Introduction to Neuroscience: Behavioral Neuroscience

Animal Navigation:
Behavioral strategies and sensory cues

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Why study animal navigation?

- **Navigation is a higher brain function that is:**
  - **Important for the animal's survival (behaviorally relevant)**
  - **Quantifiable** (spatial accuracy, straightness, time...)
  - **Closely related to learning and memory (spatial memory)**

For this reason, many researchers who are interested more generally in learning and memory, study the case of navigation and spatial memory.

- **A meeting place of the neuroethological and 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**
- **Summary**

- ***Next week: Brain mechanisms of navigation***

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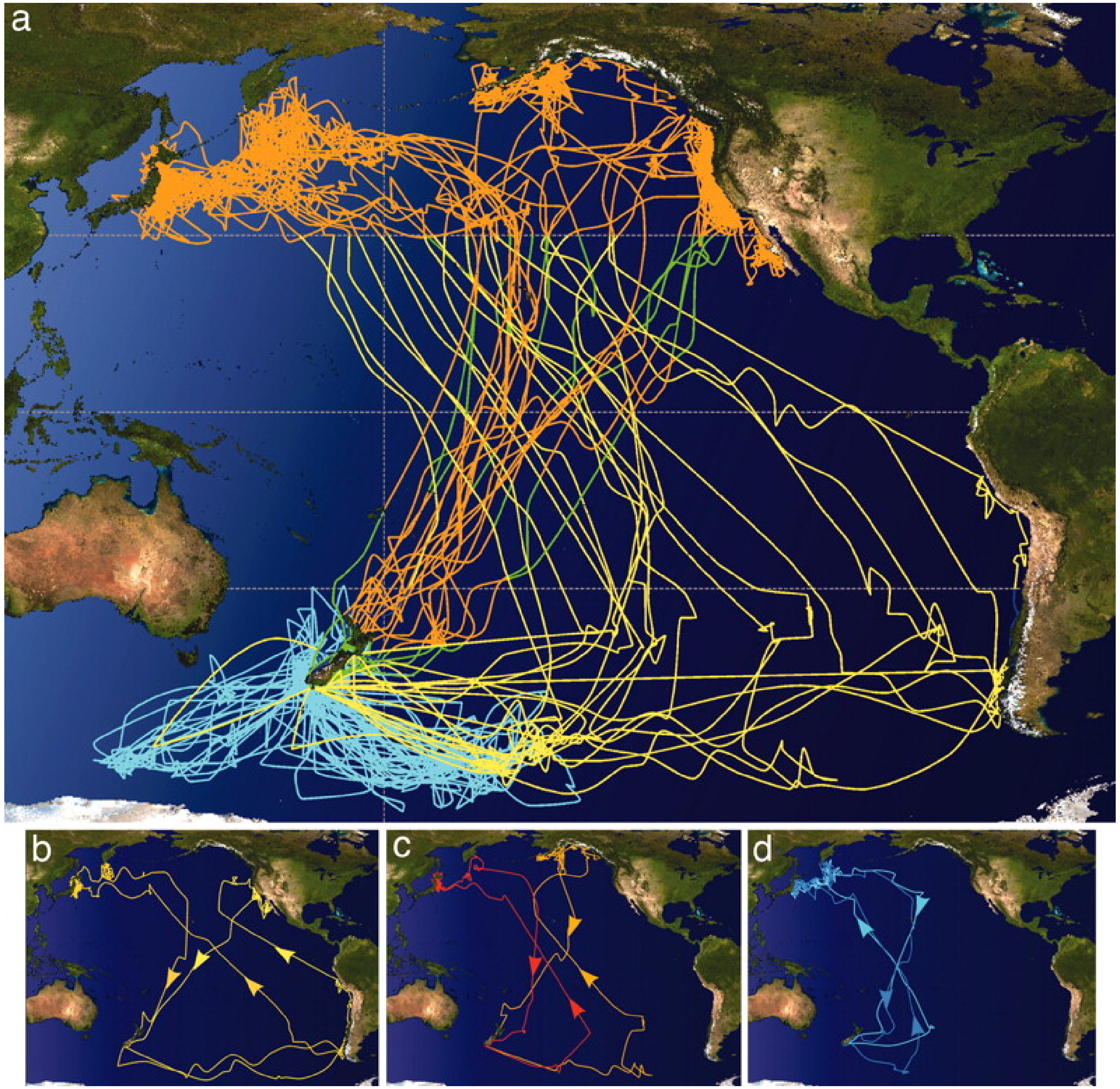
Shearwater migration across the pacific



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

Population data
from 19 birds

←3 pairs of birds

Recaptured at their breeding grounds in New Zealand

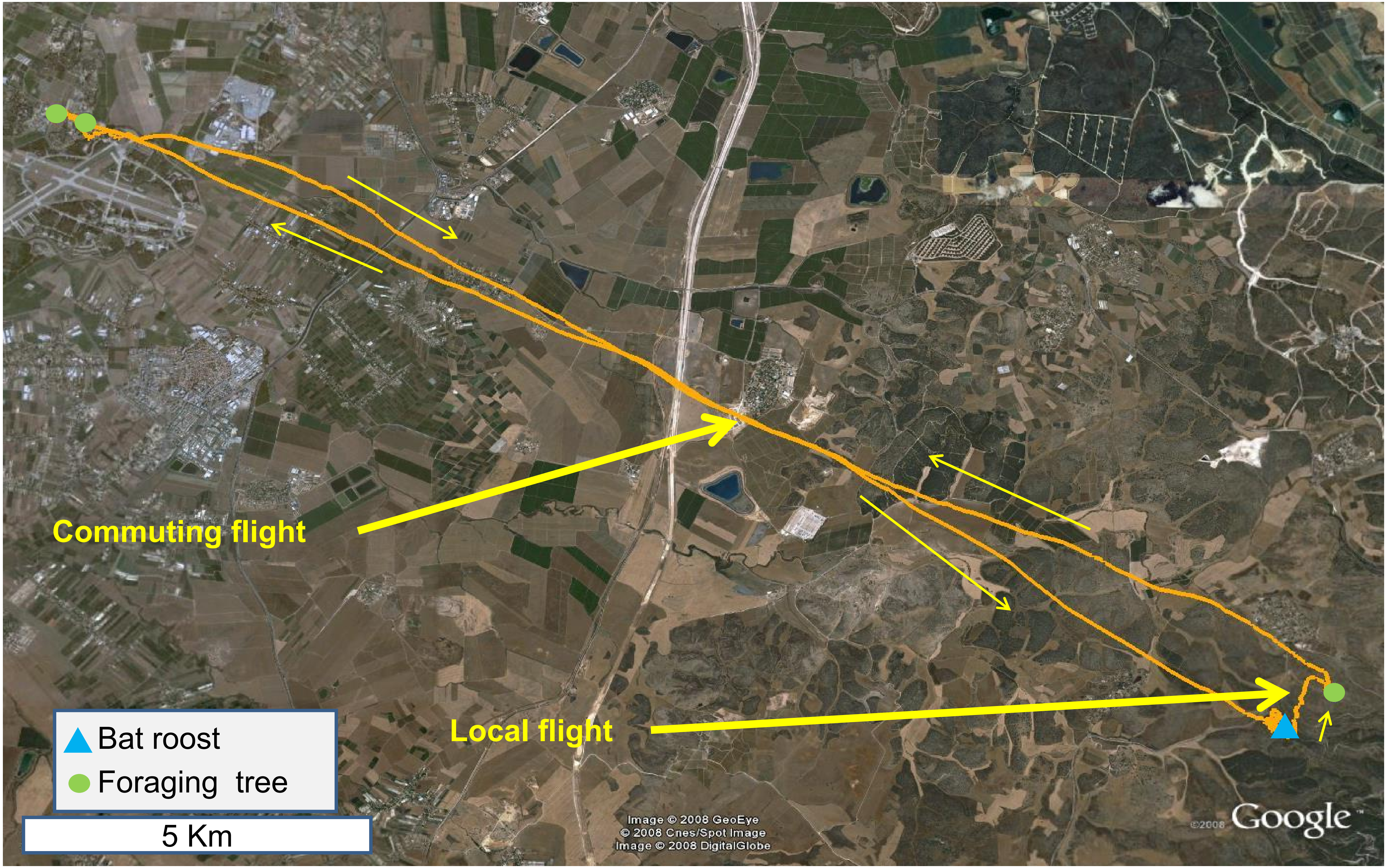
Some other famous examples

- **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

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



Characteristics of the bats' commuting flights:

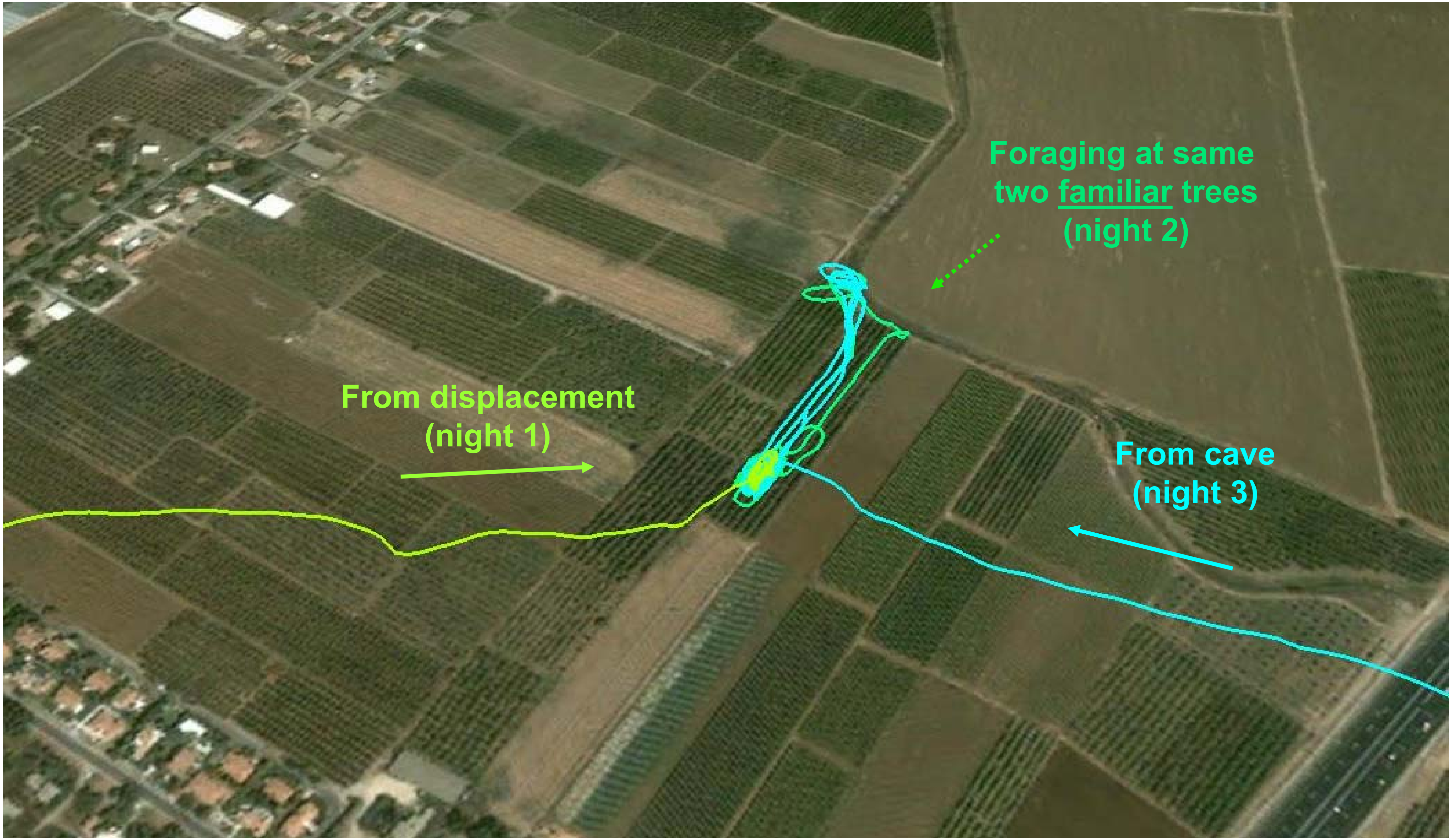
- Medium-distance flights (Typically 10–20 km one-way)
- Very straight flights (straightness index > 0.95 for almost all bats)
- Very fast (typically 30–40 km/hr, and up to 63 km/hr)
- Very high (typically 100–200 meters)
- Bats returned to the same individual tree night after night, for many nights

Tsoar, Nathan, Vyssotski, Dell'Omo, Ulanovsky (in prep)

Homing experiments

Bats displaced 45 km south

Homing experiment – bat #160



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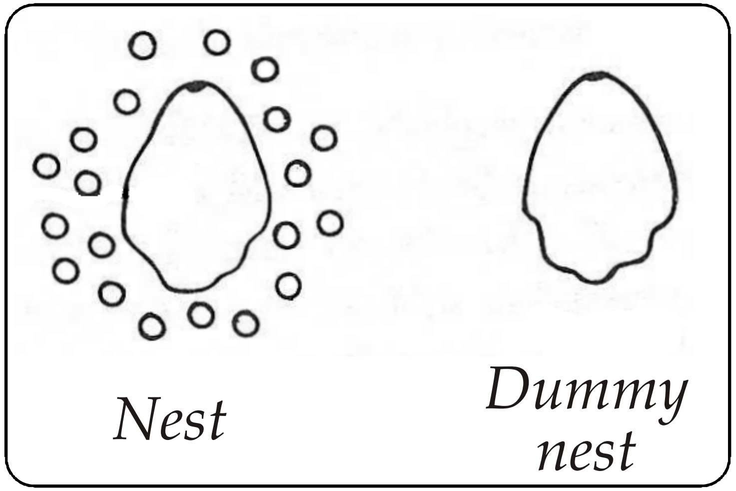
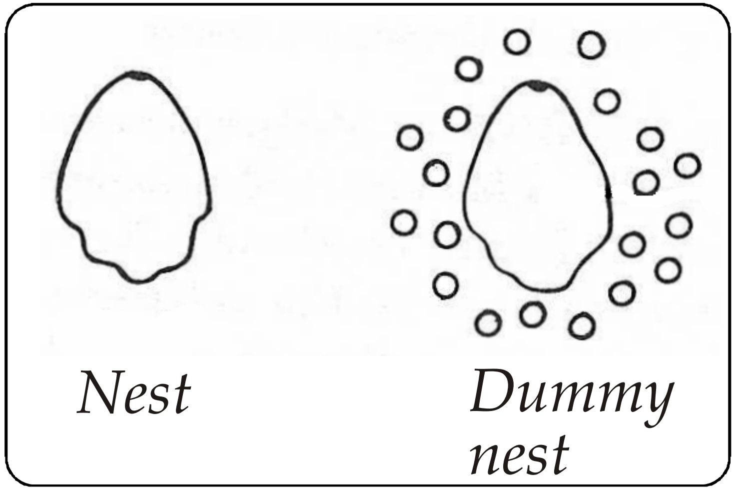
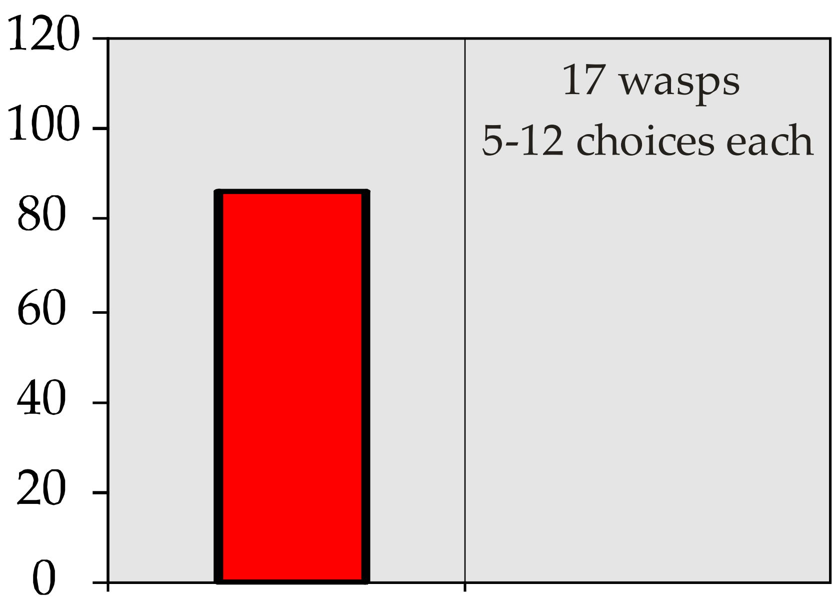
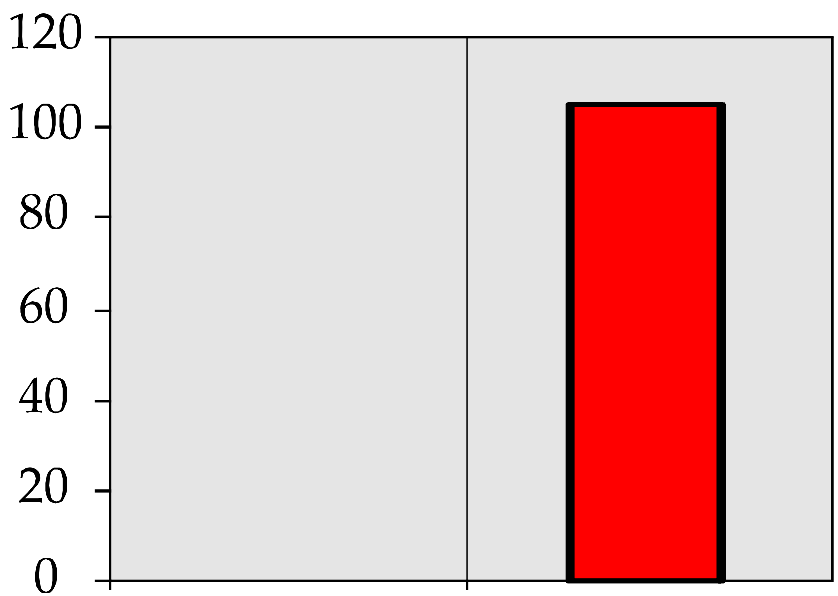
Visual Beaconing in Wasps (Tinbergen)

Beaconing: Navigation towards a directly-perceptible sensory cue.

