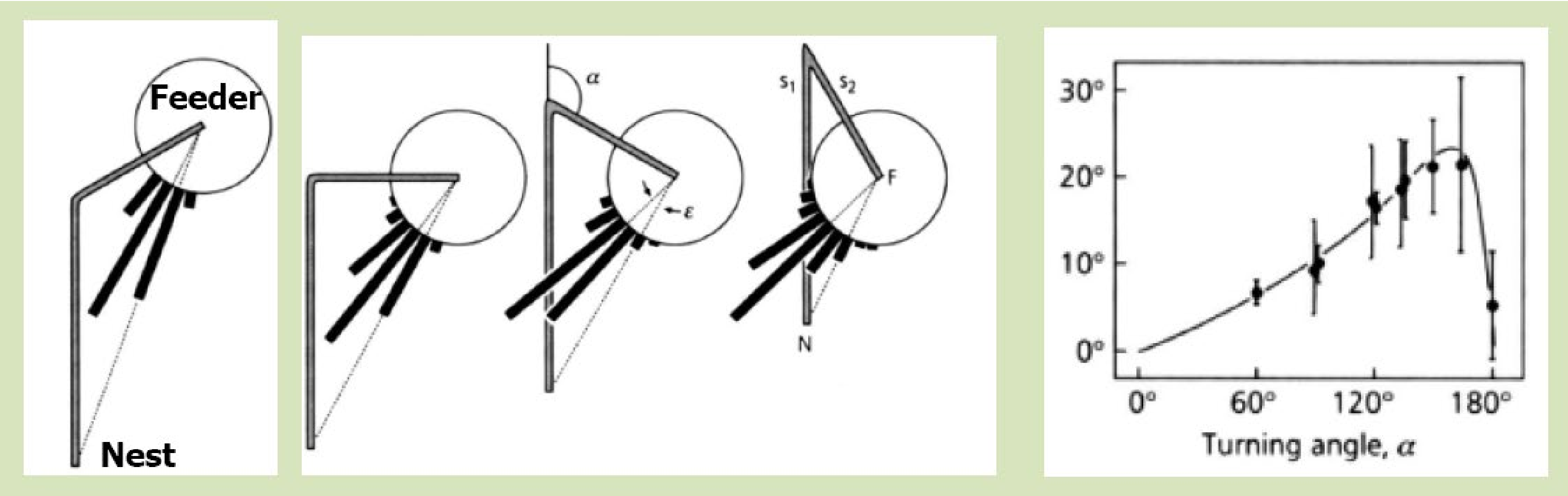


Wittlinger et al., *Science* (2006)

Measuring distance ("odometer" 'מד קילומטראז):

- **In desert ants = step counter**
- **In honeybees = optic flow**

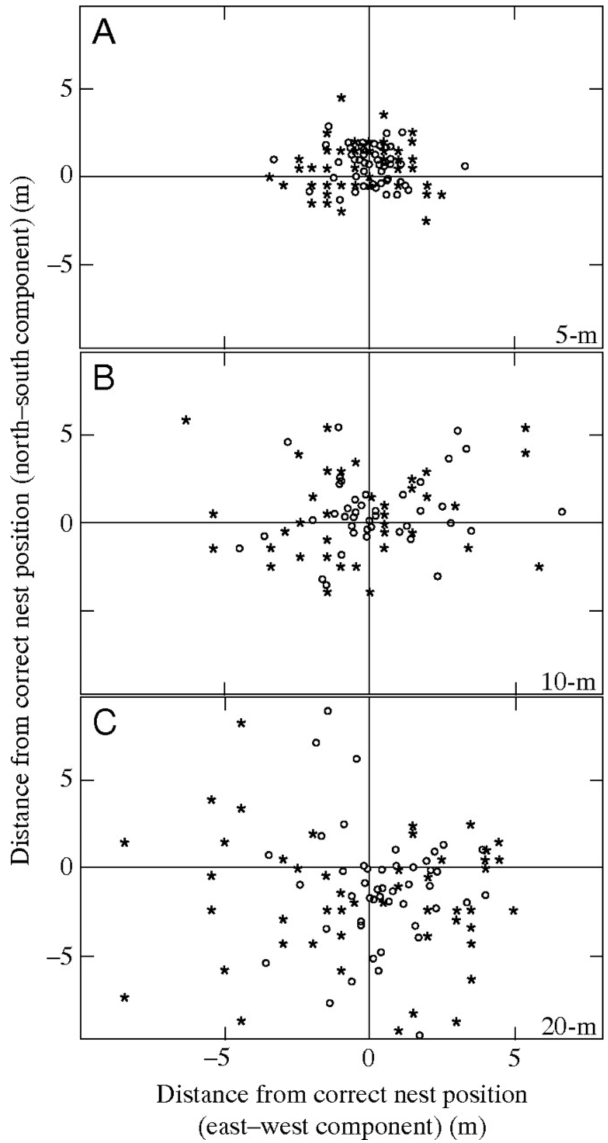
BUT: Path integration is error prone

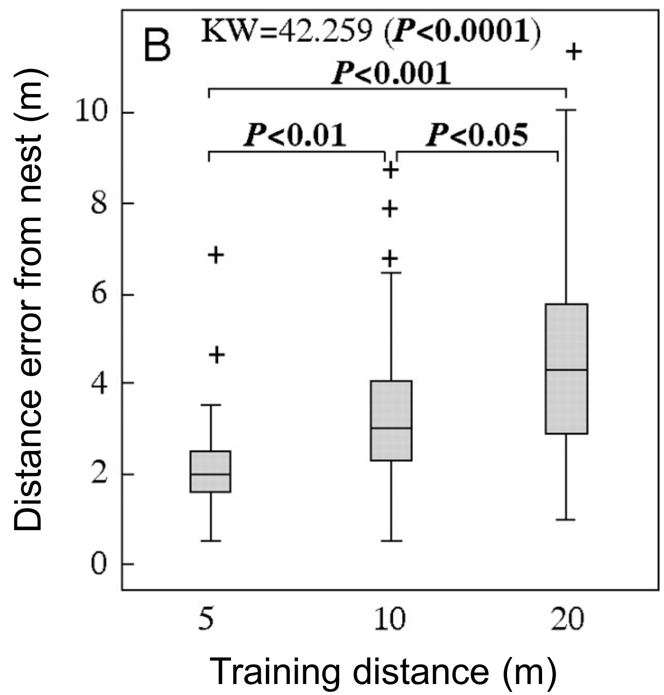


- Systematic errors sometimes > 20° in **direction**

- Random errors sometimes ~ 10° in **direction**

BUT: Path integration is error prone





In another experiment:
<u>Random errors of **~25%** in **distance**</u>

Merkle, Knaden, Wehner (2006)

- The problem: Path integration accumulates (integrates) the errors.
- Mammals are less good path integrators than the desert ant. Random errors are even larger in rodents than in ants (Etienne et al., *Nature* 1998)
- Path integration in mammals is likely most useful for “filling the gaps” when reliable external sensory information is *not* available.

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‘Cognitive Map’ theory (Tolman 1948, O’Keefe & Nadel 1978)

The cognitive map:

An abstract representation of space that allows flexible direct navigation from any start-point A to any desired end-point B.
Pro: Allows flexible navigation.
Con: Complex and detailed representation.

Still under debate whether animals truly have cognitive maps, or whether experimental results can be explained by other, simpler mechanisms.

A concept that arose historically (Tolman 1948) from laboratory work in rats = small scale navigation. The “neuropsychological” approach.

* We will talk about it more in the next lecture.

'Map-and-Compass' theory (Kramer 1953)

Kramer (1953) suggested that long-distance homing (in the field) occurs in two steps:

1. The Map step: computing your location.
2. The Compass step: computing the direction to home.

This is the basic framework to this day in studies of animal navigation in the field.

The map-and-compass: A concept very close to that of the cognitive map; arose historically (Kramer 1953) from a very different research community, that of people doing field work in birds = large scale navigation. The neuroethological approach.

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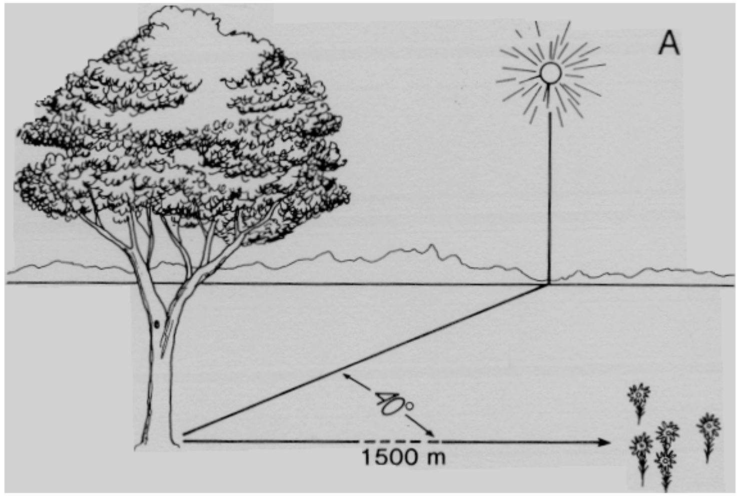
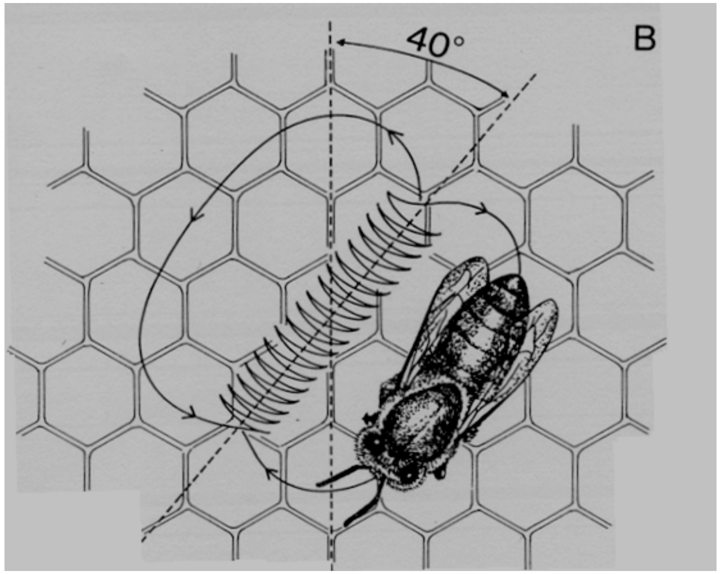
Honeybee navigation and the use of the sun compass

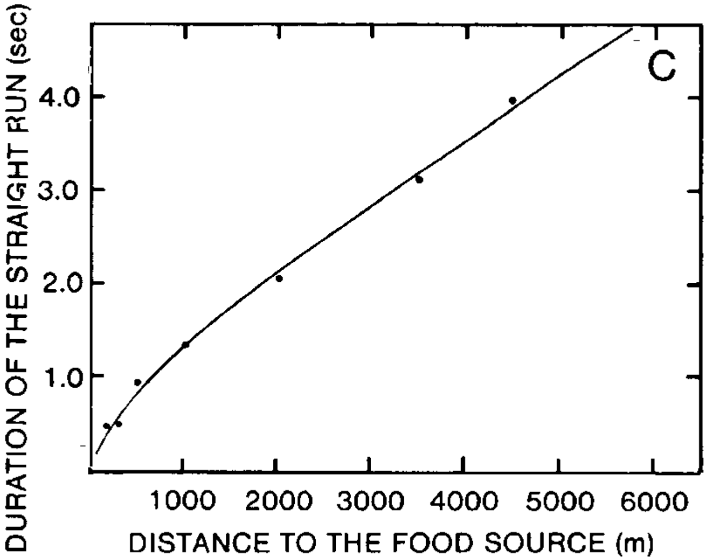
Movie (M. Srinivasan)

Honeybee navigation and the use of the sun compass

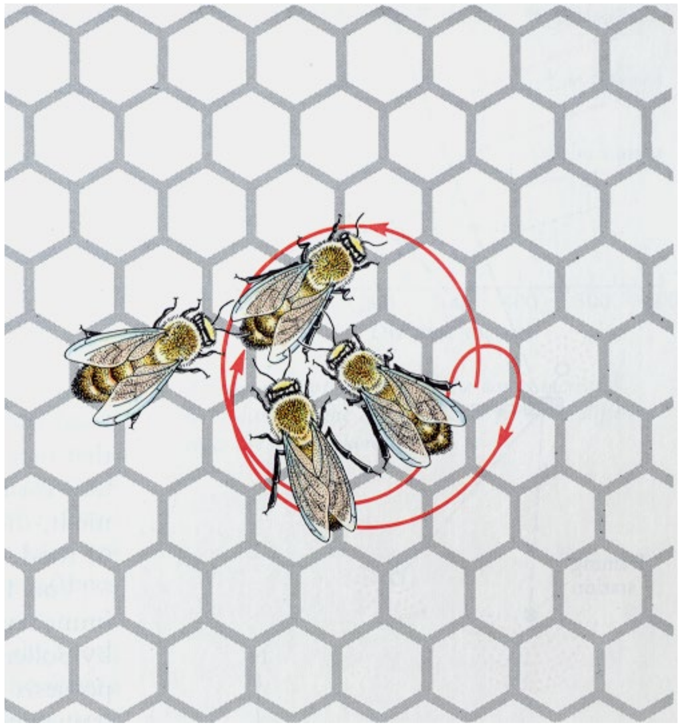
The waggle dance:
A symbolic 'language'
(Karl von Frisch)







Honeybee navigation and the use of the sun compass



Round dance

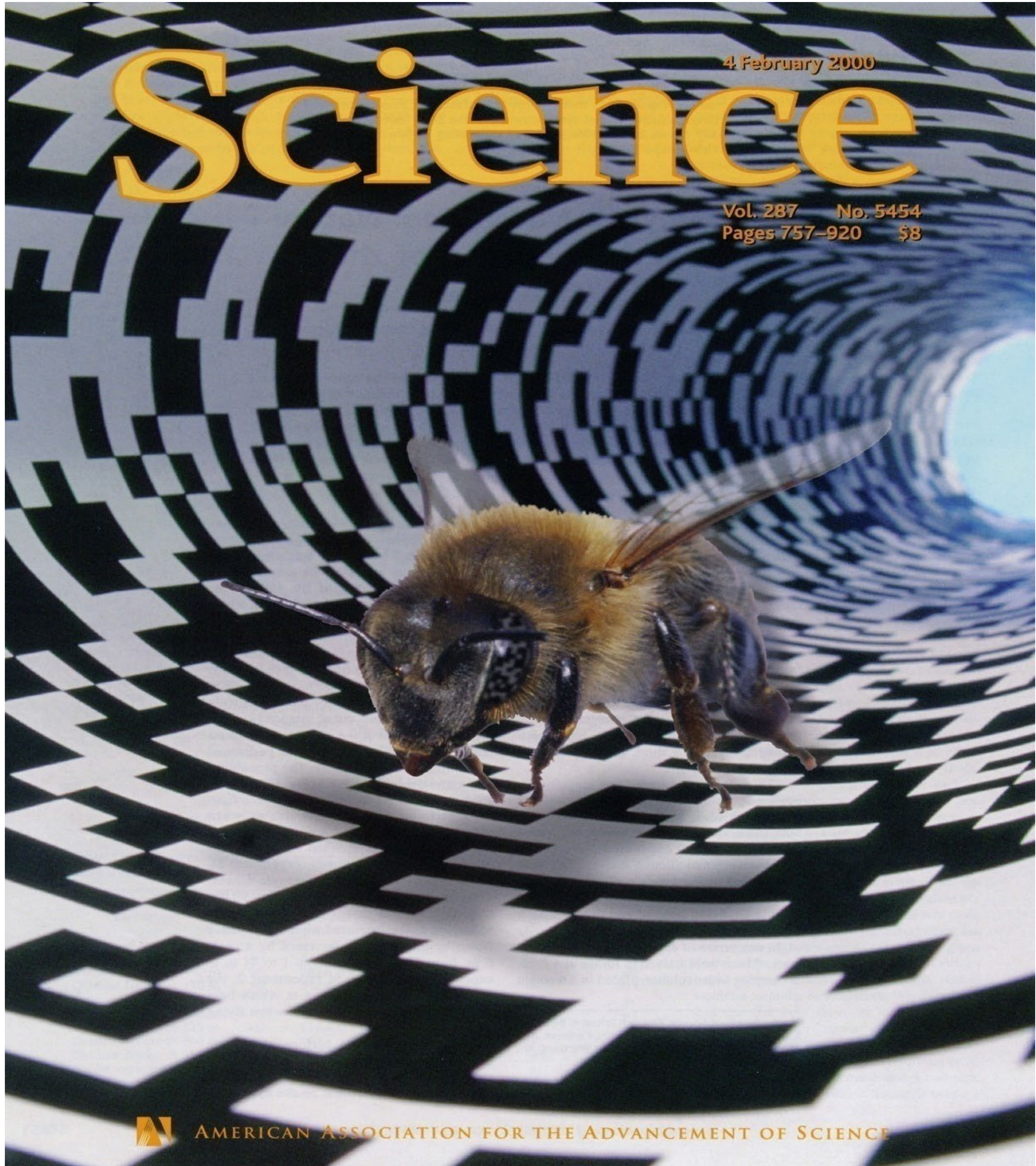
(feeder distance < 50m)

Waggle dance

(feeder distance > 50m)

You can use the waggle dance to ask how far the bee *thinks* that it flew … just like you can use the directed search of a desert ant to ask how far the ant *thinks* that it walked.

Srinivasan used this to show that the honeybee odometer is based on *optic flow*.

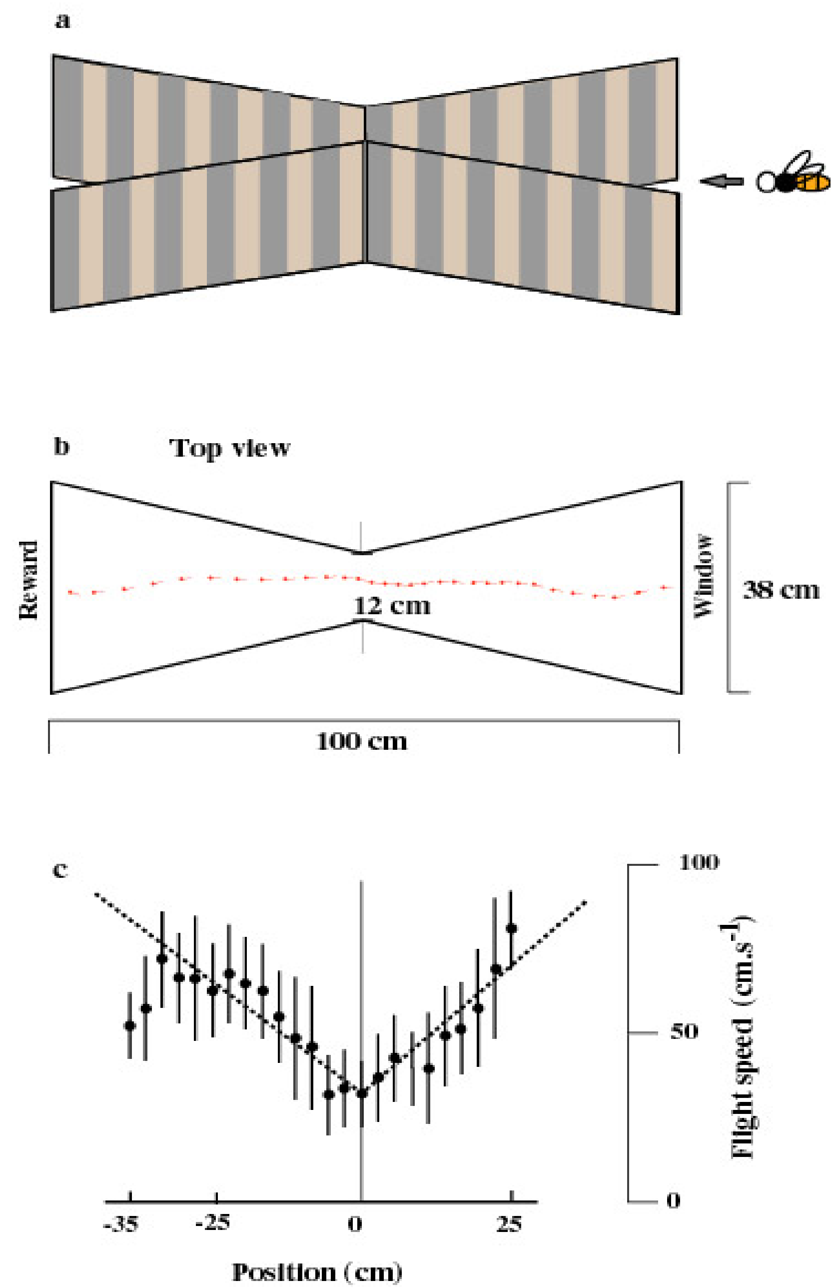


Optic flow is important for honeybees.