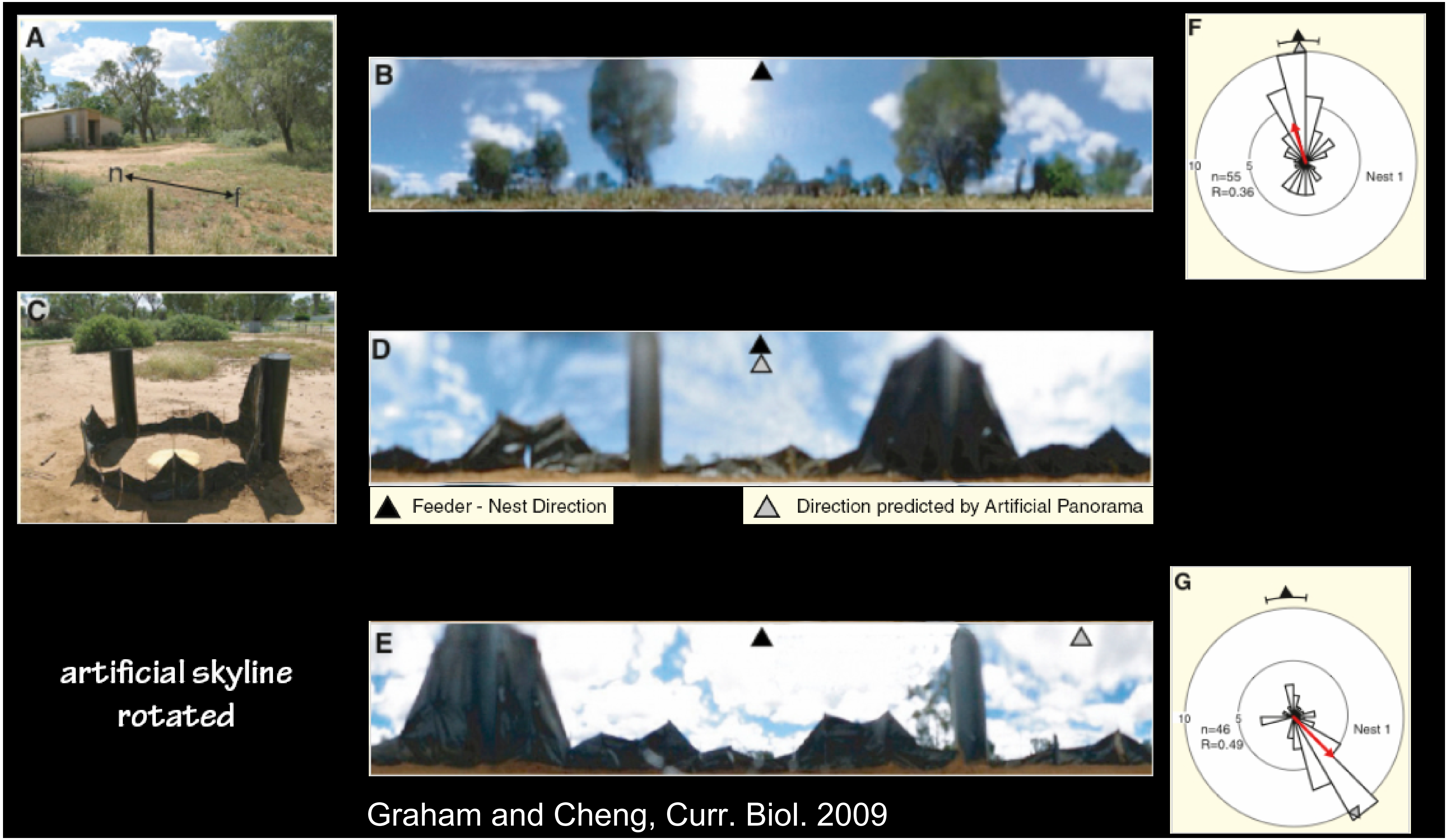






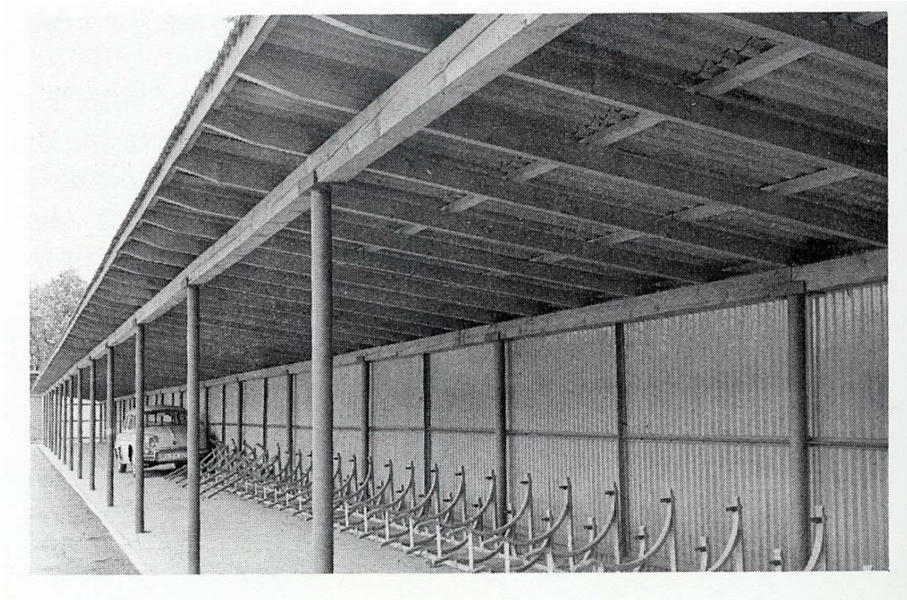


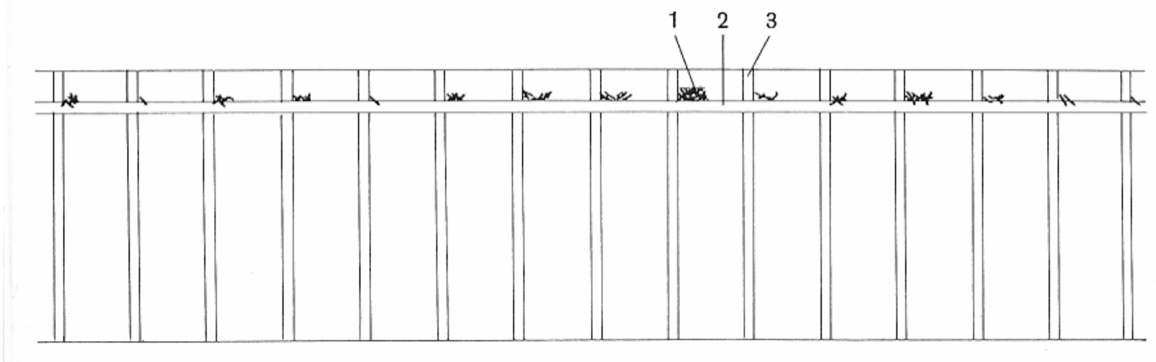
Visual Beaconing in Ants that inhabit cluttered environments

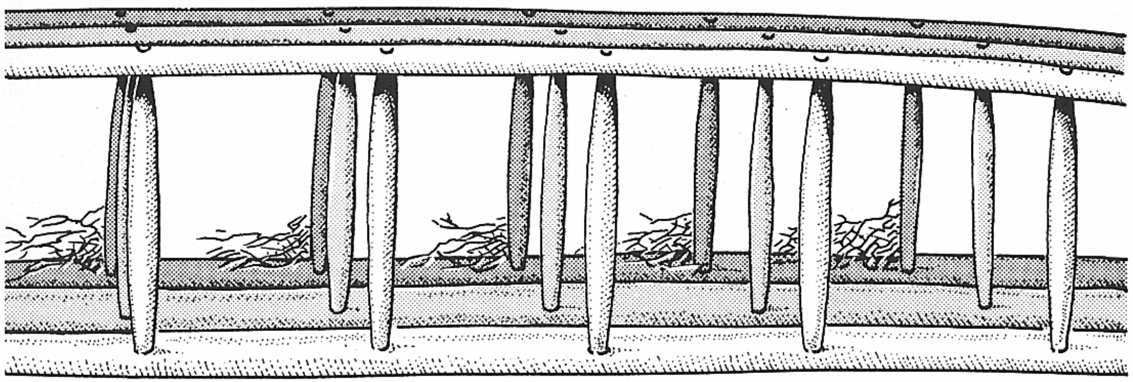


View-based Homing: The problem of visual ambiguity

Extreme example: Repetitive structures. Animals (e.g. birds) have difficulties with repetitive structures in the world.

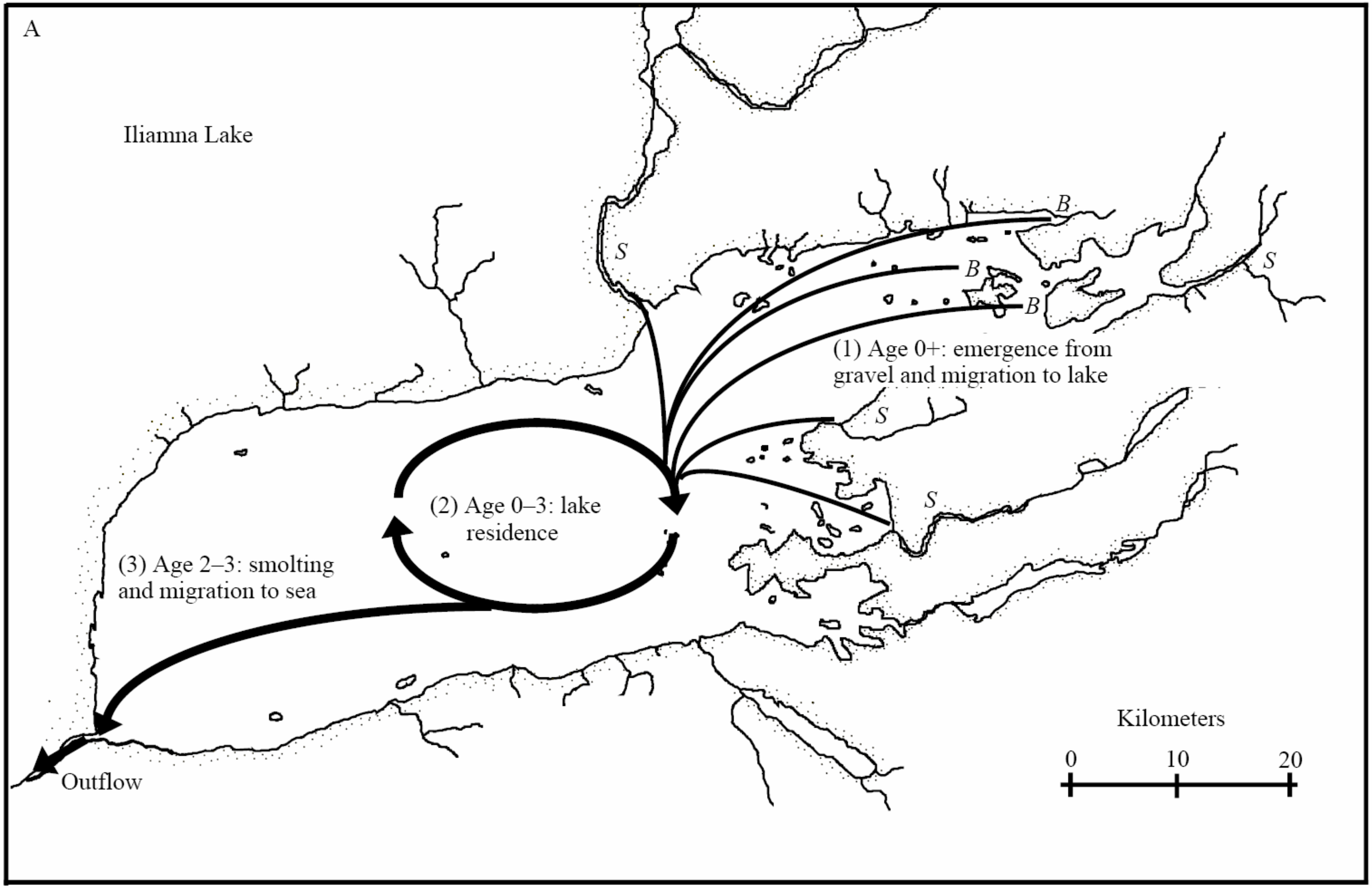






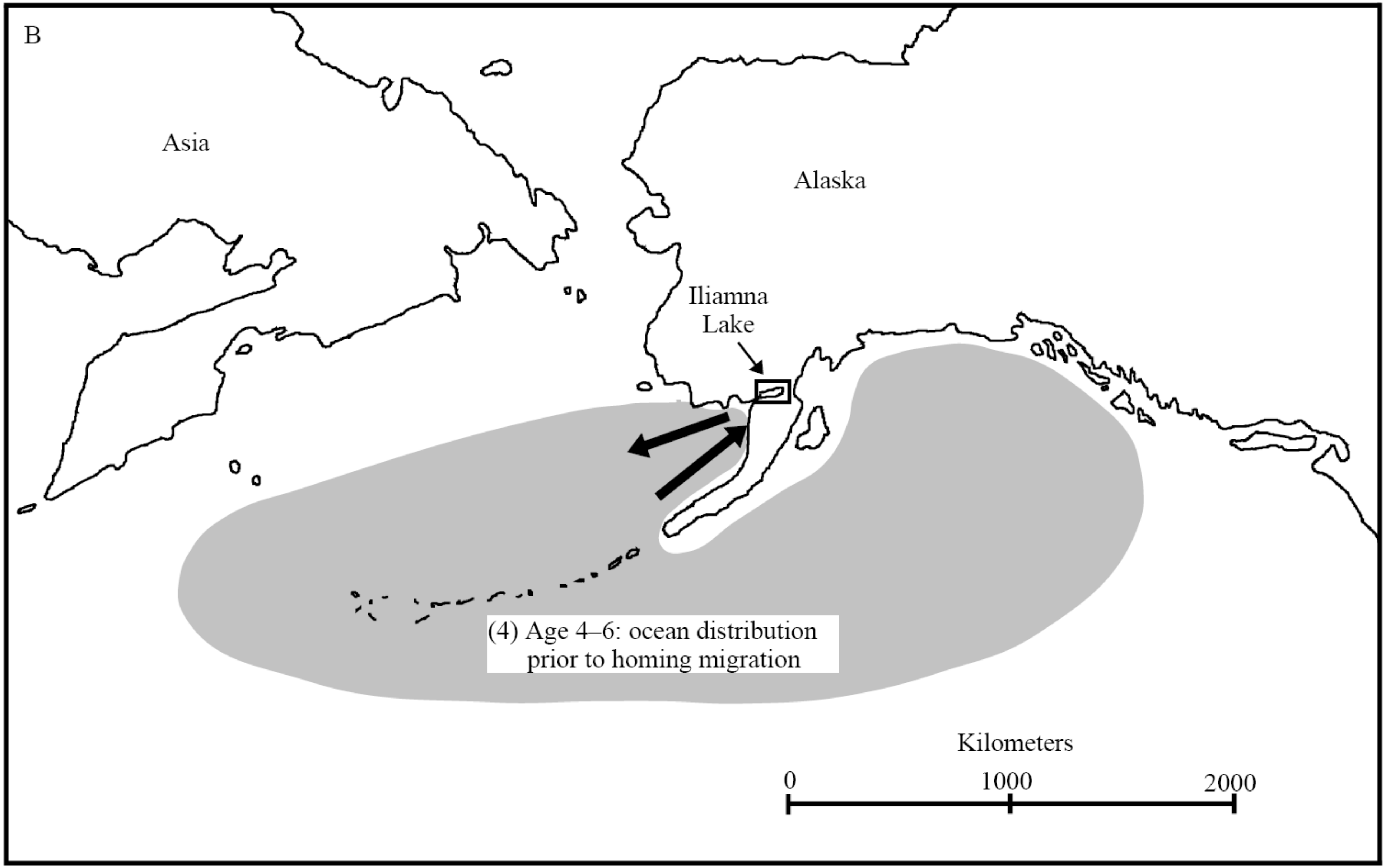
von Frisch K (1974)
Animal Architecture.
Hutchinson, London