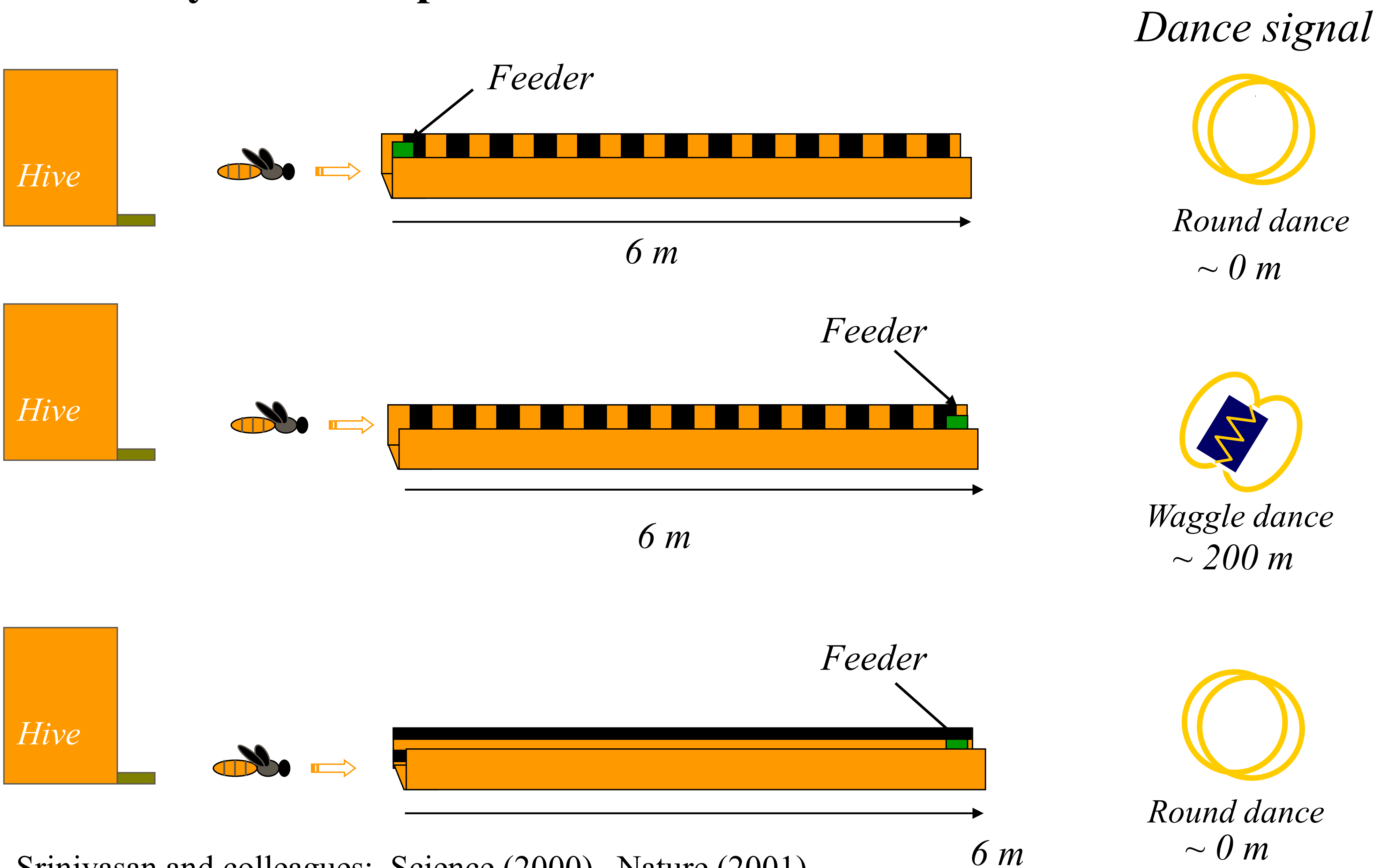
I. Optic flow controls their flight speed

Speed of flight is regulated by holding the global image velocity constant

Srinivasan, Zhang, Lehrer & Collett
J. Exp. Biol. (1996)

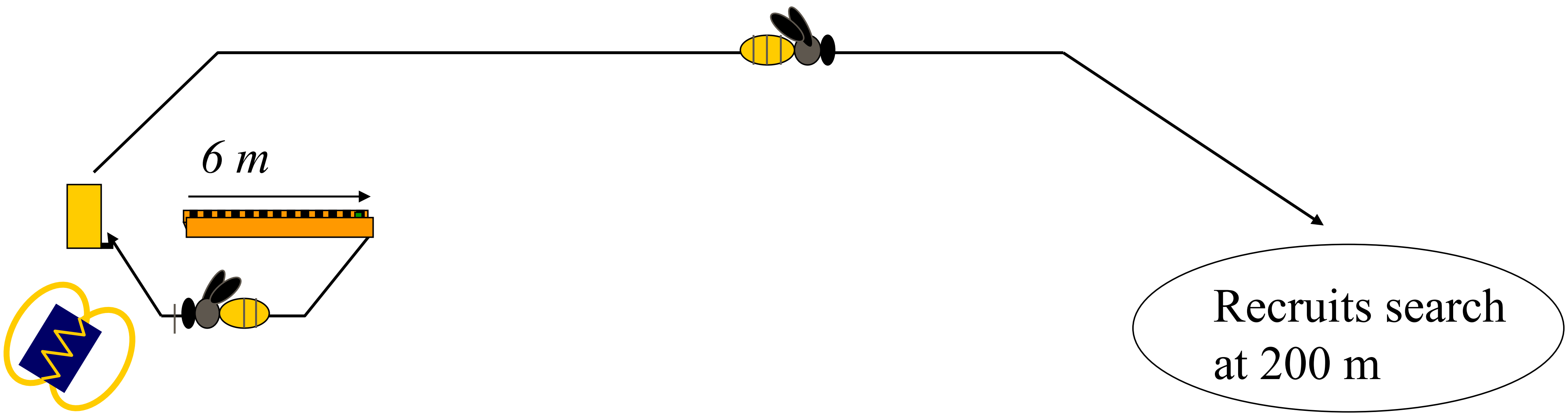


II. Honeybees use optic flow to measure distance



Srinivasan and colleagues: Science (2000) , Nature (2001)

How do the recruits respond to the dancing tunnel bees?



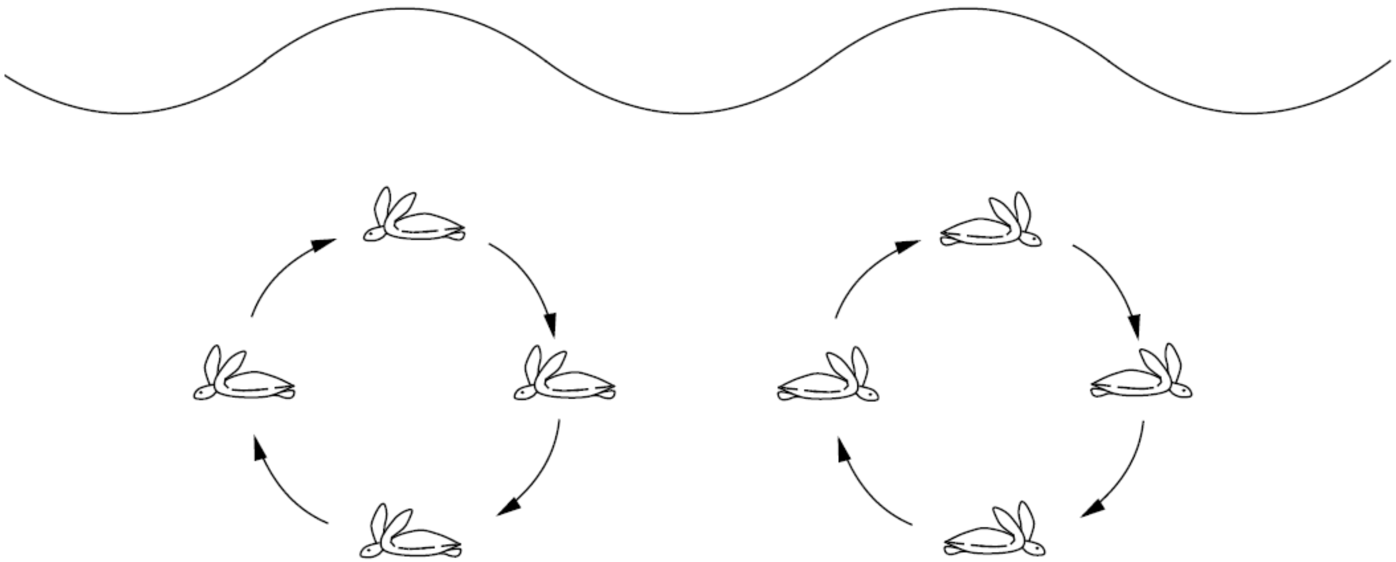
Scouts returning from 6 m tunnel signal a distance of 200 m

Esch, Zhang, Srinivasan & Tautz
Nature (2001)

Sea turtle hatchlings use the direction of waves as compass

Hypothesis: Hatchling sea turtles use wave direction to keep course into the open sea and away from shore