Olfactory Beaconing in Pacific Salmon

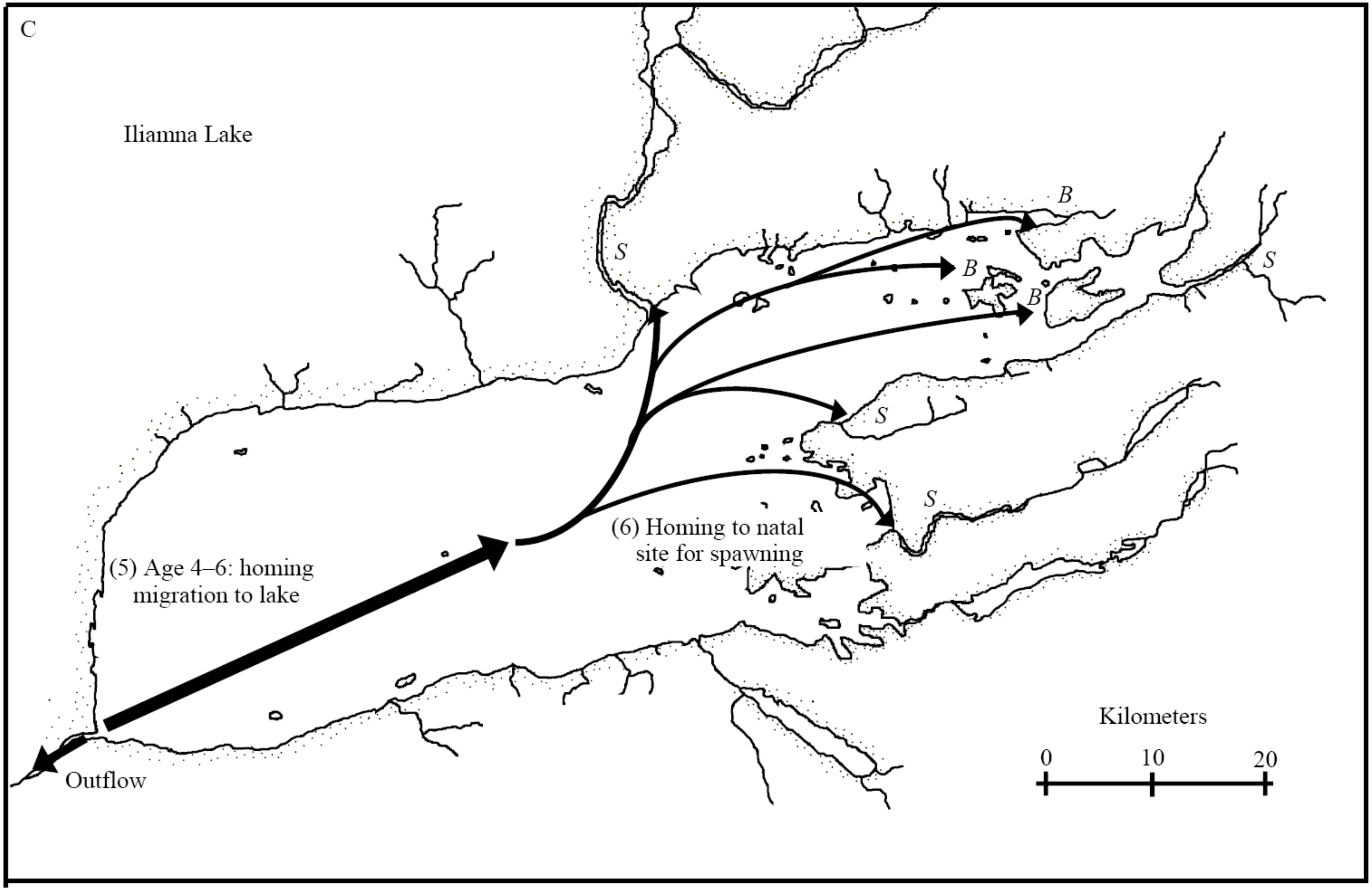


Dittman and Quinn, JEB 1996

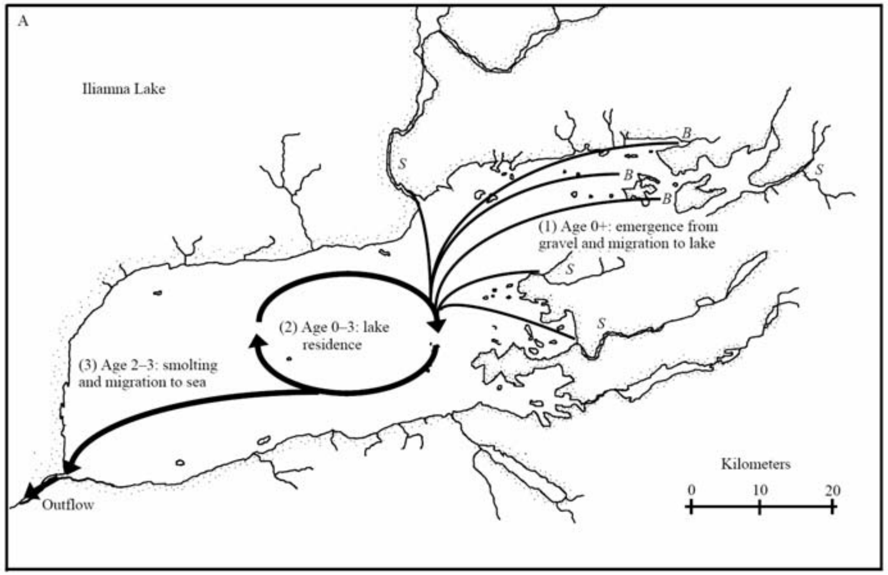
Olfactory Beaconing in Pacific Salmon

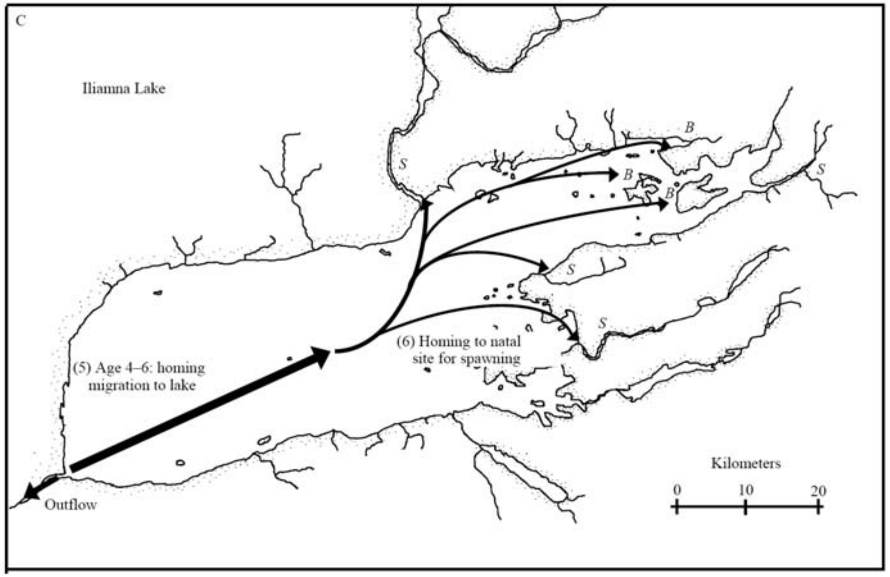


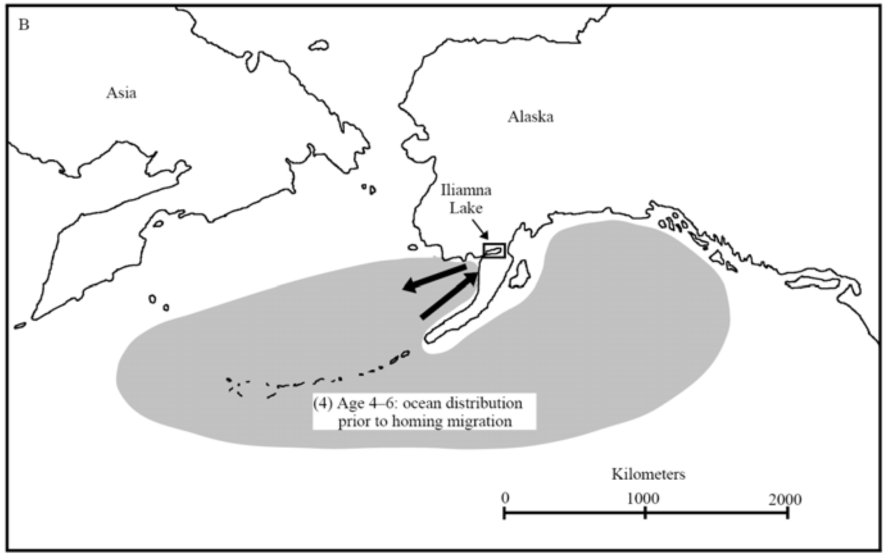
Olfactory Beaconing in Pacific Salmon



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 odor with which they were imprinted (in the wild: the odor of their stream).

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Route following (route guidance) in ants

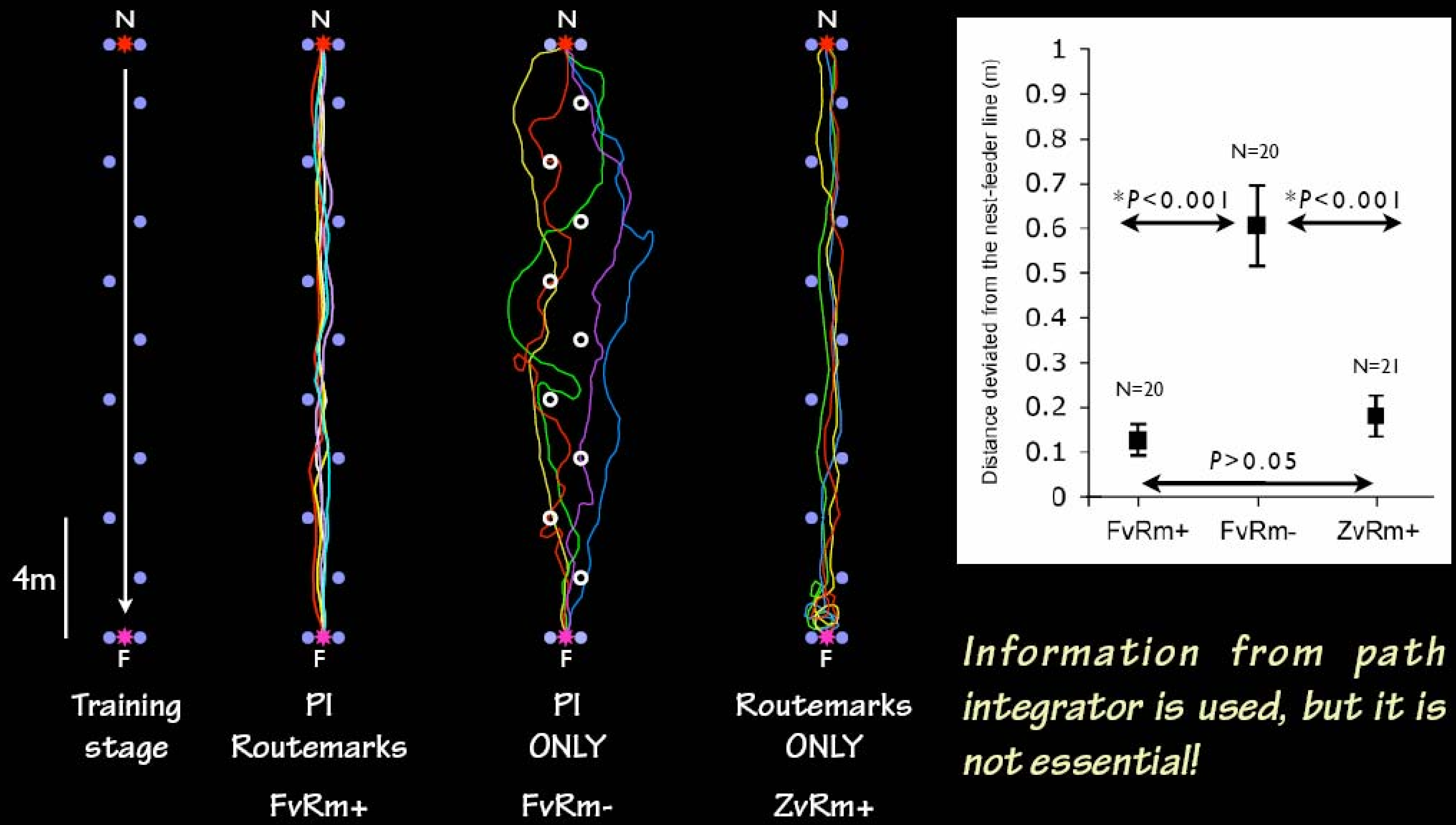
20 m long corridor of 1-m wide with cues at every 2 m interval

cylinder: 60 cm height
:16 cm diameter

Ants trained for 14 days (~300 trials)

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

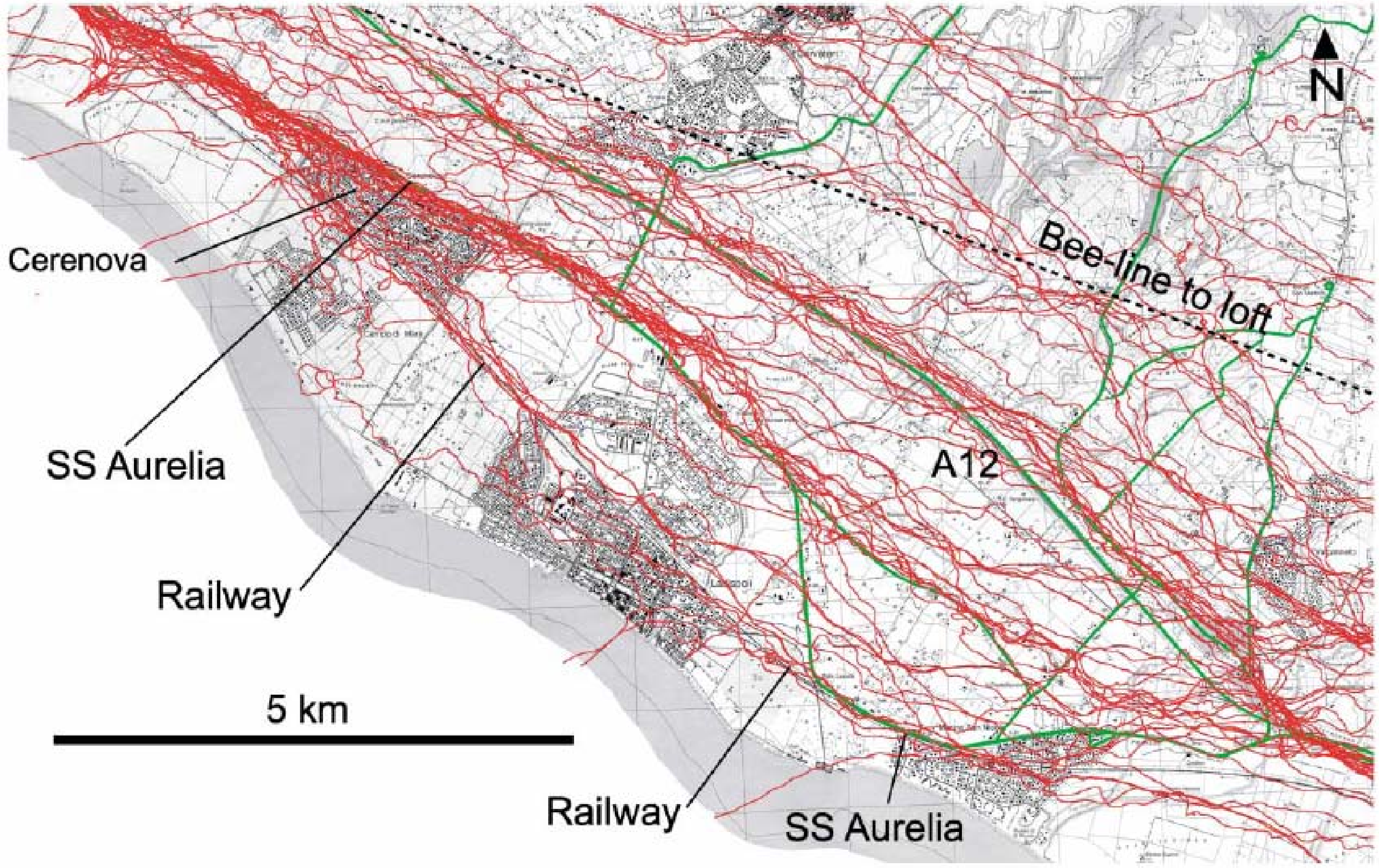
Route following (route guidance) in ants



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

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

Homing Pigeons sometimes follow highways & exits



Lipp et al. (2004)

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Path integration

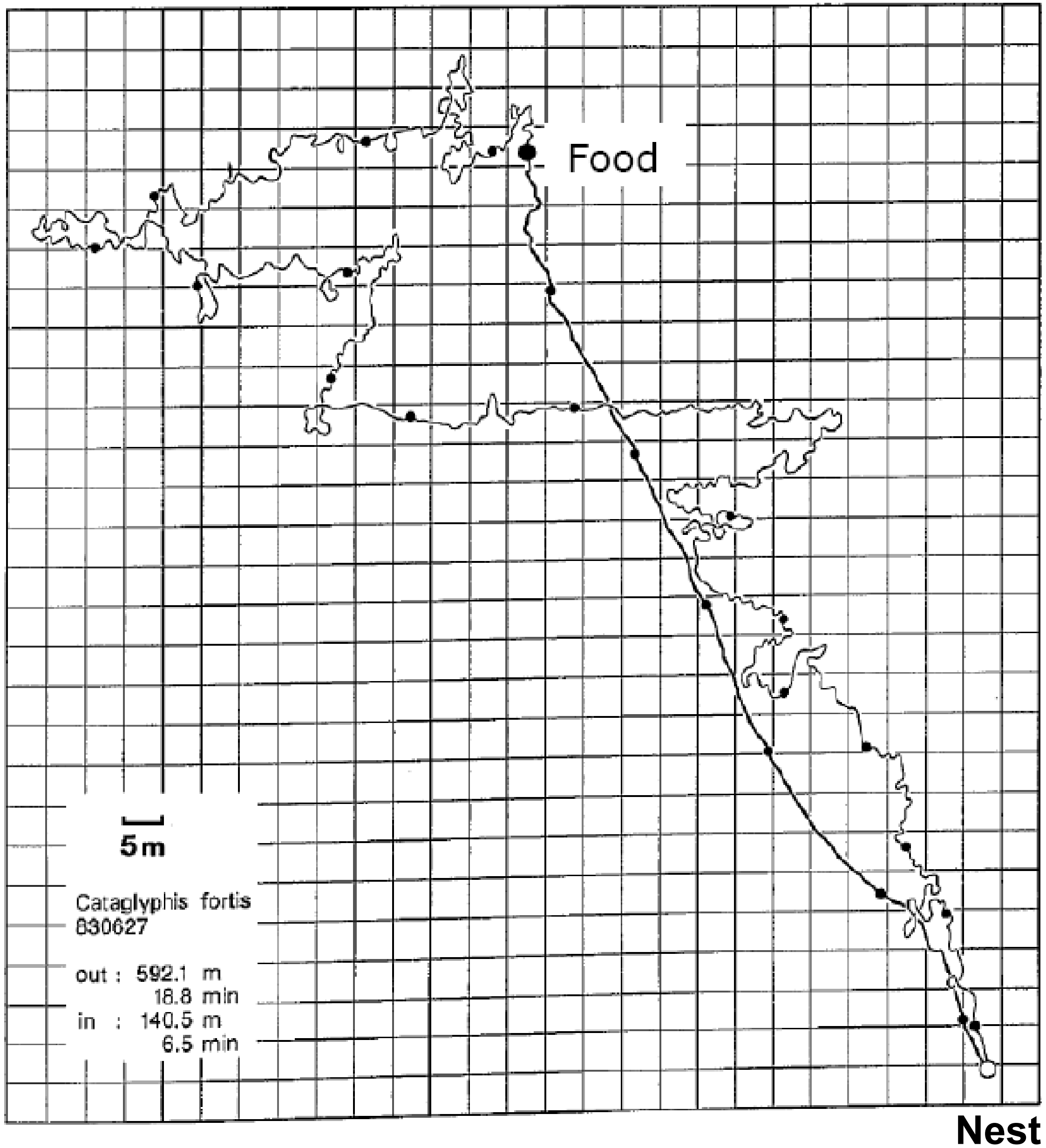
Definition of Path Integration:

"...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
- Requires no landmarks or trails