Wave direction →



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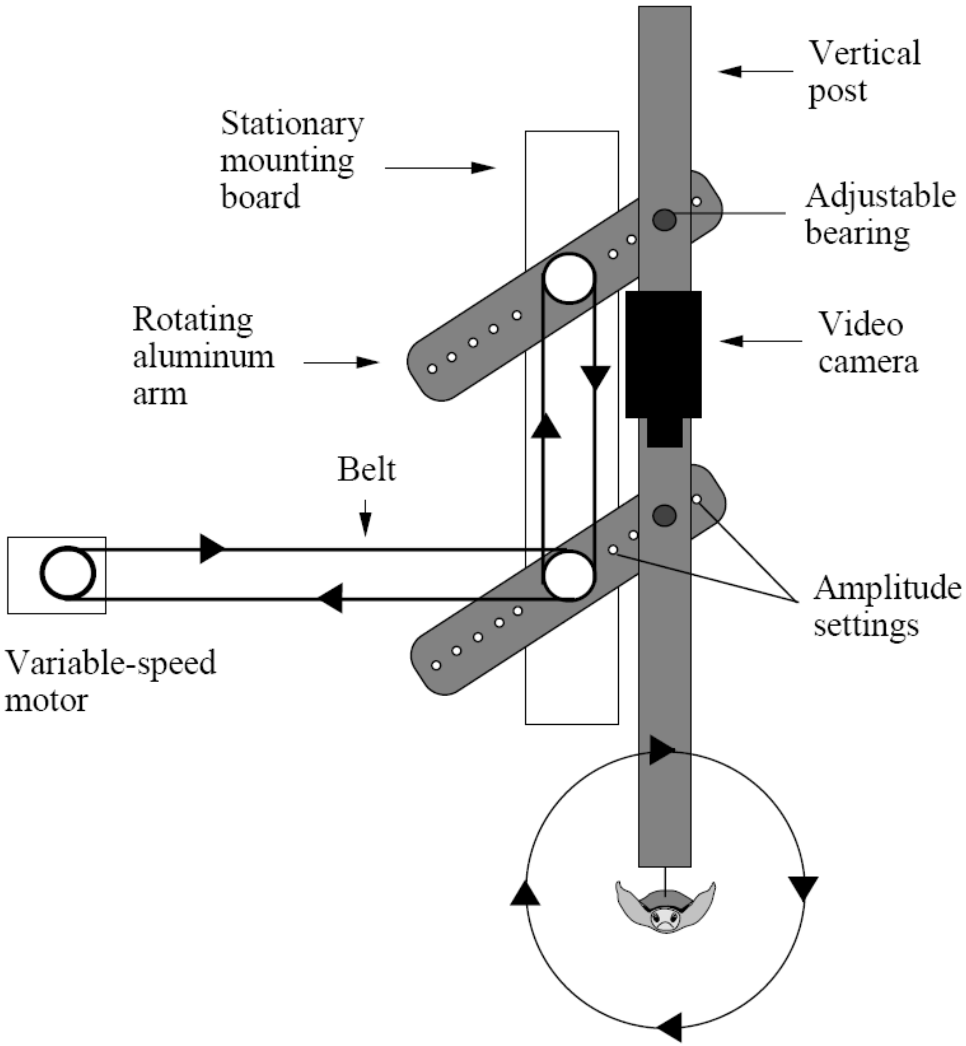
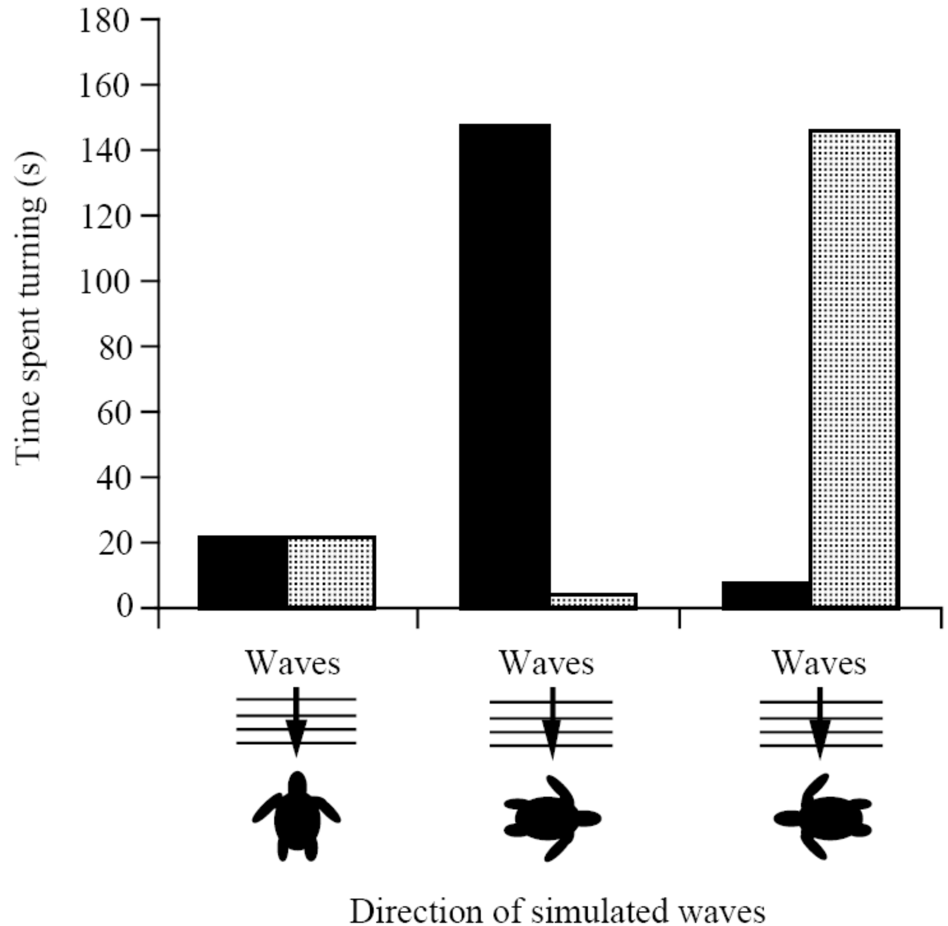




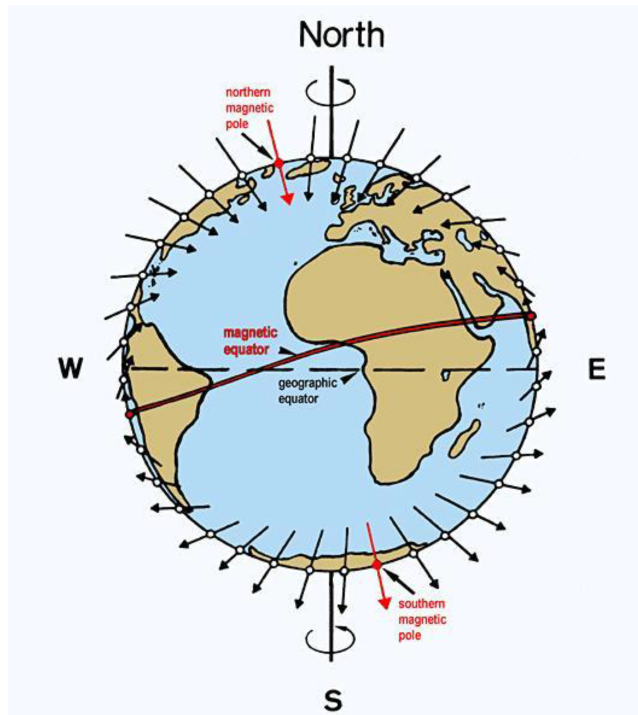
Lohmann and Lohmann (1996)

Compass mechanisms in birds

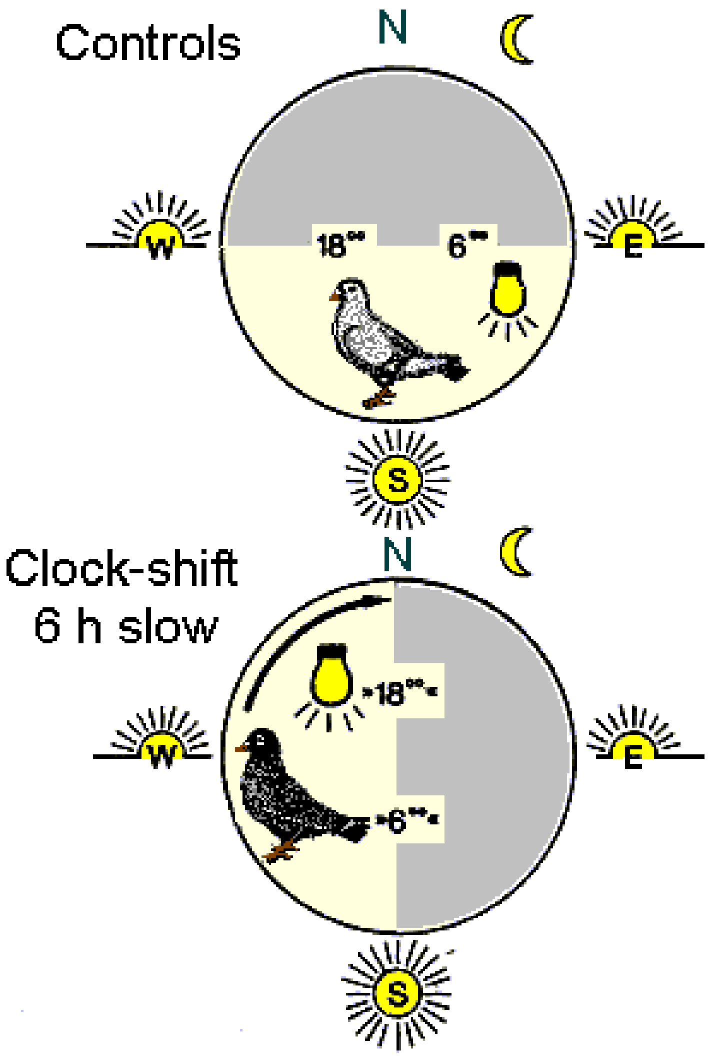
- **Celestial compass:**
  - **Stars** (in night-migratory birds): Can be manipulated in a planetarium, e.g. if rotating the simulated starry sky by 90° : birds rotate by 90°
  - **Sun**: Can be manipulated by clock-shifting