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



Lives in extremely flat and featureless salt planes in the Sahara

Rudiger Wehner

Outline of a Path Integration system

Distance:
per unit time

Direction
Rotation per
unit time

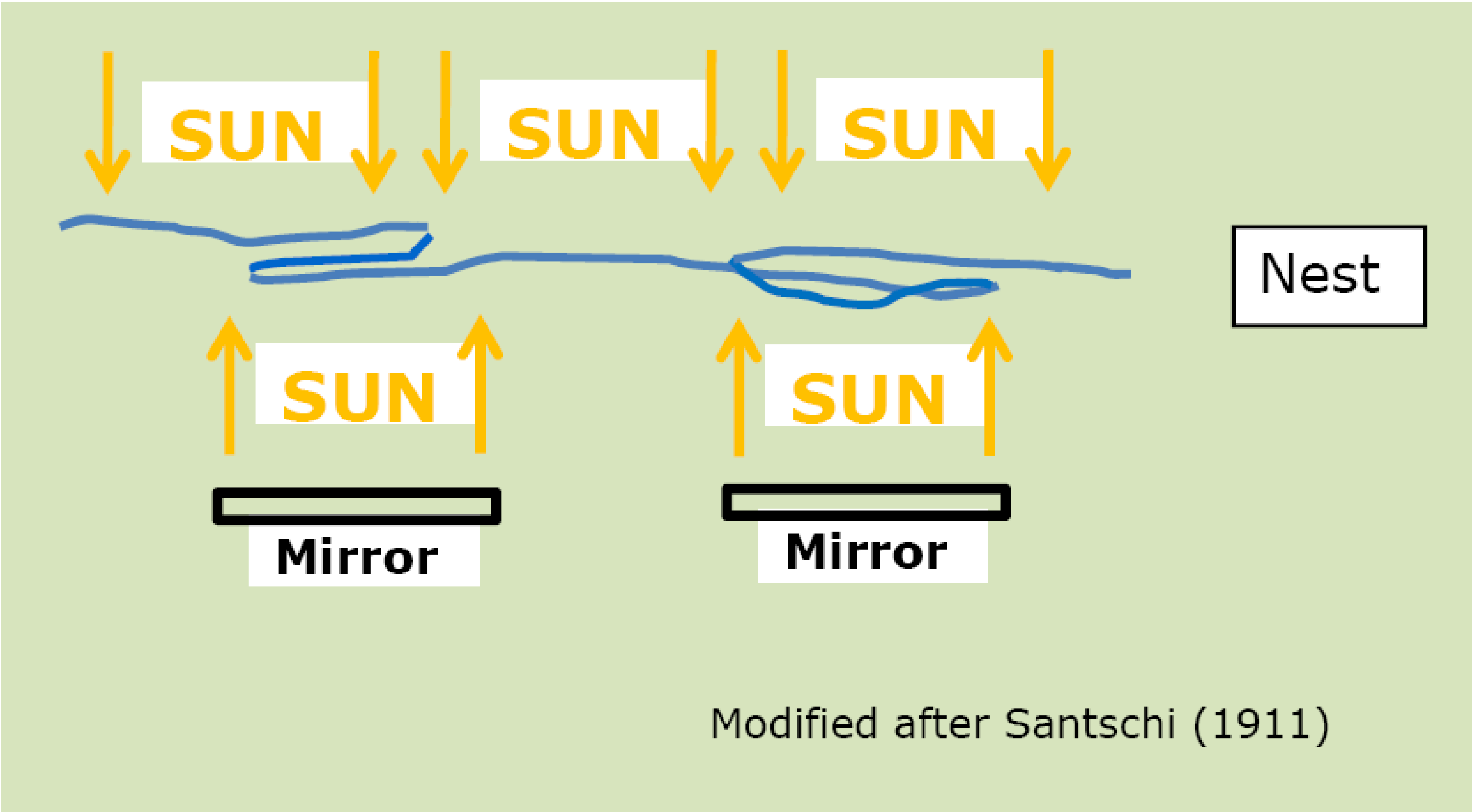
Path Integration system

"Home vector"
(estimated location =
vector relative to home)

Need mechanisms for:

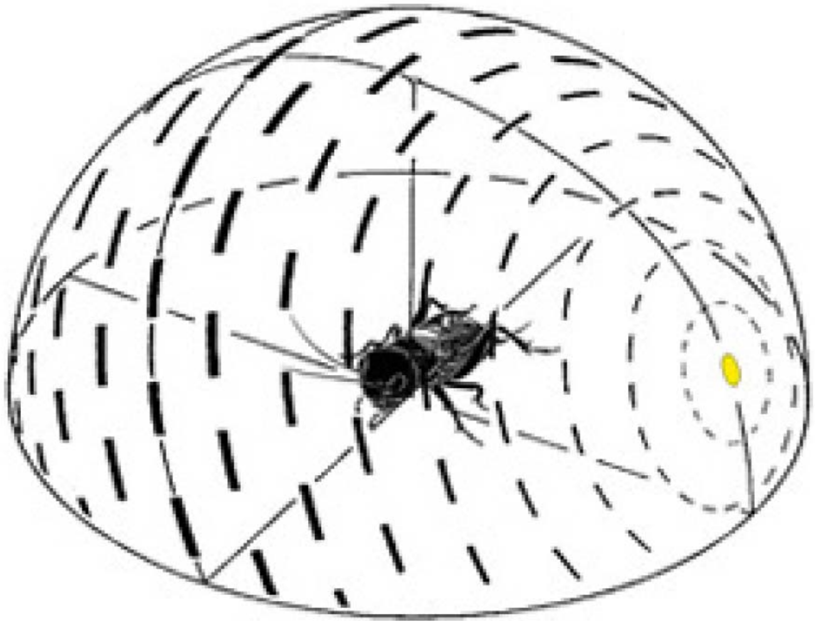
- **Measuring <u>distance</u> (per unit time)**
- **Measuring <u>direction</u> (per unit time)**

Direction cues in desert ants   I: Sun Compass



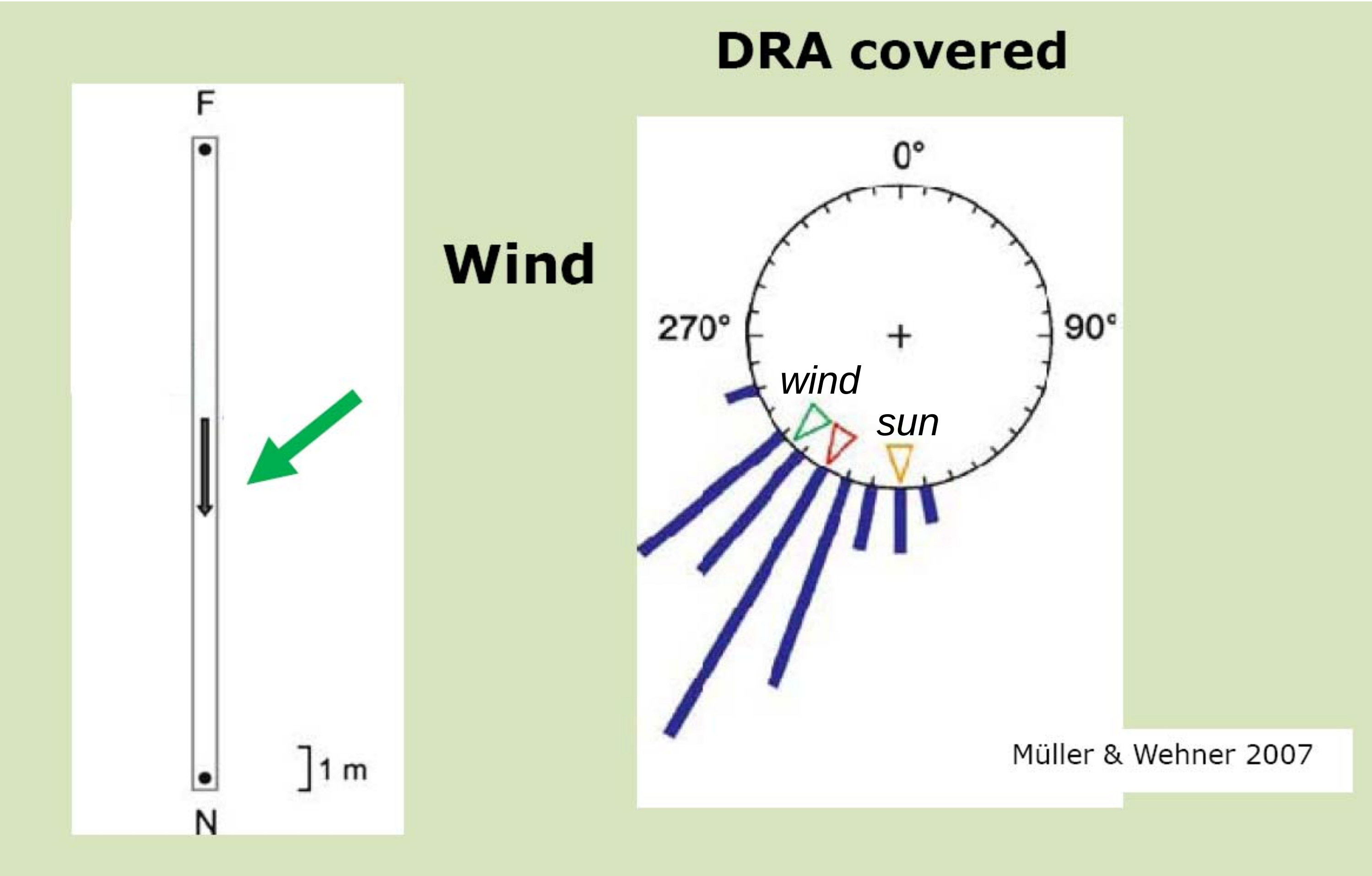
Manipulating the Sun’s direction by using a mirror showed that ants use a <u>sun compass</u>.

Direction cues in desert ants II : Polarization Compass



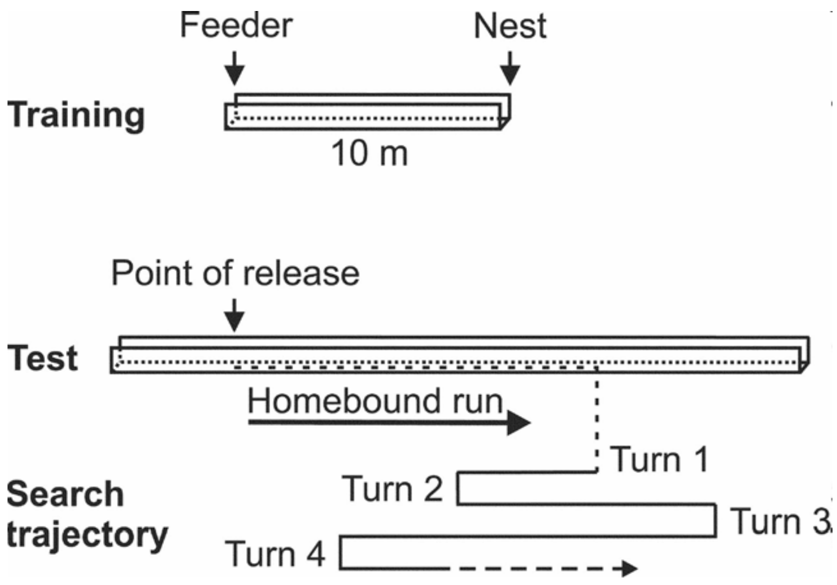
Insects can see the polarization pattern of the sky in the Dorsal Rim Area of their compound eyes. Experiments with rotating polarization filters have shown that desert ants indeed functionally use a polarization compass.

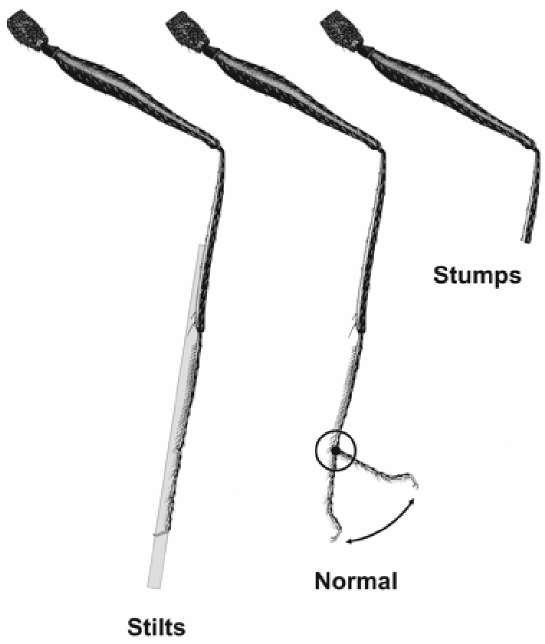
Direction cues in desert ants III : Wind

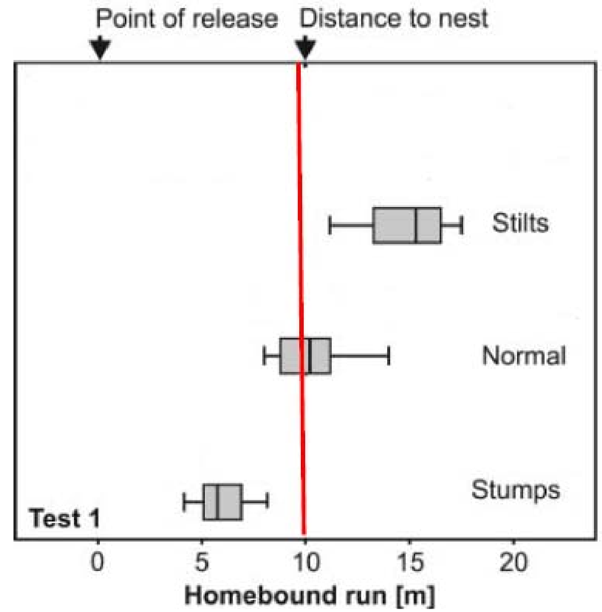


When sun and polarization directional cues are unavailable, the desert ant uses a wind compass.

Distance measurement (odometer) in desert ants: Step Counter







Wittlinger et al., *Science* (2006)

Measuring <u>distance (“odometer”</u> מד קילומטראז'):

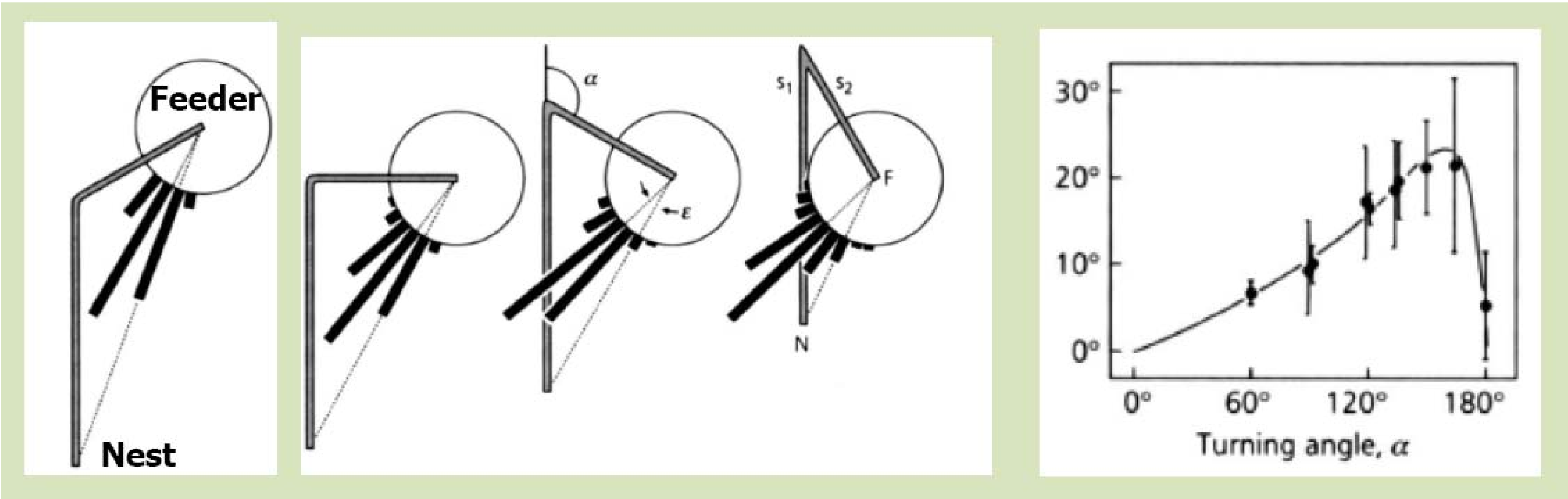
- **In <u>desert ants</u> = <u>step counter</u>**
- **In <u>honeybees</u> = <u>optic flow</u>**

(Srinivasan *et al.*, see in your reading material)

Path integration only in X,Y, not in the third dimension

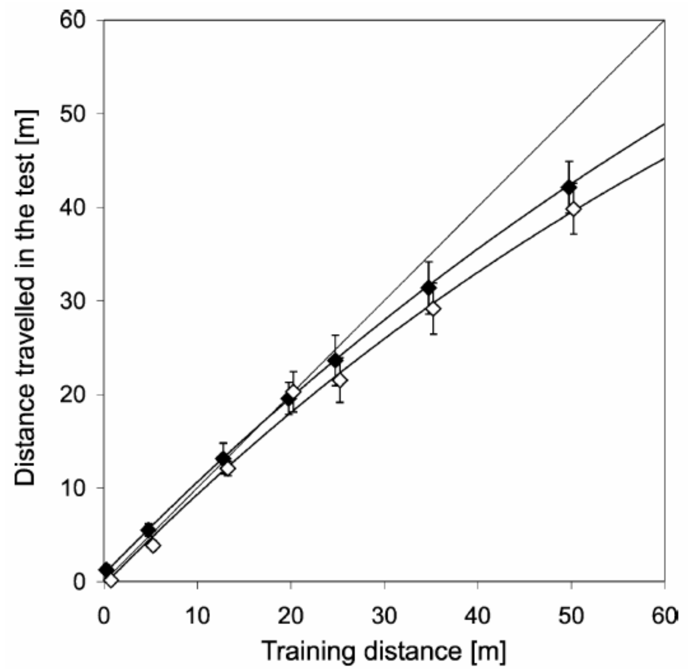
Wohlgemuth et al., *Nature* (2001)

BUT: Path integration is error prone



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

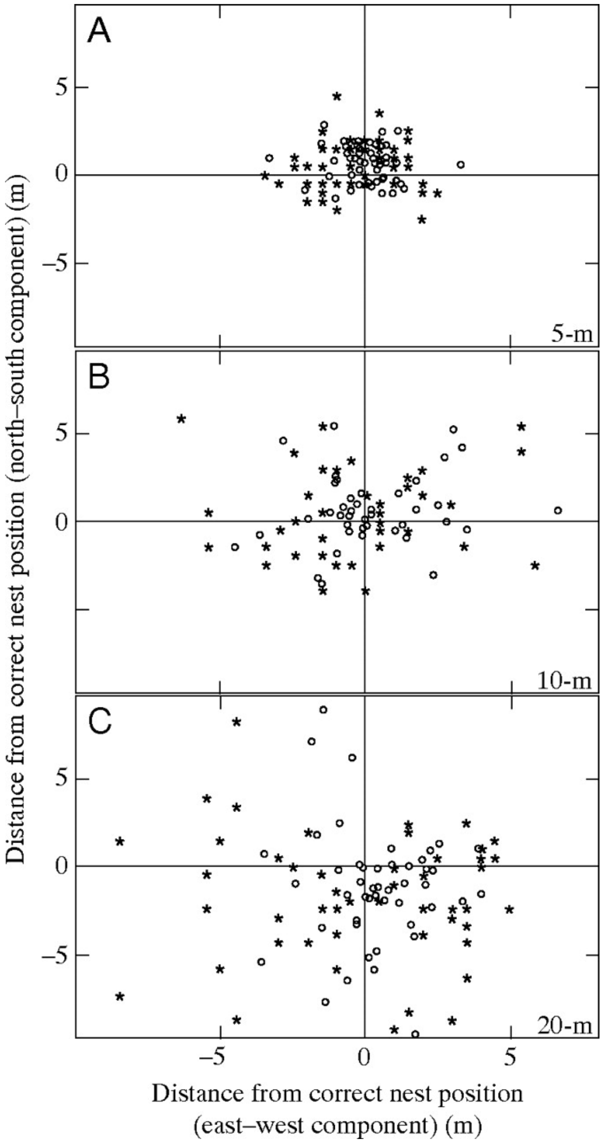
- Random errors sometimes ~ 10° in **direction**

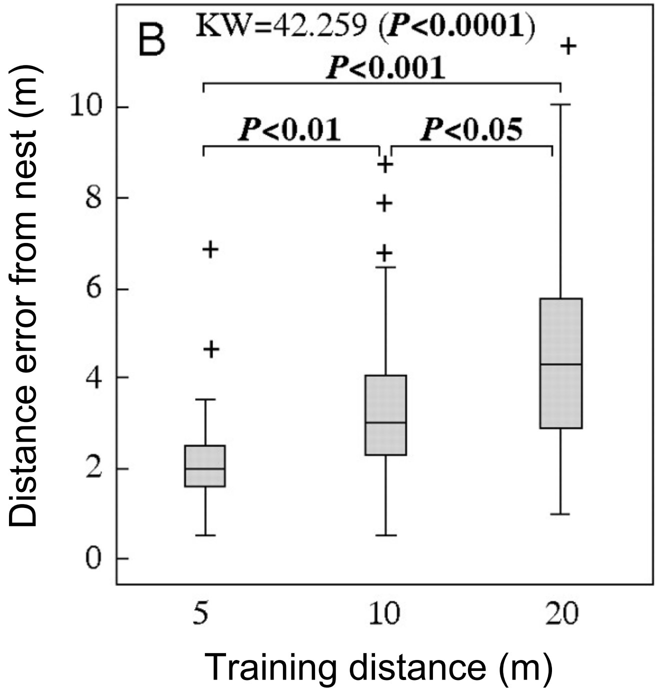


- Systematic errors (underestimation) of ~20% in **distance**
- Random errors (variability) of ~10% in **distance**

Sommer & Wehner (2004)

BUT: Path integration is error prone



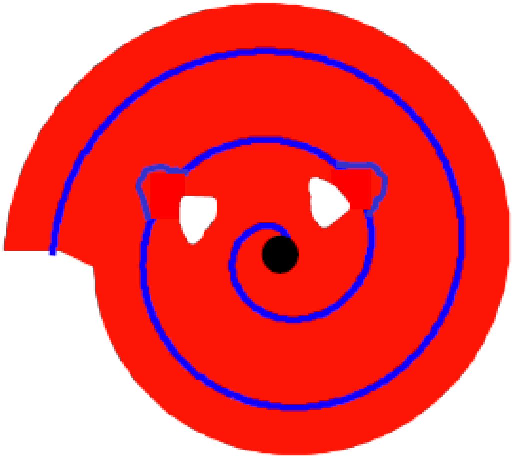


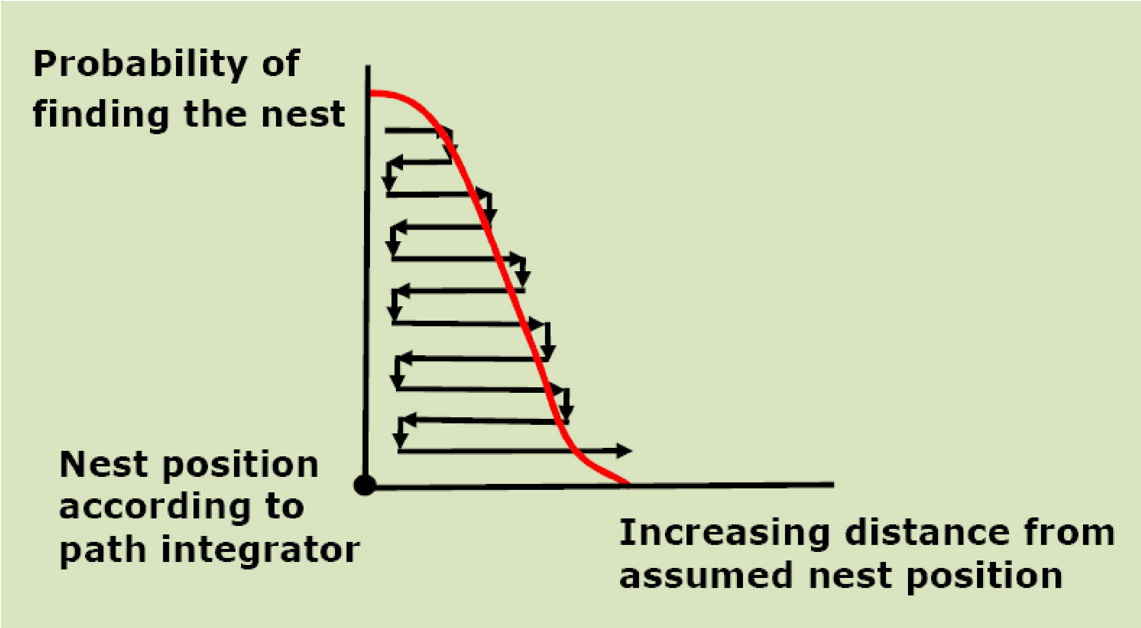
In another experiment:
Random errors of **~25%** in **distance**

Merkle, Knaden, Wehner (2006)

Mammals are less good path integrators that the desert ant. Random errors are even larger in rodents than in the ant (Etienne et al, *Nature* 1998).

Backup strategy in the desert ant: Systematic Search





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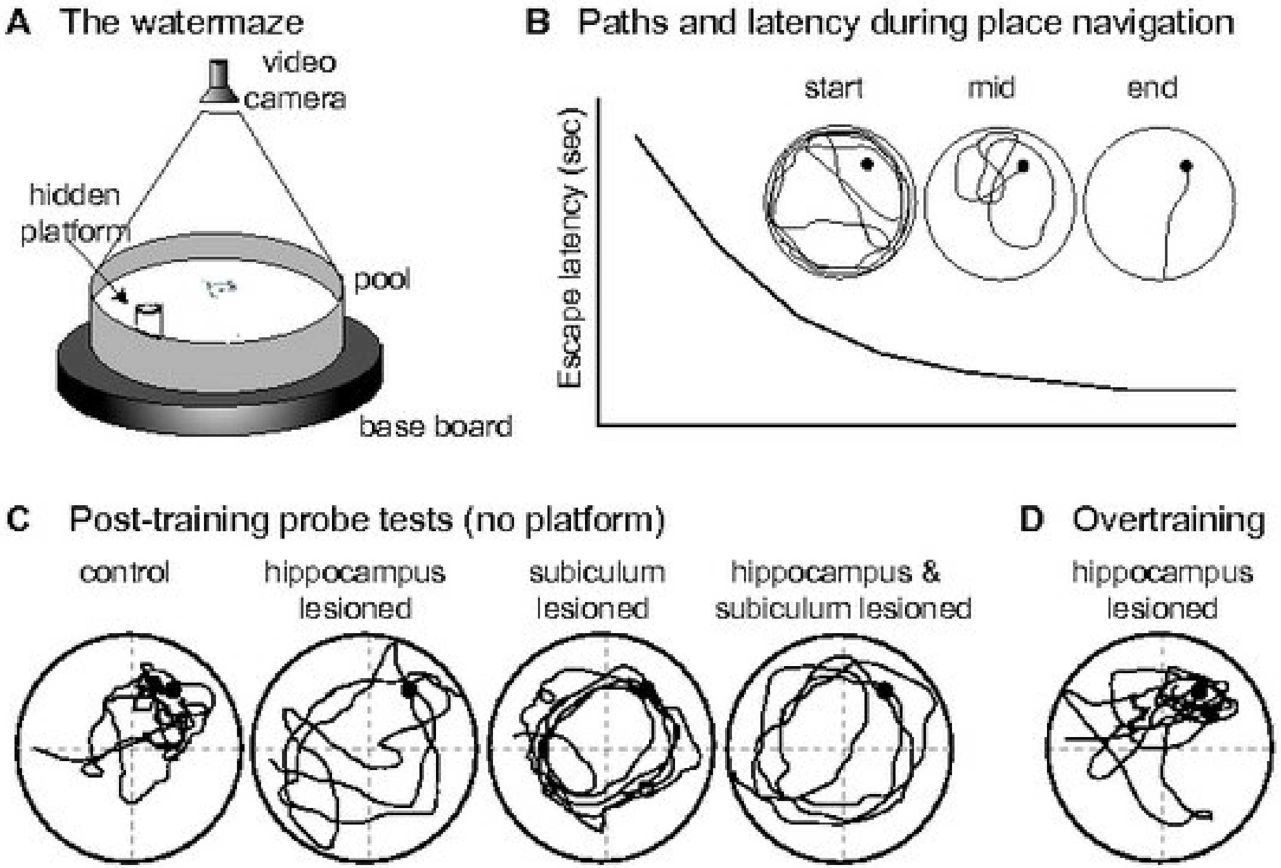
'Cognitive Map' theory (Tolman 1948, O'Keefe & Nadel 1978)



The cognitive map: A concept that arose historically (Tolman 1948) from <u>laboratory</u> work in rats = <u>small</u> scale navigation. The <u>neuropsychological</u> approach.

‘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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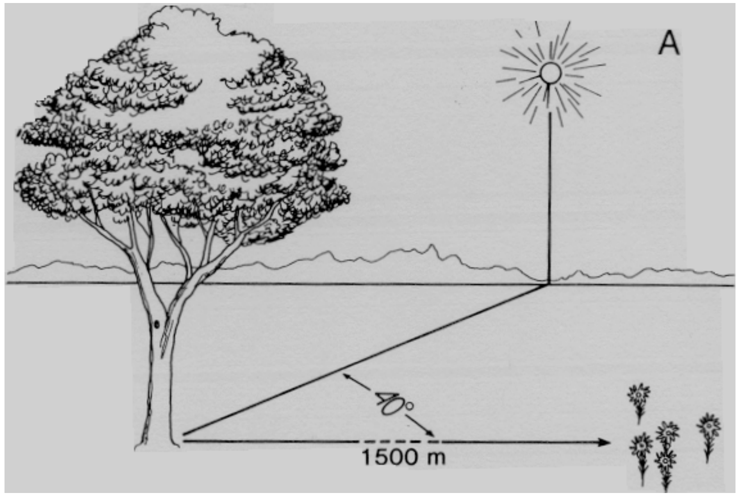
Compass Mechanisms

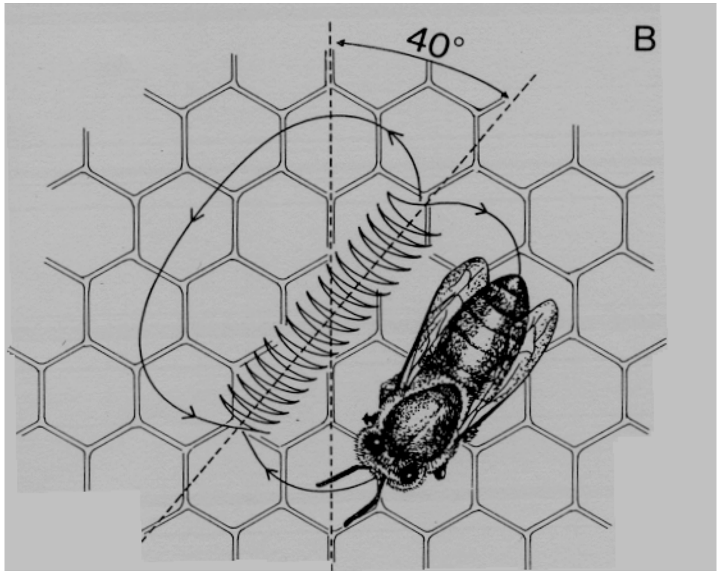
- ‘Compass’ from path integration (integrating vestibular cues: semicircular canals)
- Distal visual cues (e.g. mountains)
- Polarization compass: In insects, and possibly by Vikings (‘sun-stone’, Cordierite?)
- Wind
- Sun
- Waves
- Stars
- Magnetic

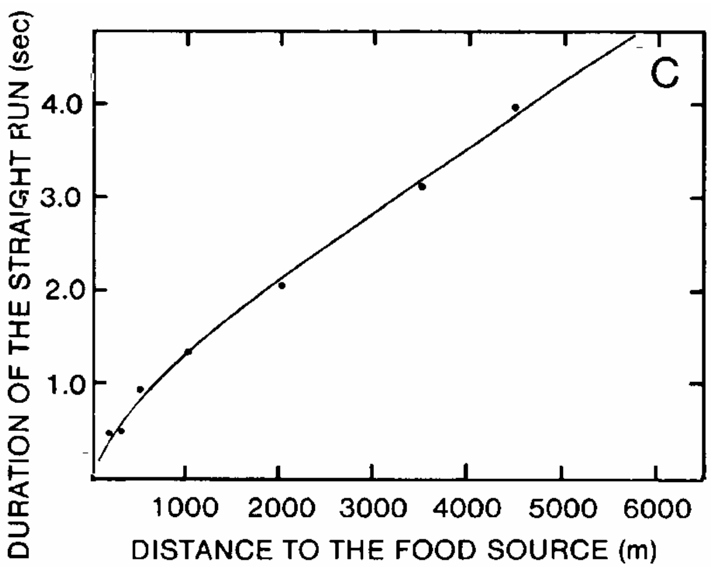
- ... Several others...

Honeybee navigation and the use of the sun compass

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



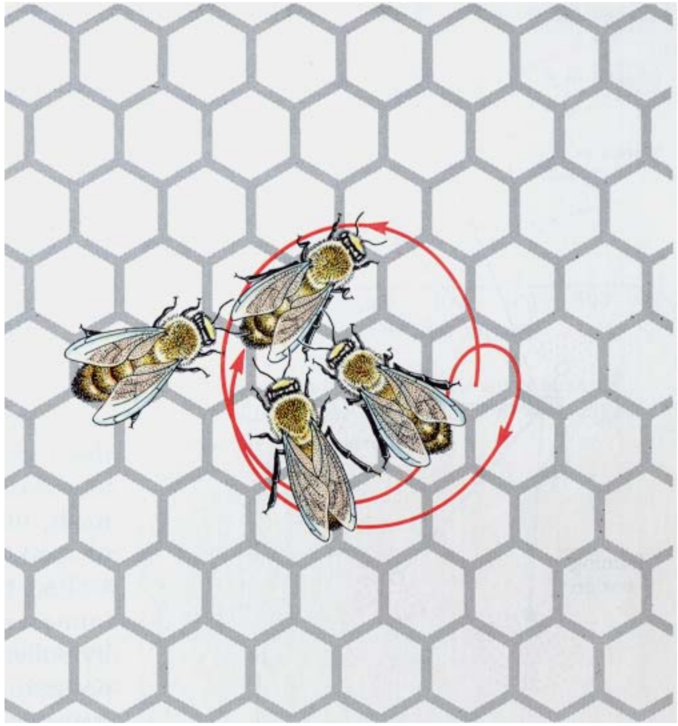




Honeybee navigation and the use of the sun compass

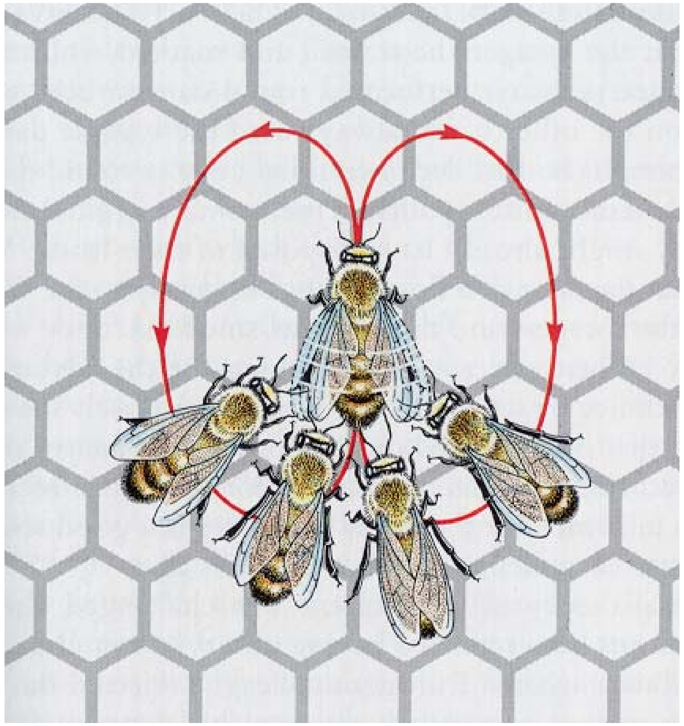
Movie (M. Srinivasan)

Honeybee navigation and the use of the sun compass



Round dance

(feeder distance < 50m)