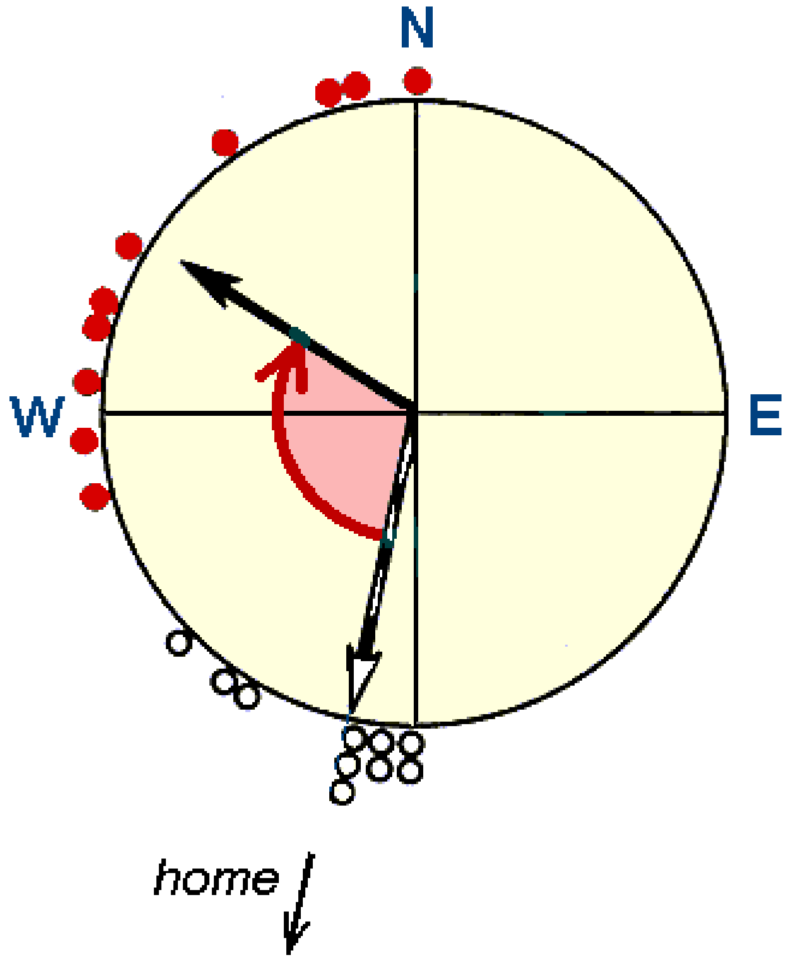
- **Magnetic compass** (based on the geomagnetic field)

(note that the geomagnetic field can be used both for **compass** and for **locational** information – as we'll see later)



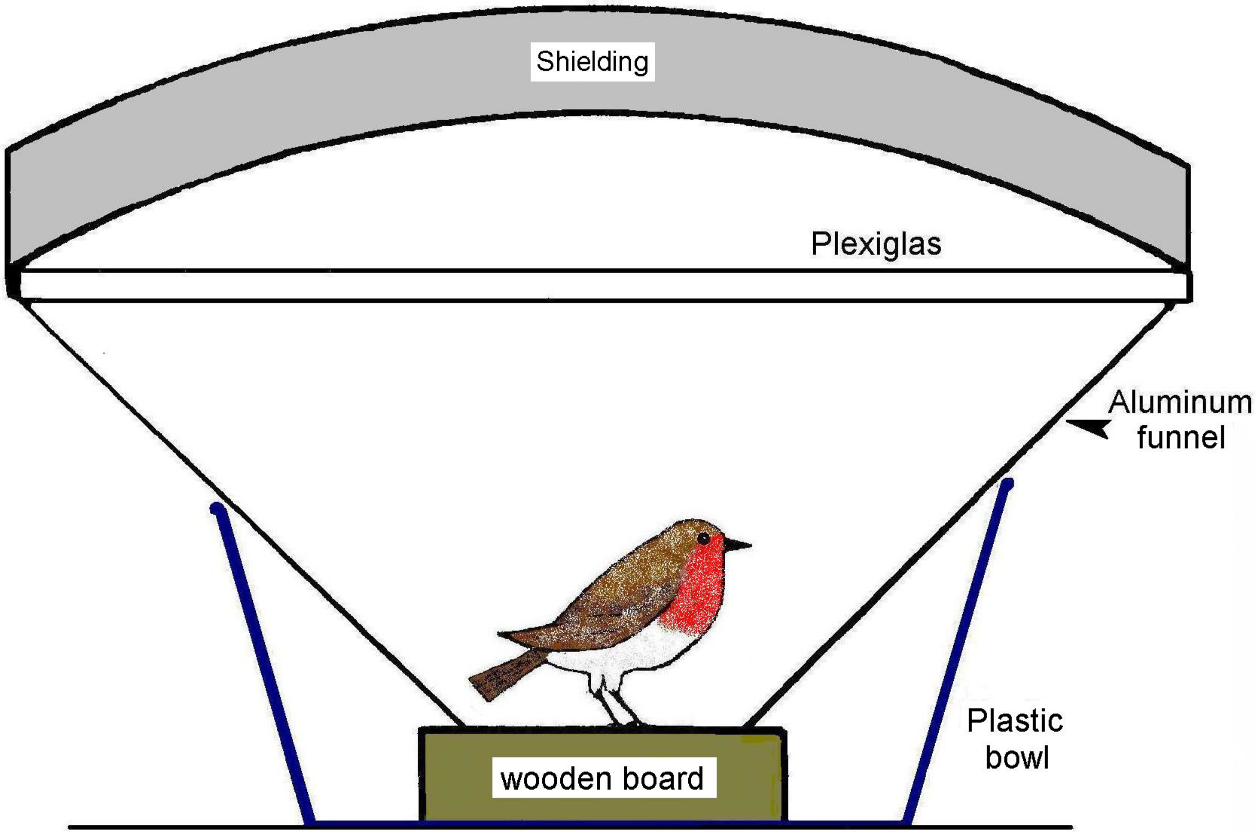
Demonstrating sun compass in pigeons





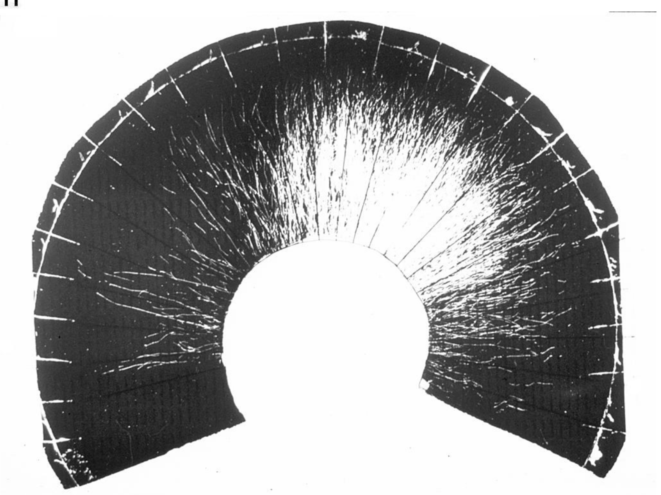
Demonstrating magnetic compass navigation in migratory birds in captivity

These laboratory experiments rely on the behavioral phenomenon of *Zugunruhe* (migratory restlessness)

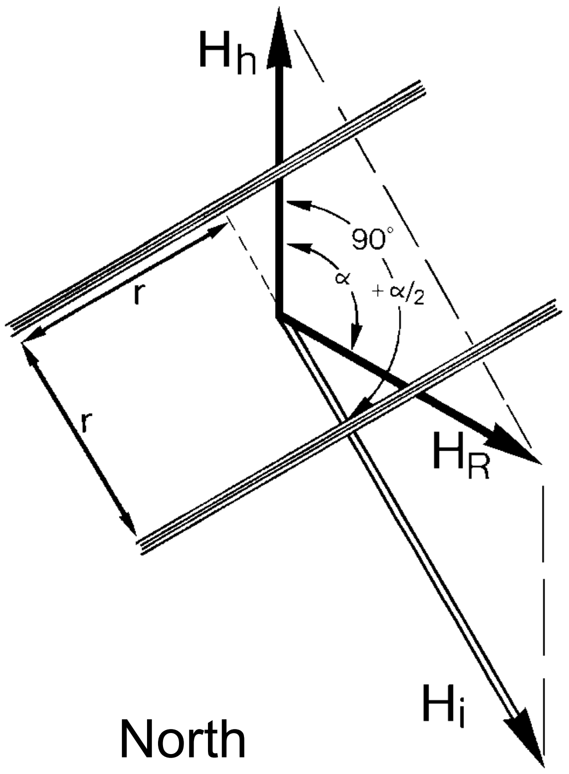


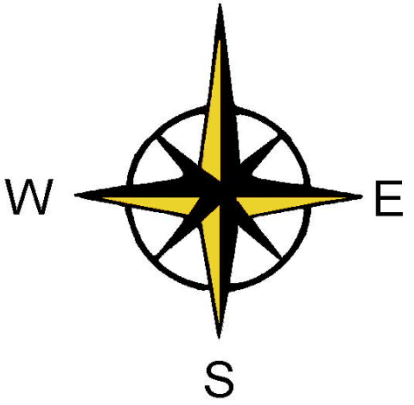
Funnel cage by Emlen & Emlen (1966)