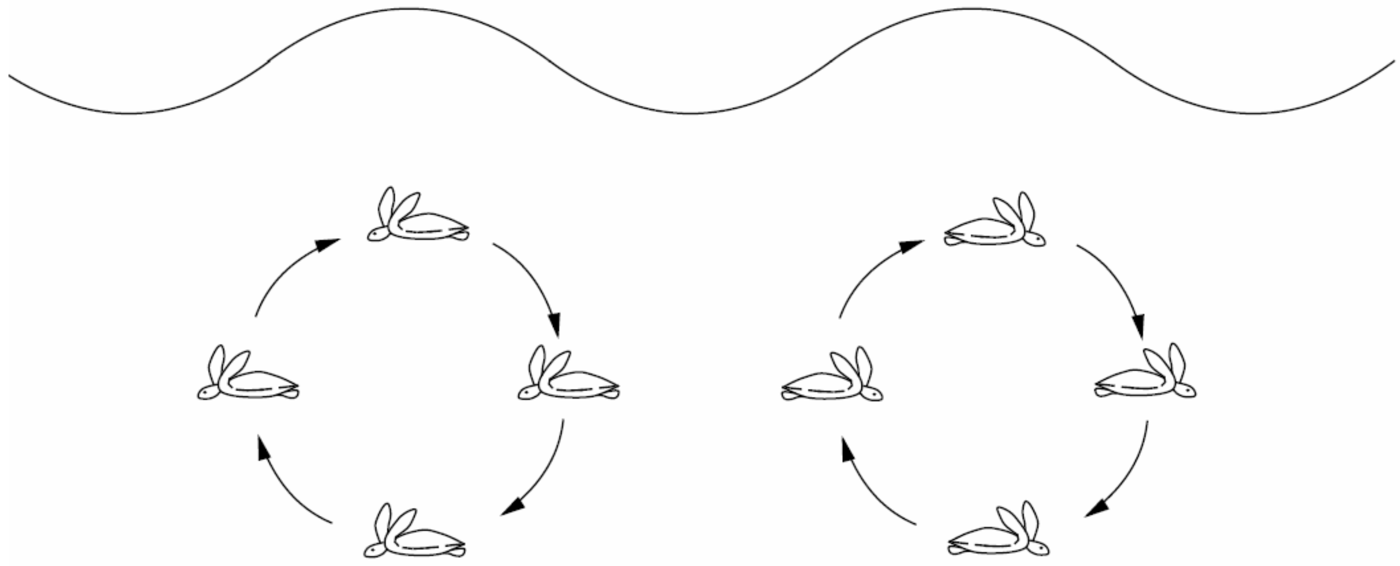
Waggle dance

(feeder distance > 50m)

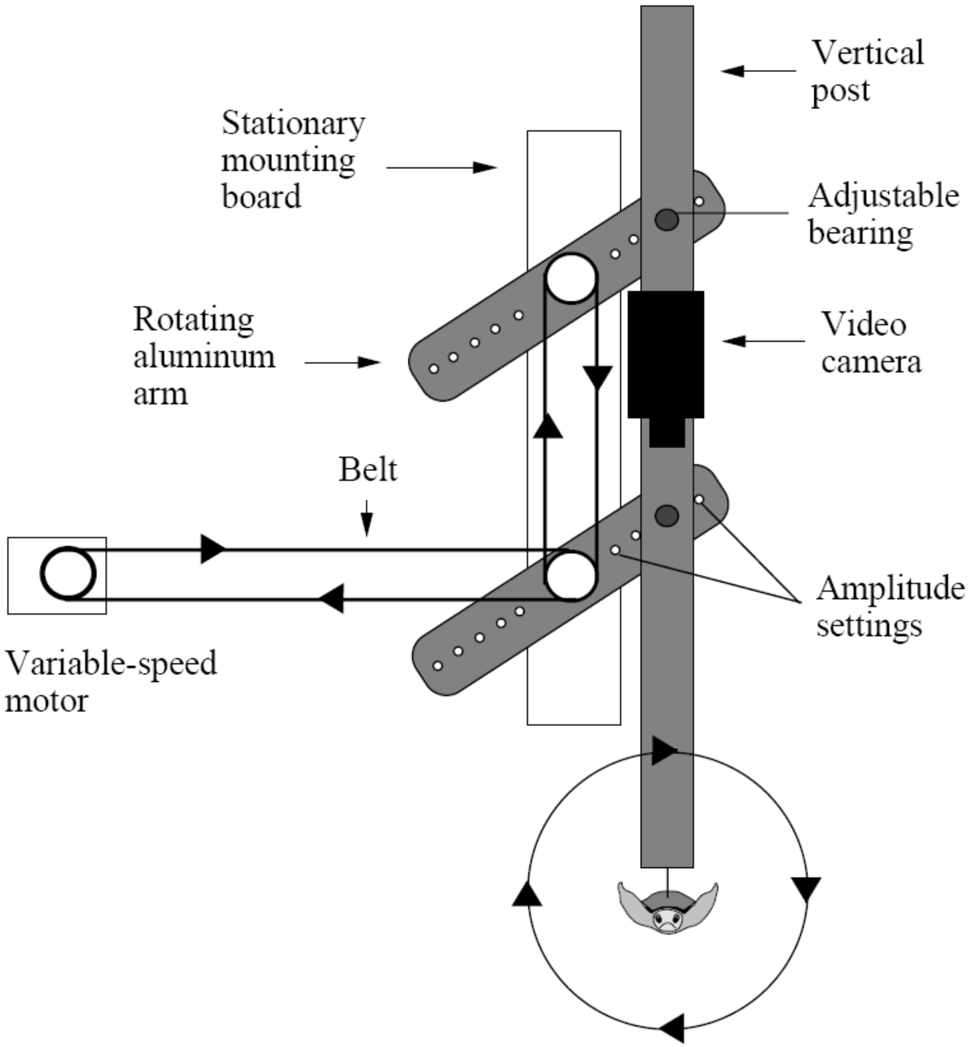
Sea turtle hatchlings use the direction of waves as compass

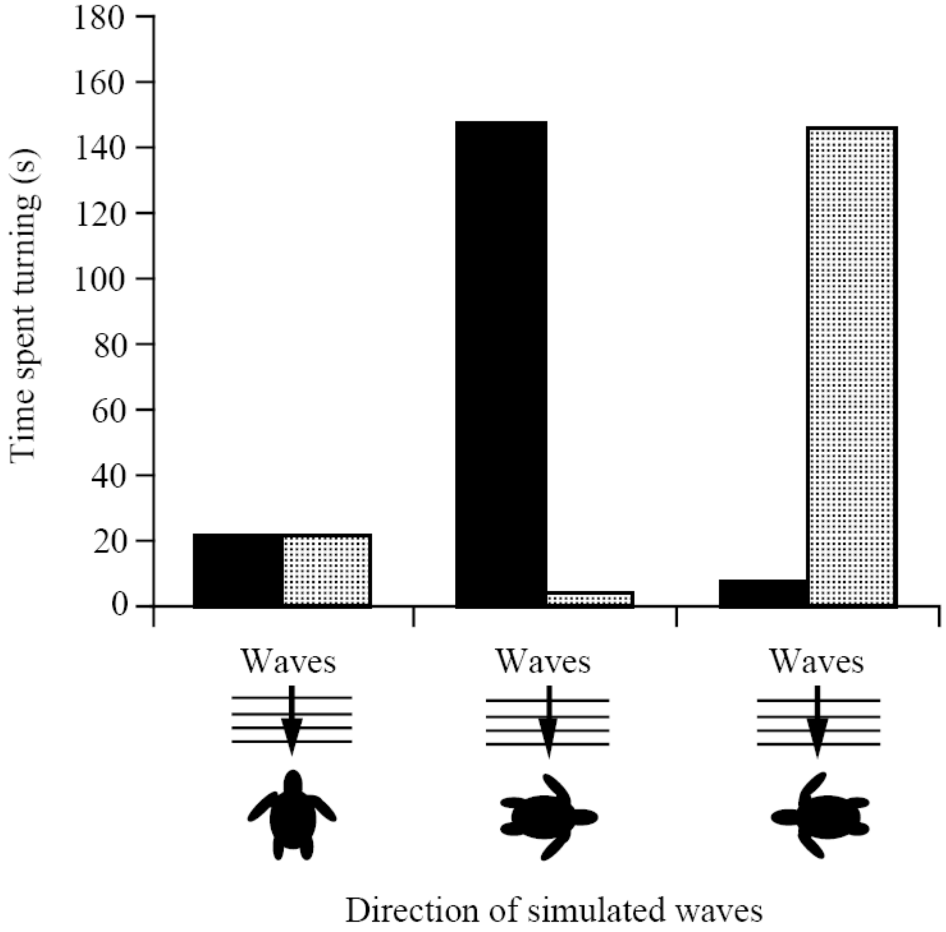
Hypothesis: Hatchling sea turtles use wave direction to keep course into the open sea and away from shore

Wave direction →



Sea turtle hatchlings use the direction of waves as compass



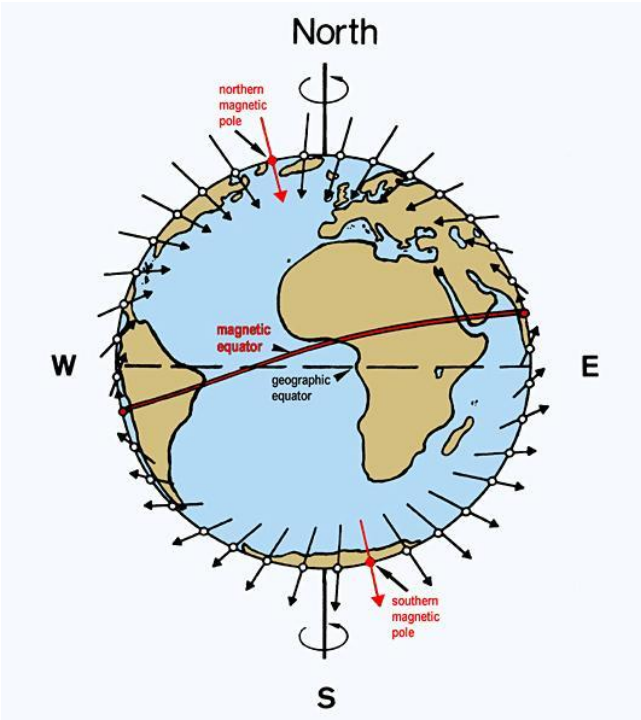


Lohmann and Lohmann (1996)

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

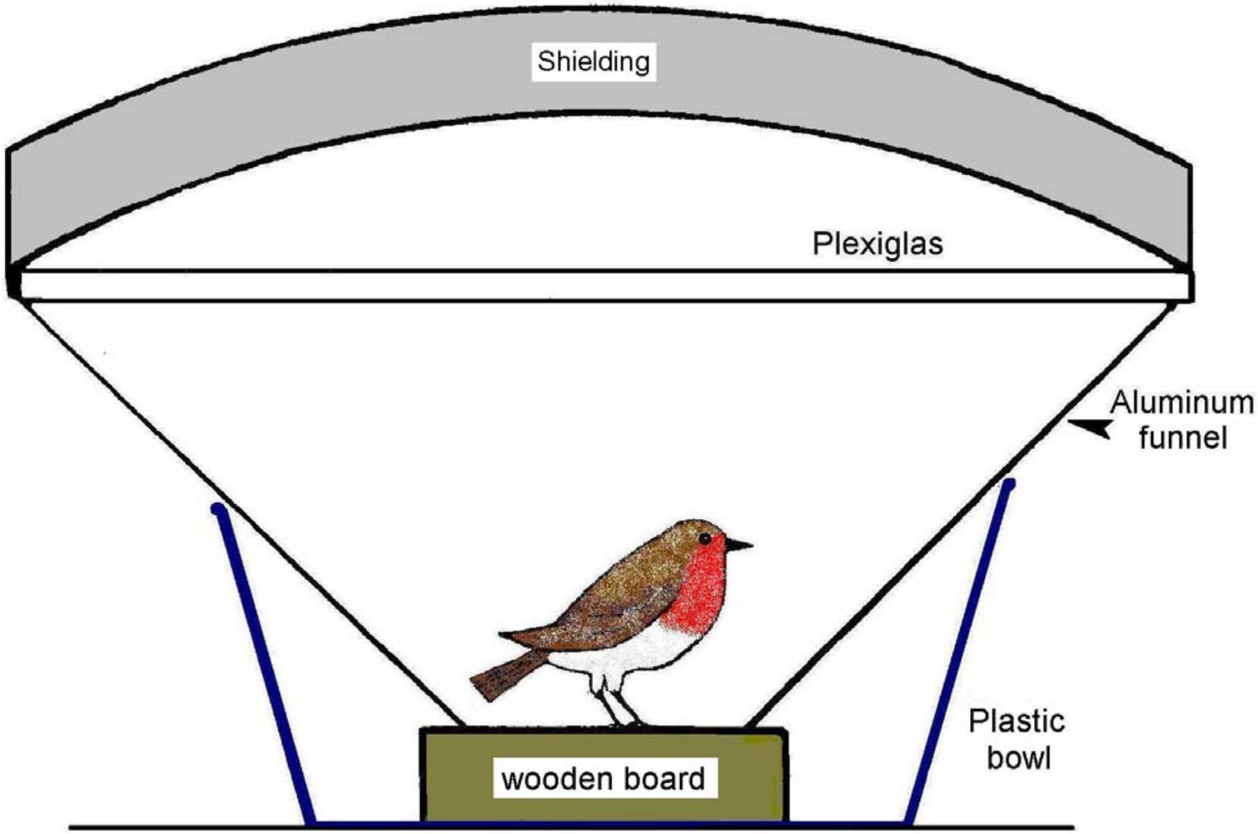
- **Magnetic compass** (based on the geomagnetic field)



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

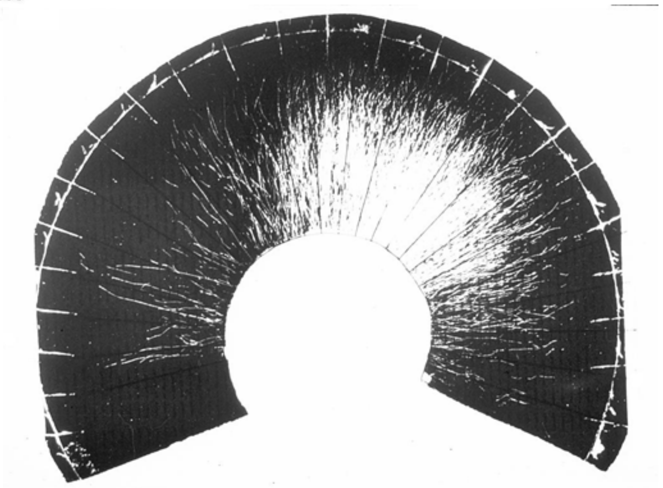
Demonstrating magnetic compass navigation in migratory birds in captivity

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

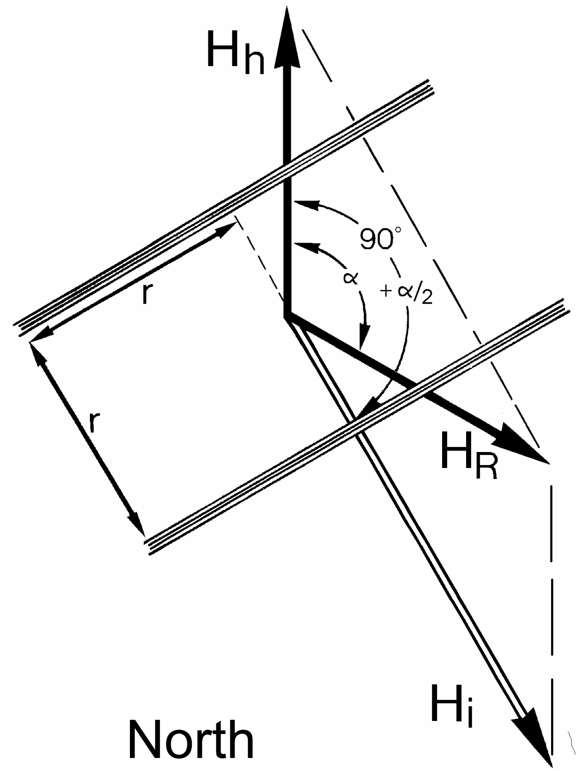


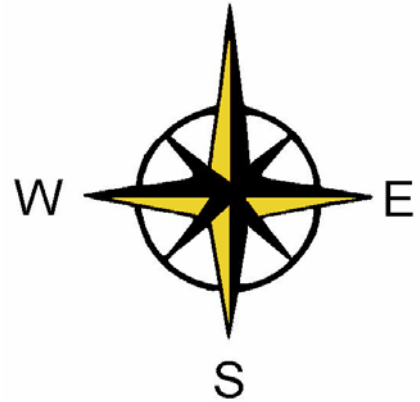
Funnel cage by Emlen & Emlen (1966)

Funnel cage lined with coated paper



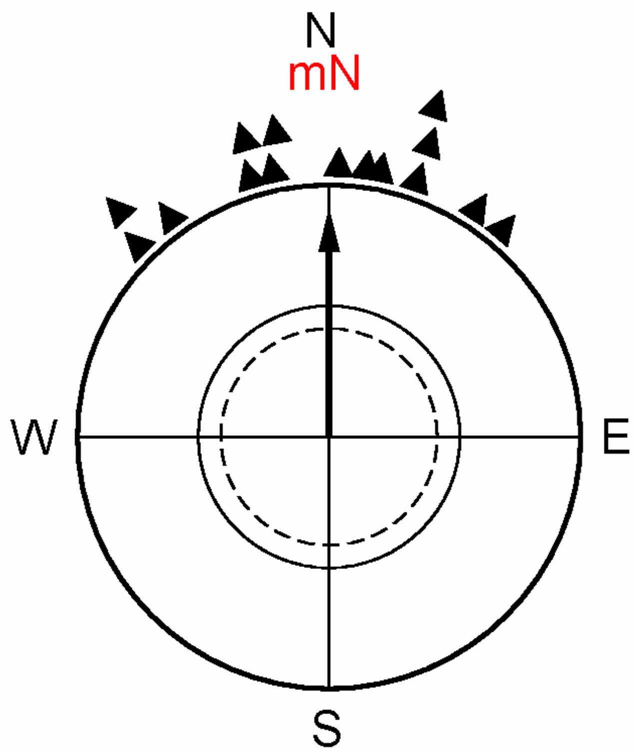
Demonstrating magnetic compass navigation in migratory birds in captivity





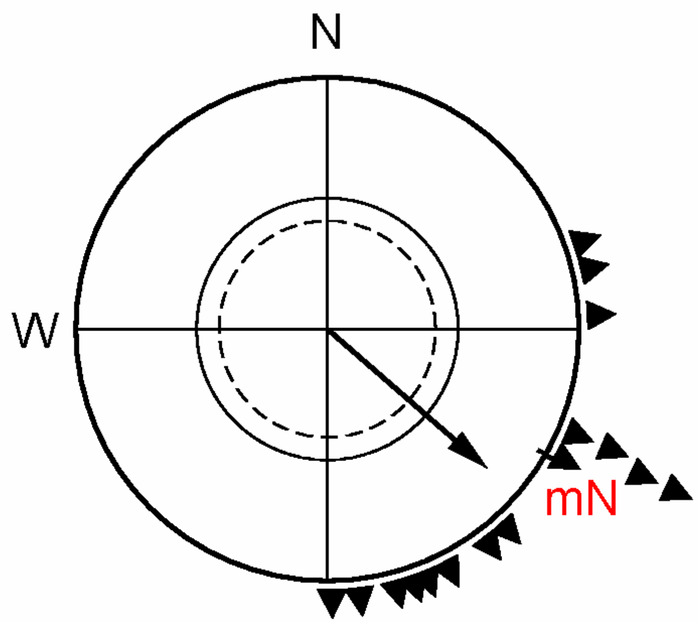
Demonstrating magnetic compass navigation in migratory birds in captivity

European Robins



local geomagnetic field
Control

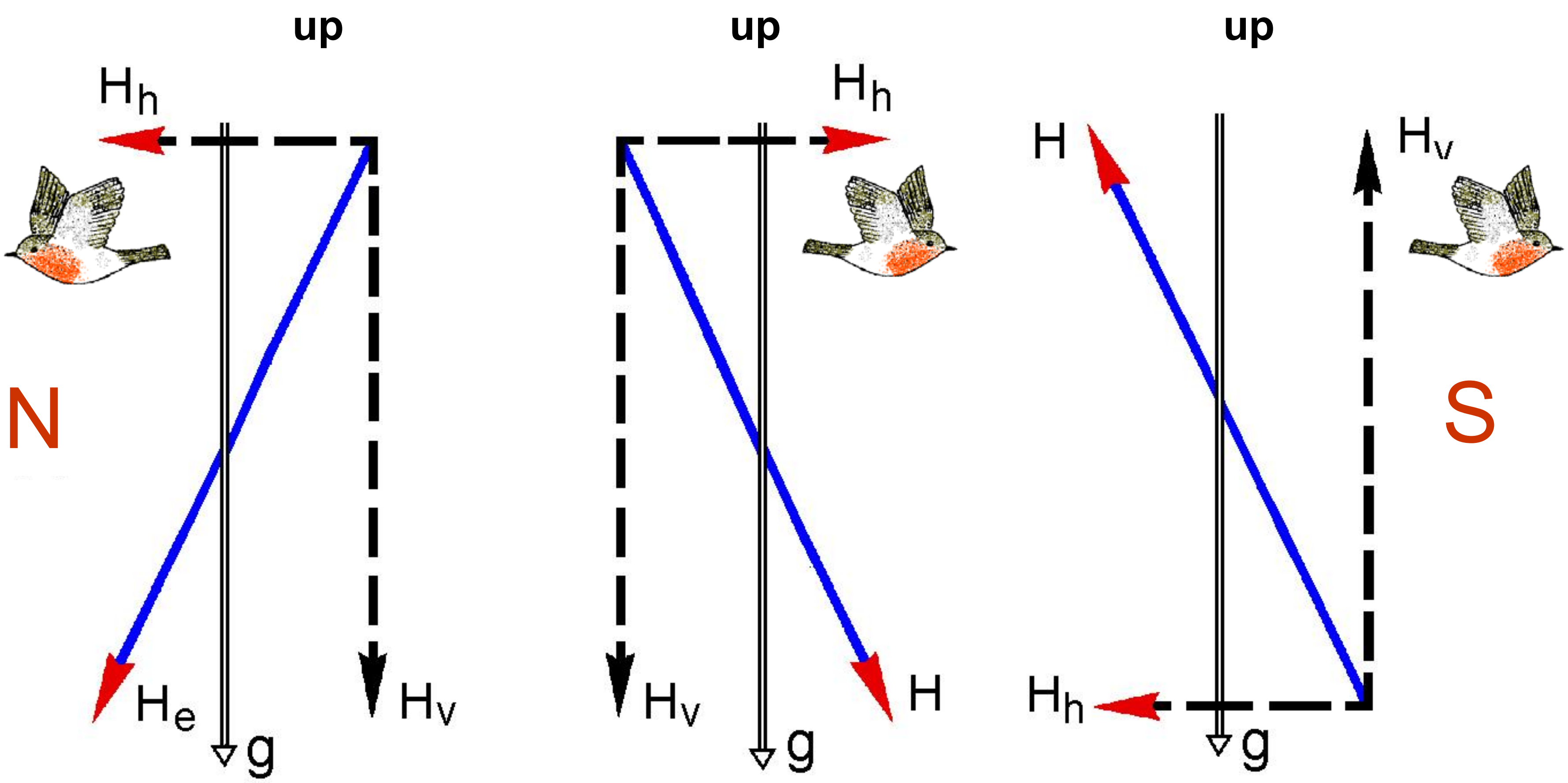
$\Rightarrow$ $N = mN$



magnetic North
turned 120° to ESE

$\Rightarrow$ $SE = mN$

Inverting the vertical component of the magnetic field



local geomagnetic field

horizontal component reversed

vertical component inverted

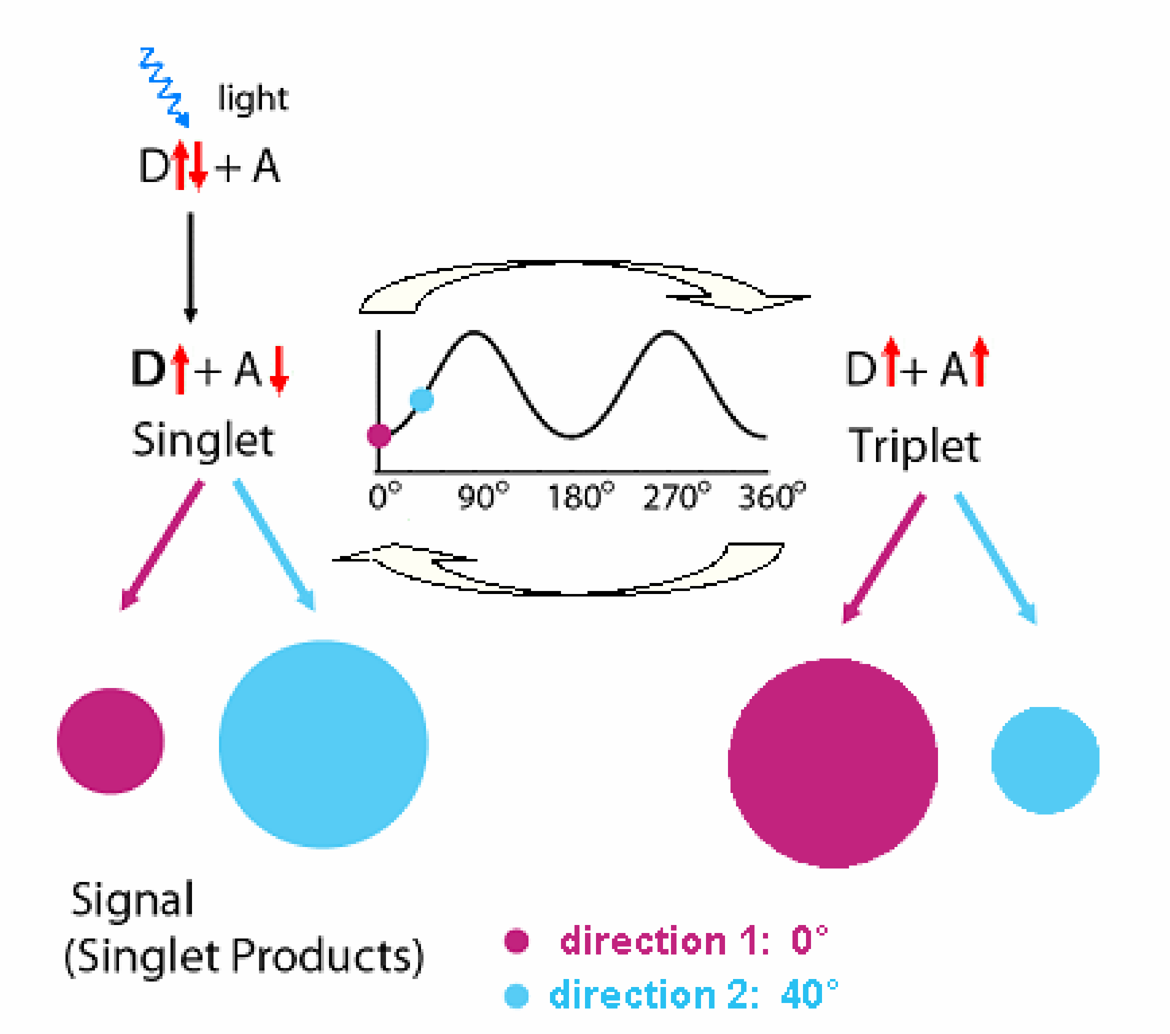
⇨ $N = mN$ ⇨ $S = mN$ ⇨ $S = mS$

Inverting the vertical component of the magnetic field

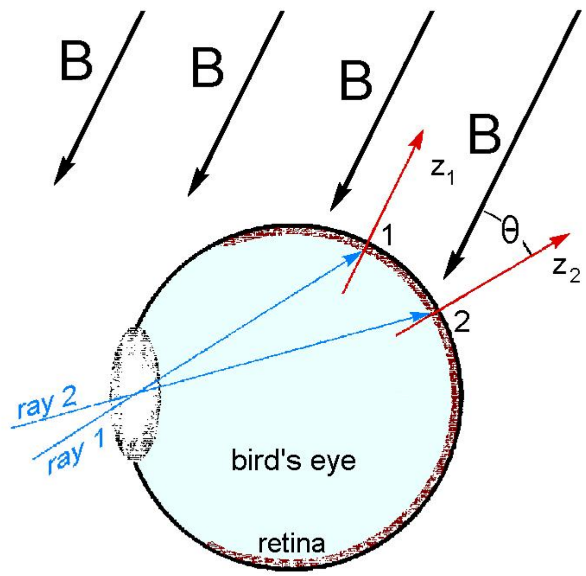
The avian magnetic compass is
an *'inclination compass'*

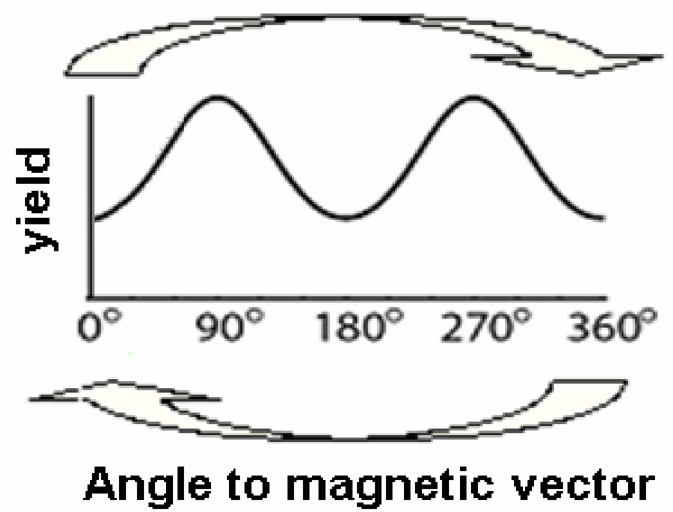
Birds do not distinguish
between magnetic
North and South,
but between
"poleward" (***»p«***) and
"equatorward" (***»e«***)

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

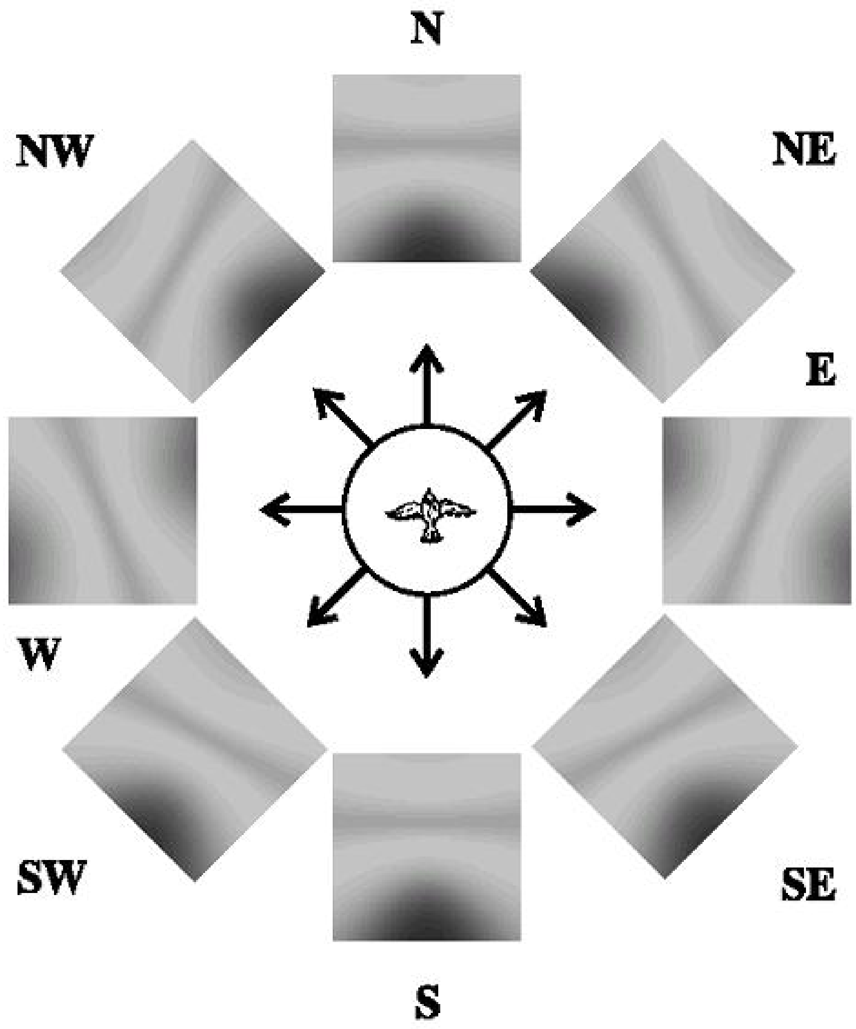


Radical pair model





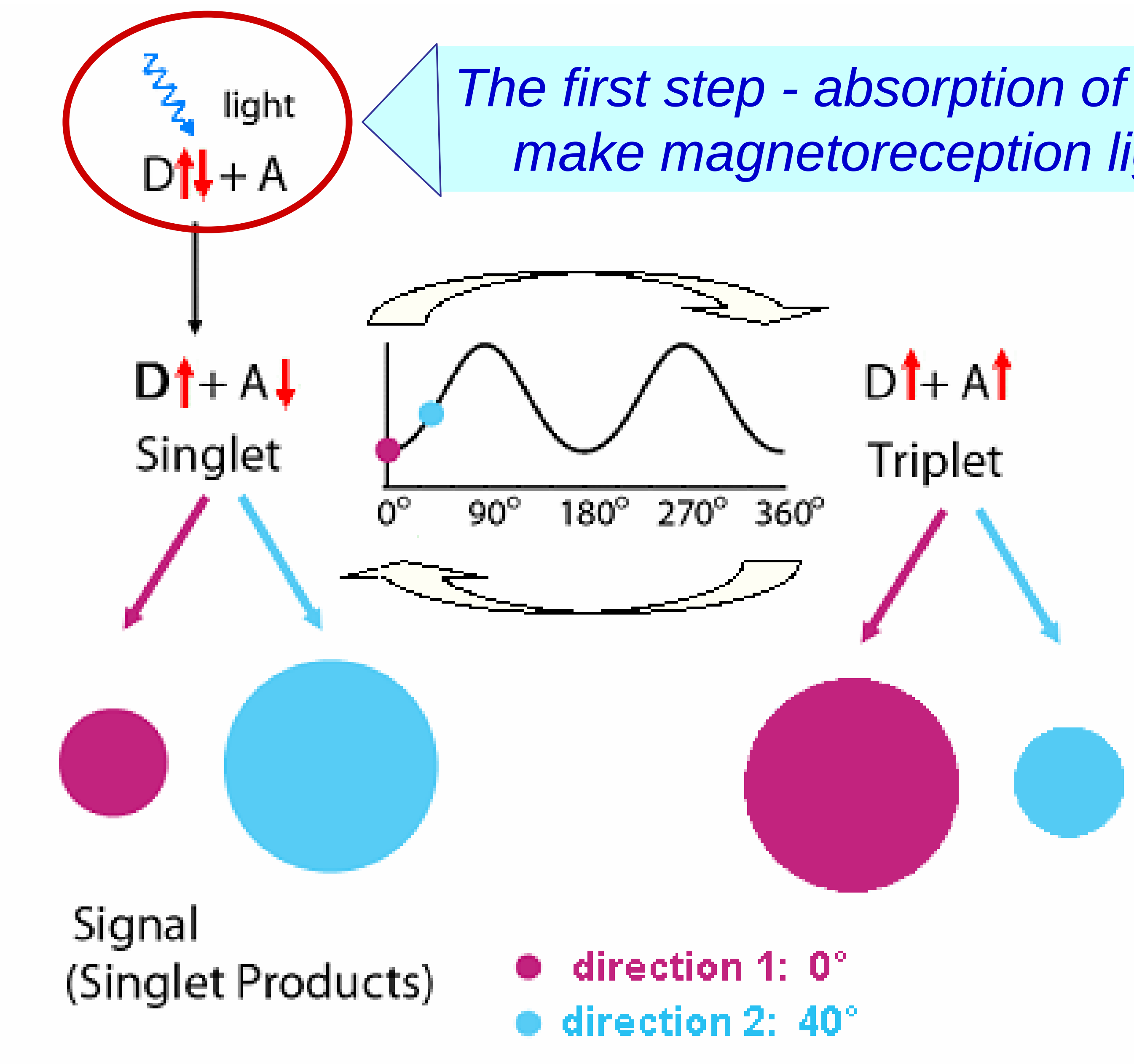
According to the model: Pattern of radical-pair reactions on the bird's retina is modulated by the geomagnetic field as the bird flies to different directions



(from Ritz et al. 2000)