Funnel cage lined with coated paper



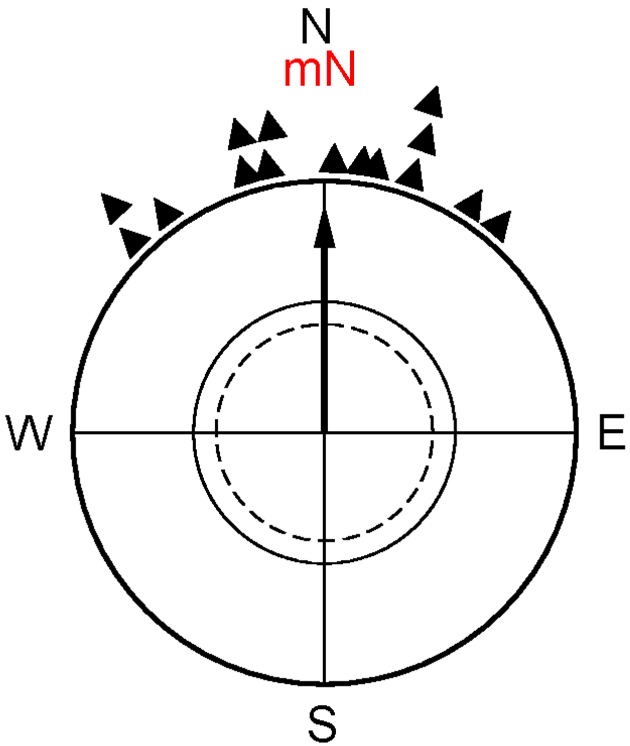
Demonstrating magnetic compass navigation in migratory birds in captivity





Demonstrating magnetic compass navigation in migratory birds in captivity

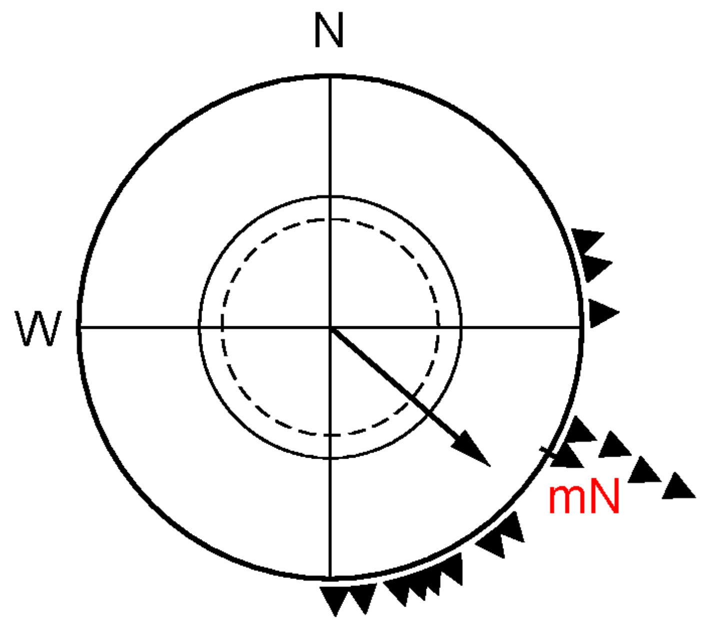
European Robins



local geomagnetic field

Control

⇨ *N = mN*

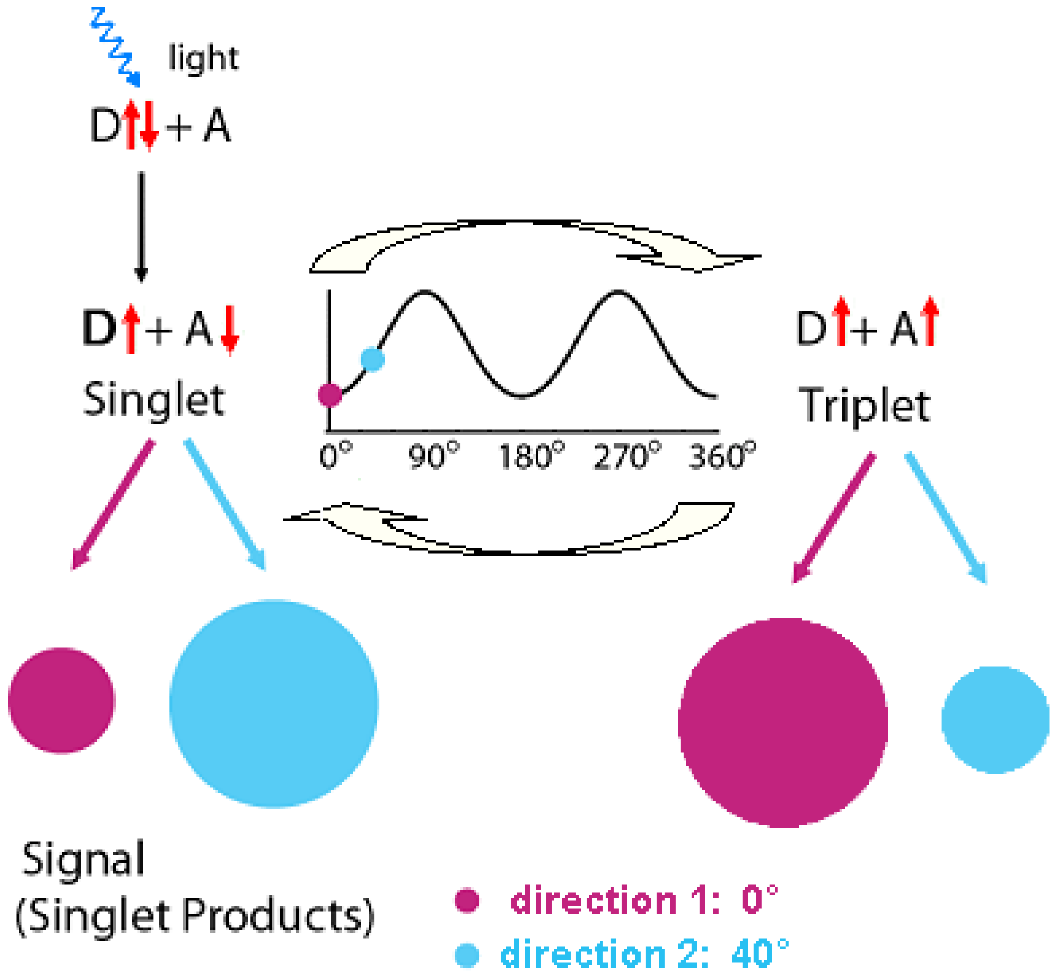


magnetic North

turned 120° to ESE

⇨ *SE = mN*

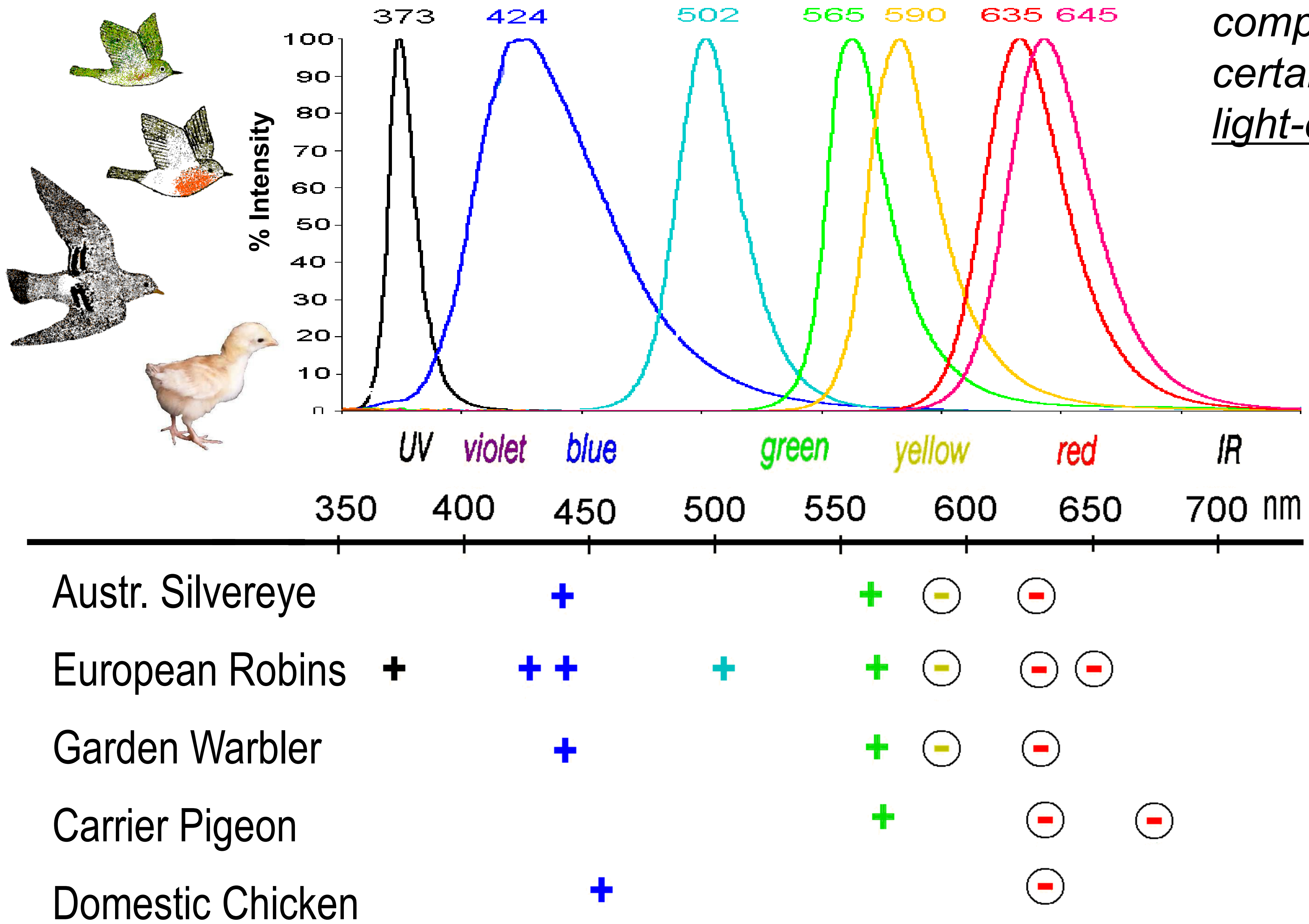
Mechanism of magnetic compass in night-migratory birds (e.g. European robins): Light- and magnetic-field-dependent radical-pair reaction ?



Candidate molecules:
Cryptochromes, which are located in the bird‘s retina

Testing the radical pair model

Magnetic compass in certain birds is <u>light-dependent</u>



Compass Mechanisms: Summary

- ‘Compass’ from path integration (integrating vestibular cues: semicircular canals)
- Distal visual cues (e.g. mountains)
- Polarization compass: In insects
- Wind
- Sun
- Waves
- Stars
- Magnetic

- Others…

Outline of today's lecture

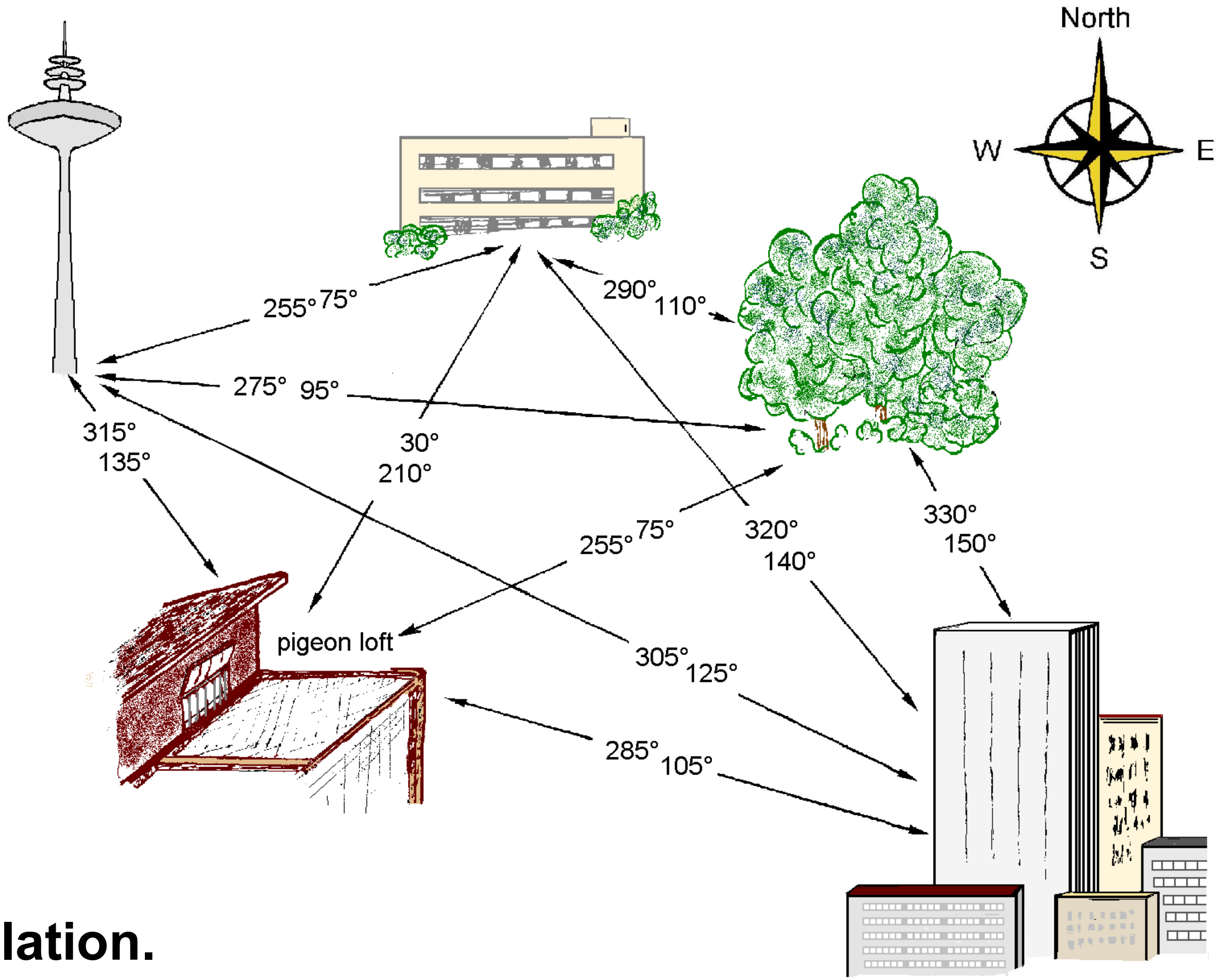
- Introduction: Feats of animal navigation
- Navigational strategies:
  - Beaconing
  - Route following
  - Path integration
  - Map and Compass / Cognitive Map
- Sensory cues for navigation:
  - Compass mechanisms
  - **Map mechanisms**
- Brain mechanisms of Navigation (brief introduction)
- Summary

Map mechanisms

Three main map mechanisms:

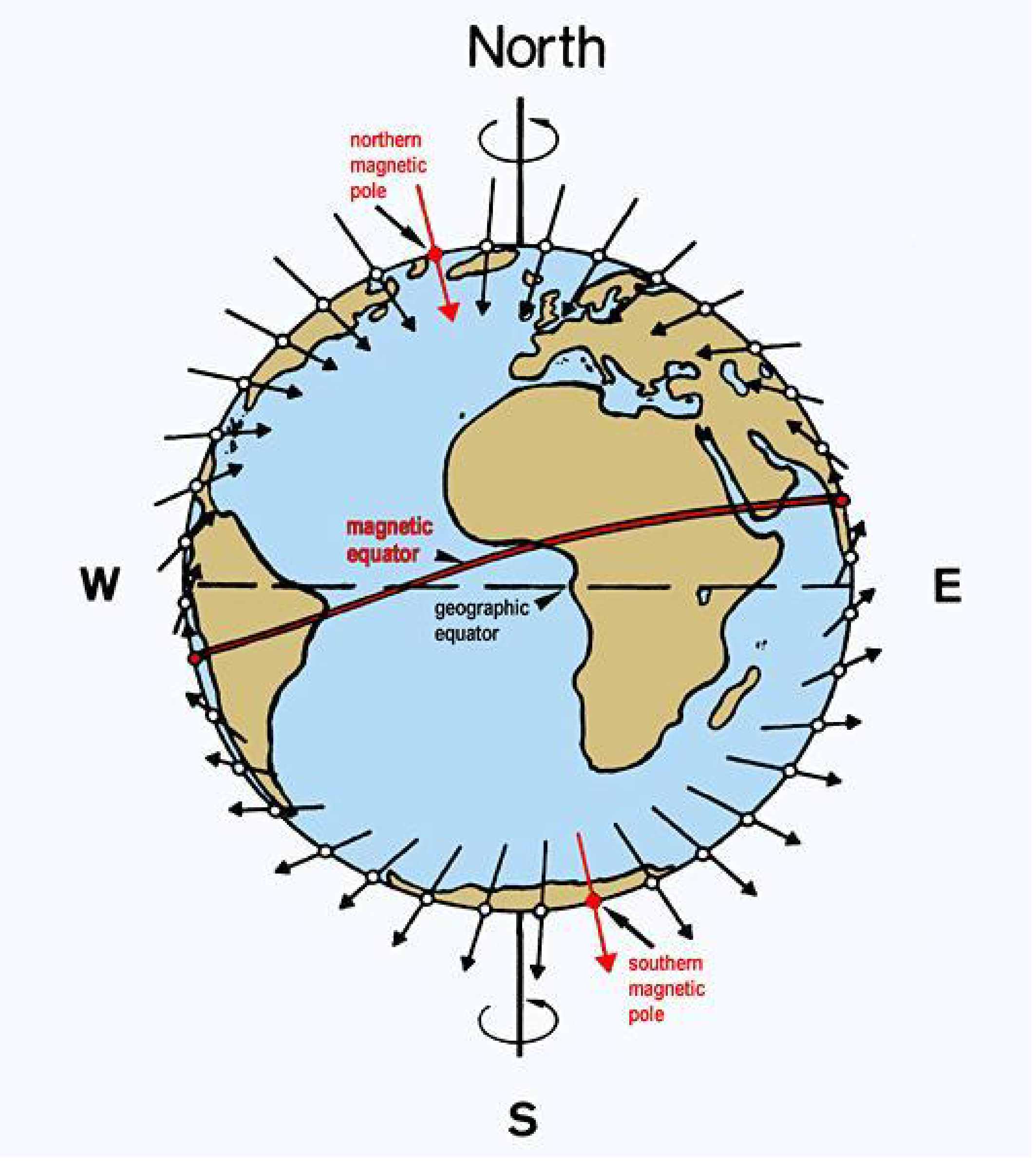
- 'Mosaic map' based on visual landmarks
- Magnetic map
- Olfactory bi-gradient map

The concept of ‘Mosaic Map’ based on familiar landmarks

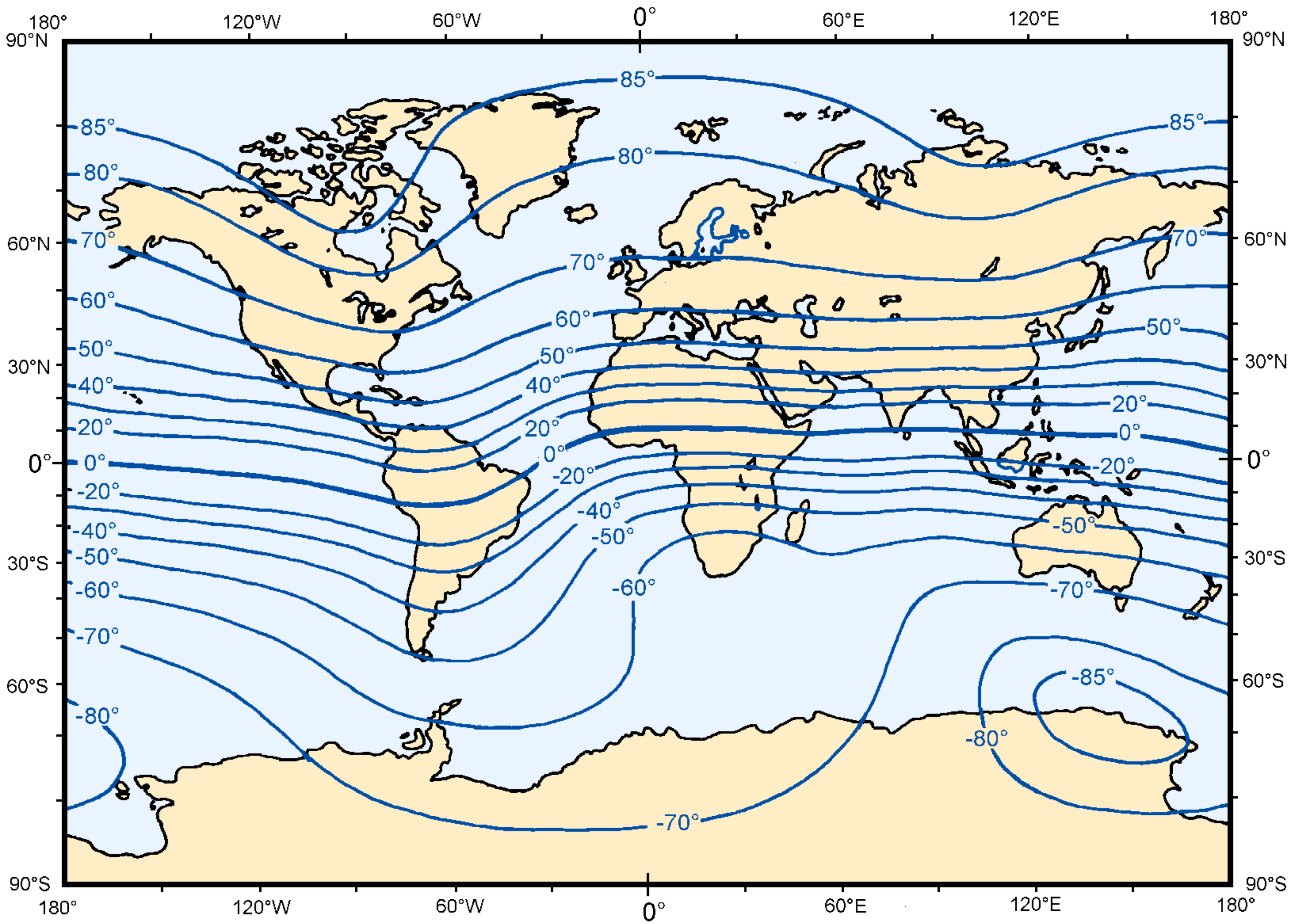


- **Self-triangulation.**
- **Piece-wise map: using different sets of landmarks in different locations (hence `Mosaic`).**

The magnetic field of the earth

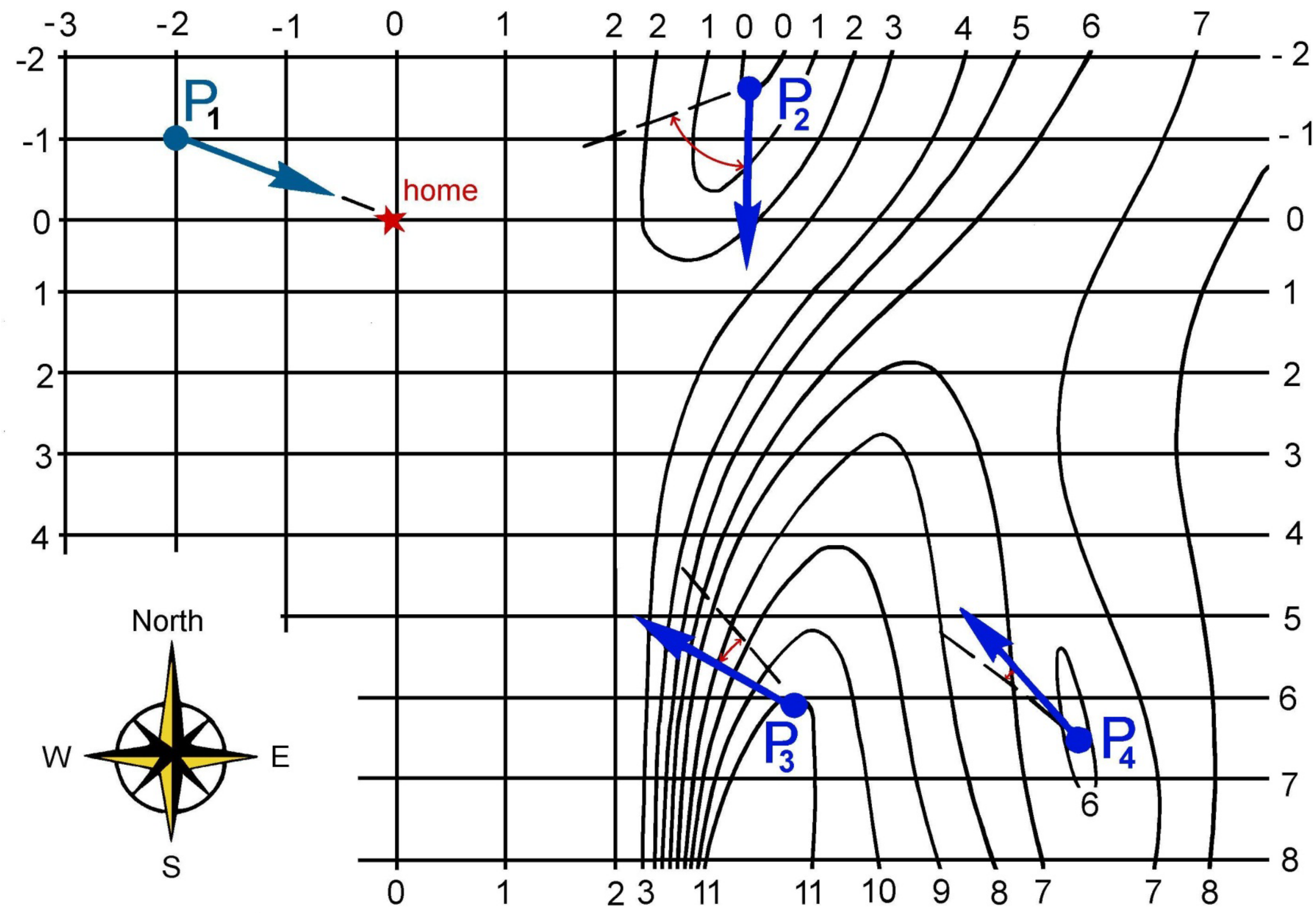


Magnetic Inclination provides information about Latitude



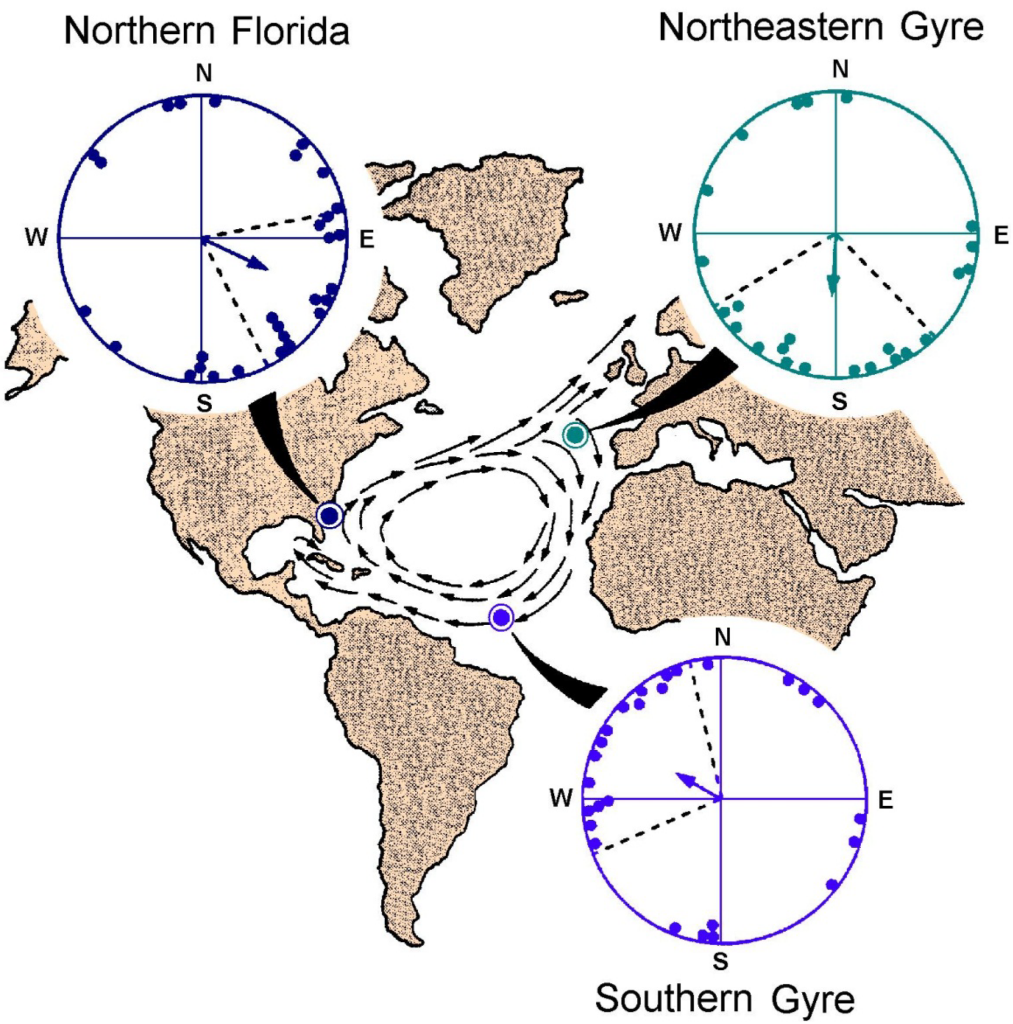
- **Magnetic Declination** (deviation of magnetic north from true north) provides some information about *Longitude* (at least close to the poles).

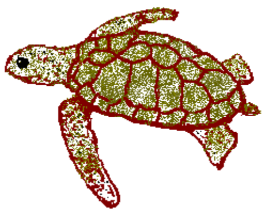
Magnetic Anomalies might provide detailed local map information



Evidence for usage of magnetic map information in sea turtles

Trigger effect in young marine turtles, *Caretta caretta*





- The magnetic conditions in specific areas elicit different directional tendencies.
- Mechanism of magnetic map sensing: unclear. Possibly magnetite crystals.

(Lohmann & Lohmann, Nature 2002)

Questions ?