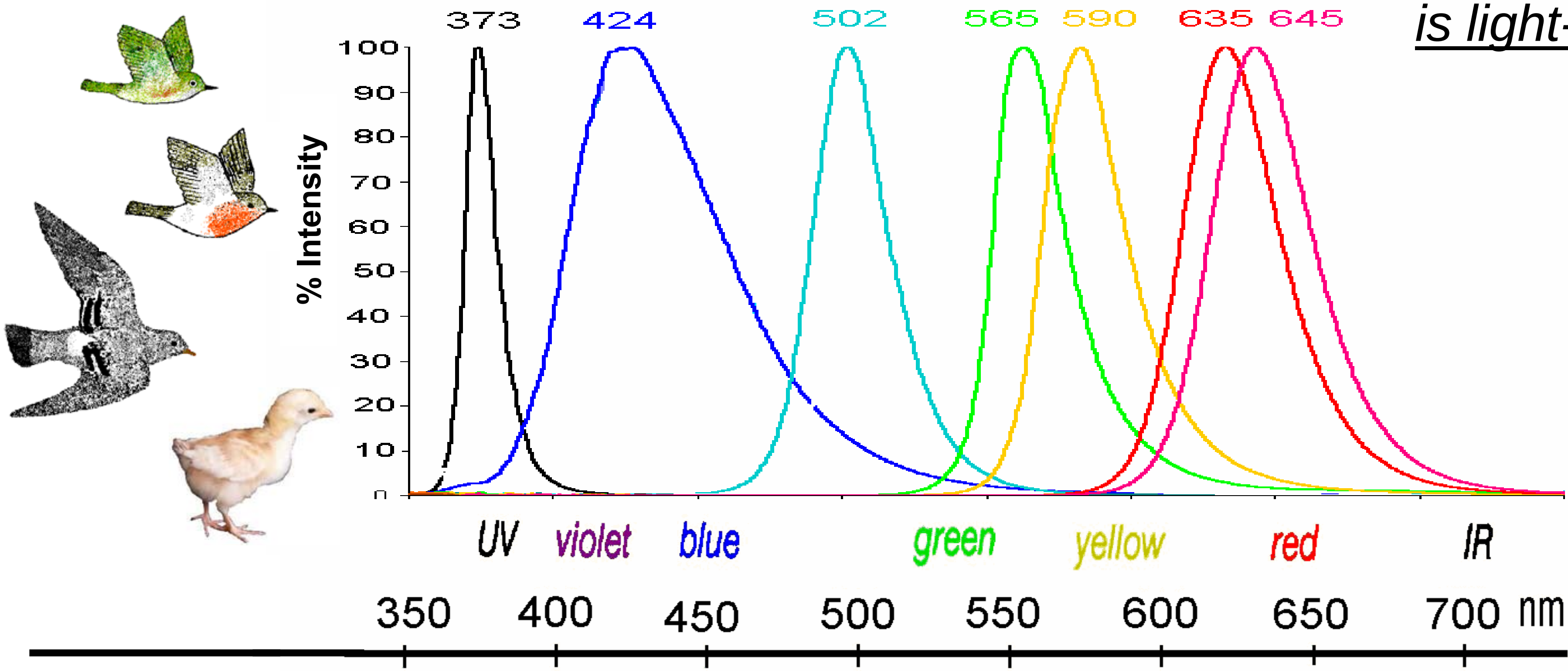
Testing the radical pair model

The first step - absorption of a photon - would make magnetoreception light-dependent



Testing the radical pair model

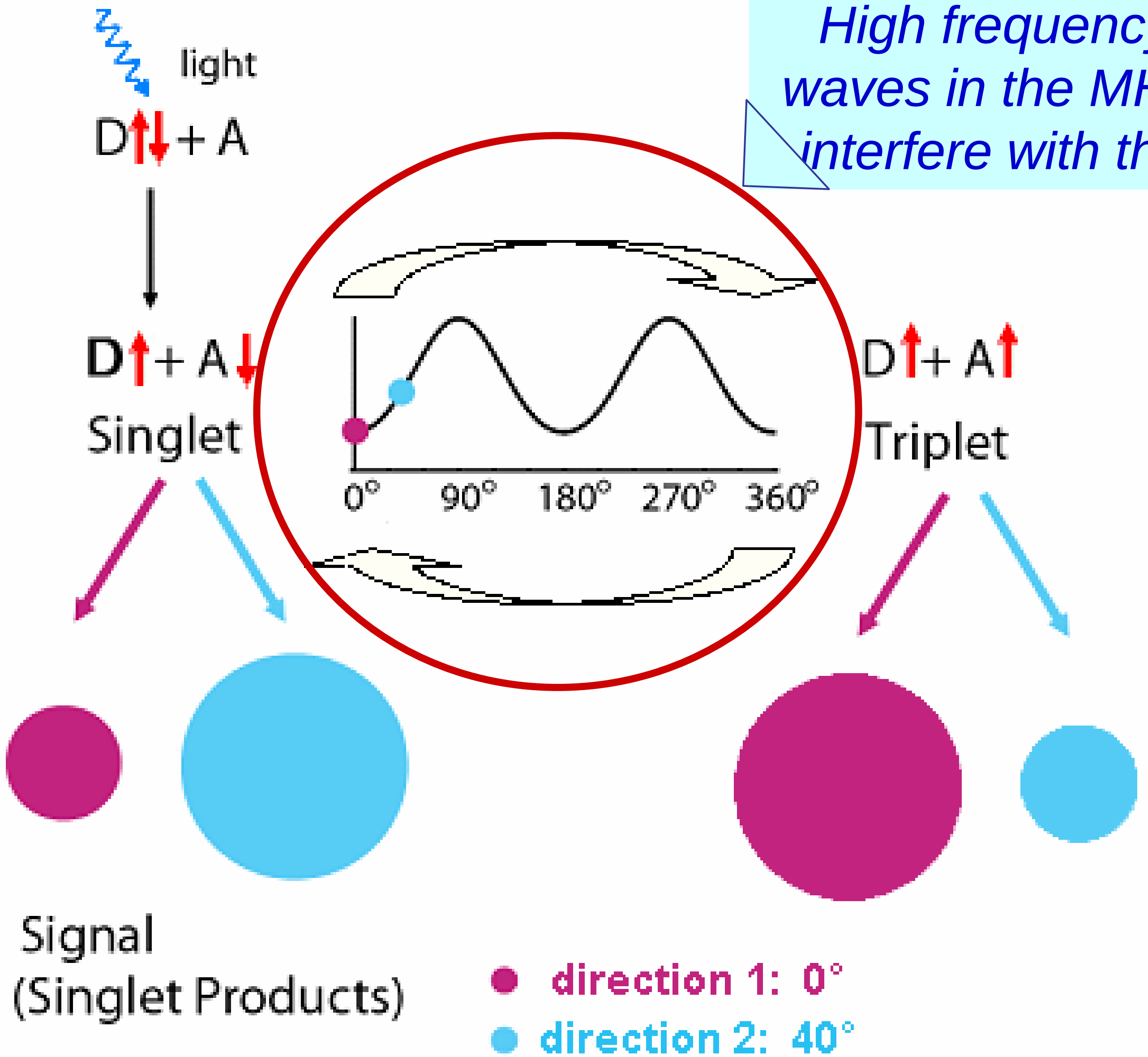
Magnetoreception
<u>is light-dependent</u>



Austr. Silvereye			+			+	−	−		
European Robins	+	+	+		+	+	−	−	−	
Garden Warbler			+			+	−	−		
Carrier Pigeon						+		−		−
Domestic Chicken				+				−		

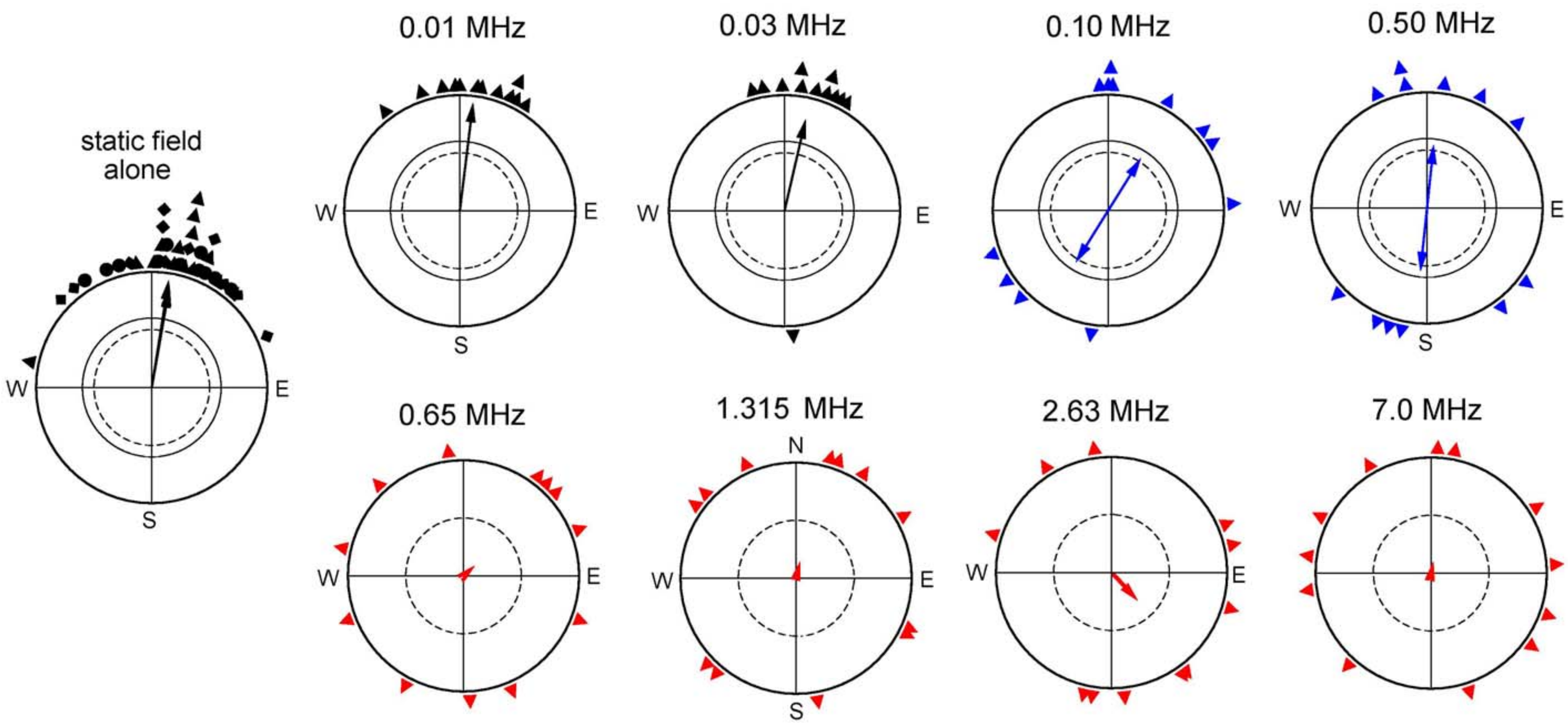
Testing the radical pair model

High frequency electromagnetic (radio) waves in the MHz frequency range should interfere with the singlet-triplet transition!



Testing the radical pair model

0.65 – 7.0 MHz radio waves indeed interfere!



Candidate molecule that can form the crucial radical pairs: **Cryptochrome**. Was recently found in the retina of European Robins, in cells that projects into a brain area involved in magnetic processing („Cluster N“).

Caveat: According to the model, Cryptochrome molecules need to be anchored perpendicularly to retina, which was not shown yet, and it‘s unclear how this could occur.

Demonstrating sun compass in pigeons

Equations for calculating the *sun's position*:

$$\sin \mathbf{h} = \sin \varphi \cdot \sin \delta + \cos \varphi \cdot \cos \delta \cdot \cos t$$

$$\sin \mathbf{A} = \frac{\sin t \cdot \cos \delta}{\cos h}$$

$$\cos \mathbf{A} = \frac{\sin \varphi \cdot \sin h - \sin \delta}{\cos \varphi \cdot \cos h}$$

h = sun altitude

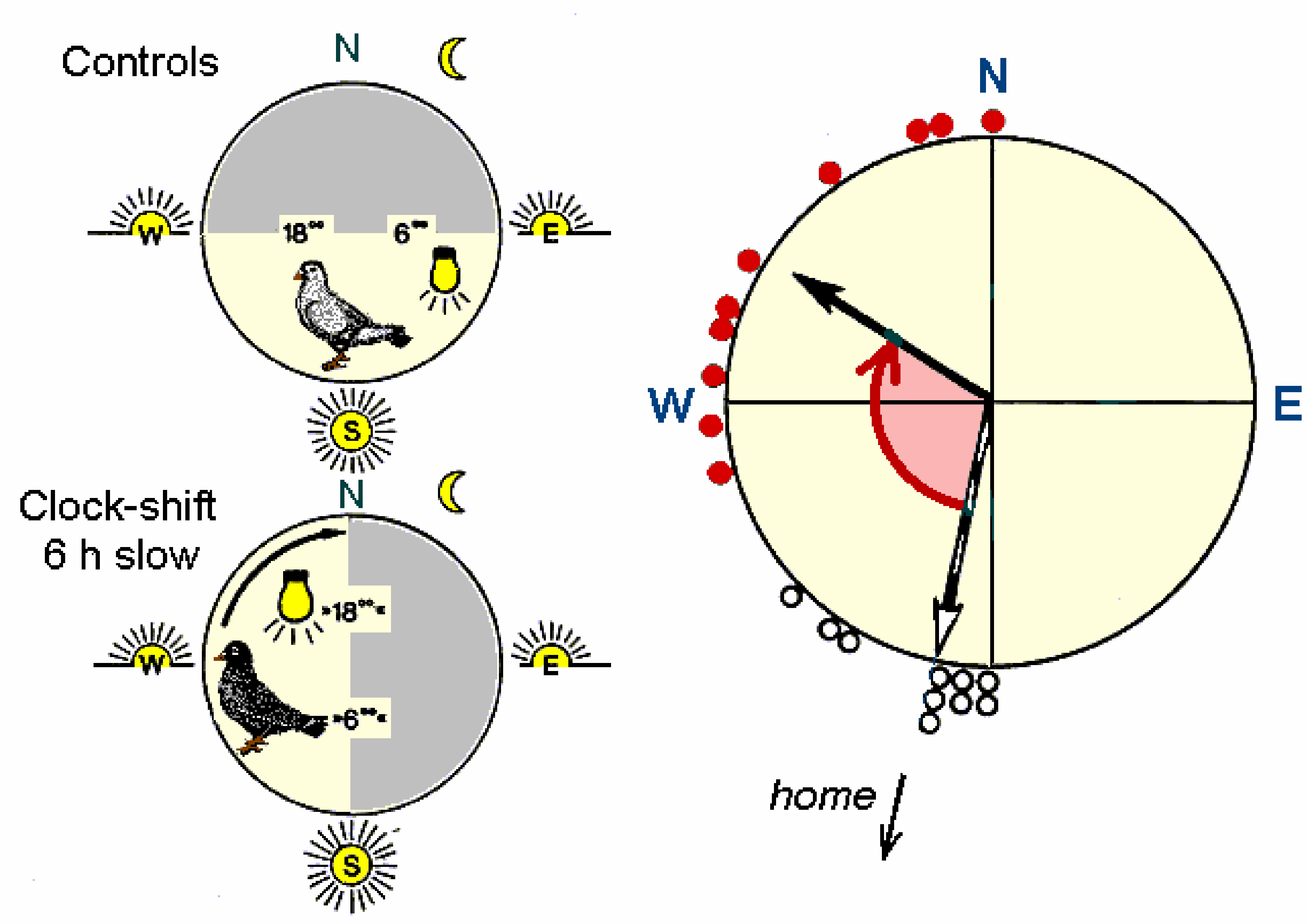
A = sun azimuth

t = hour angle of the sun

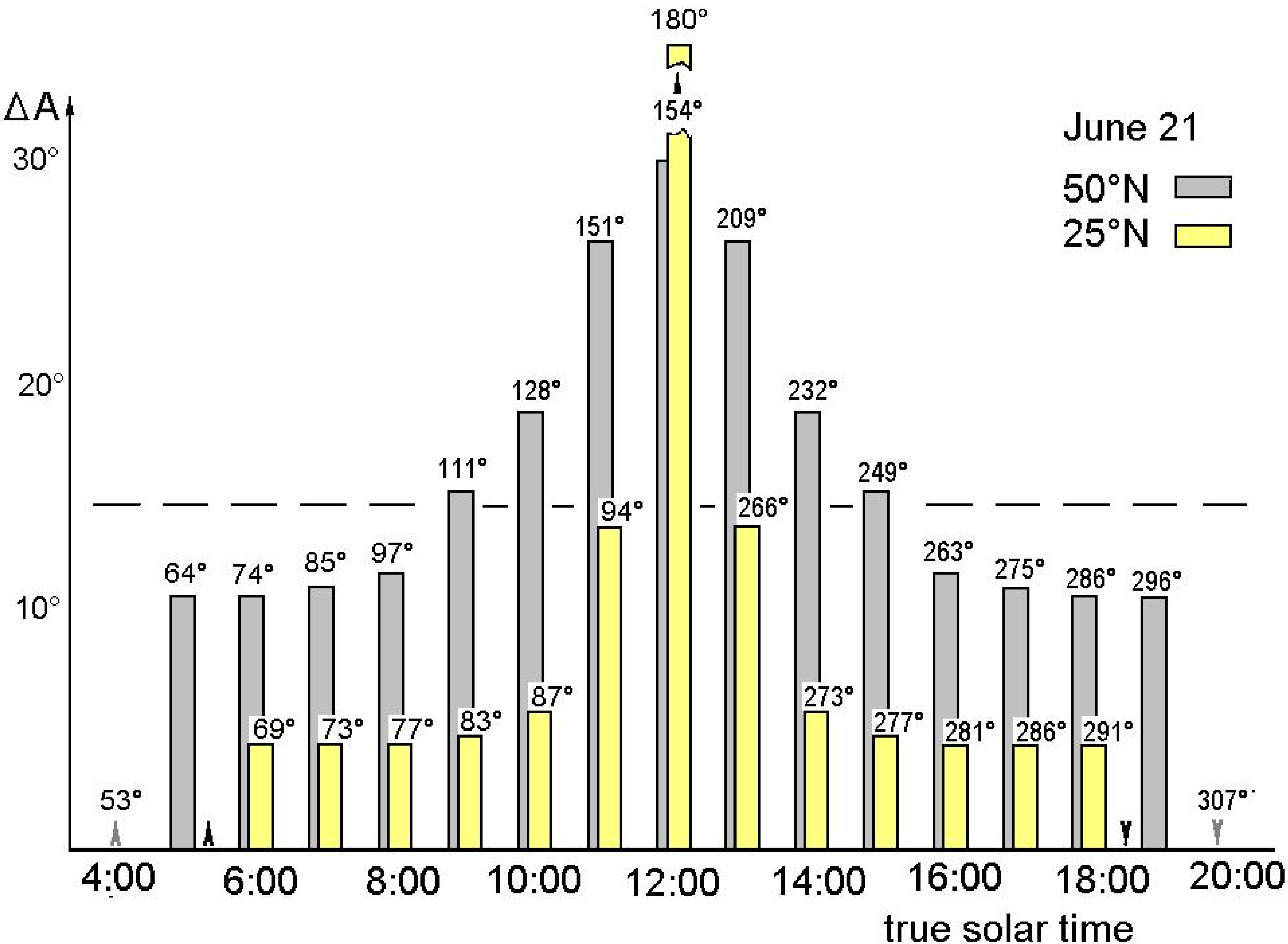
δ = sun declination (seasonal)

φ = geographic latitude

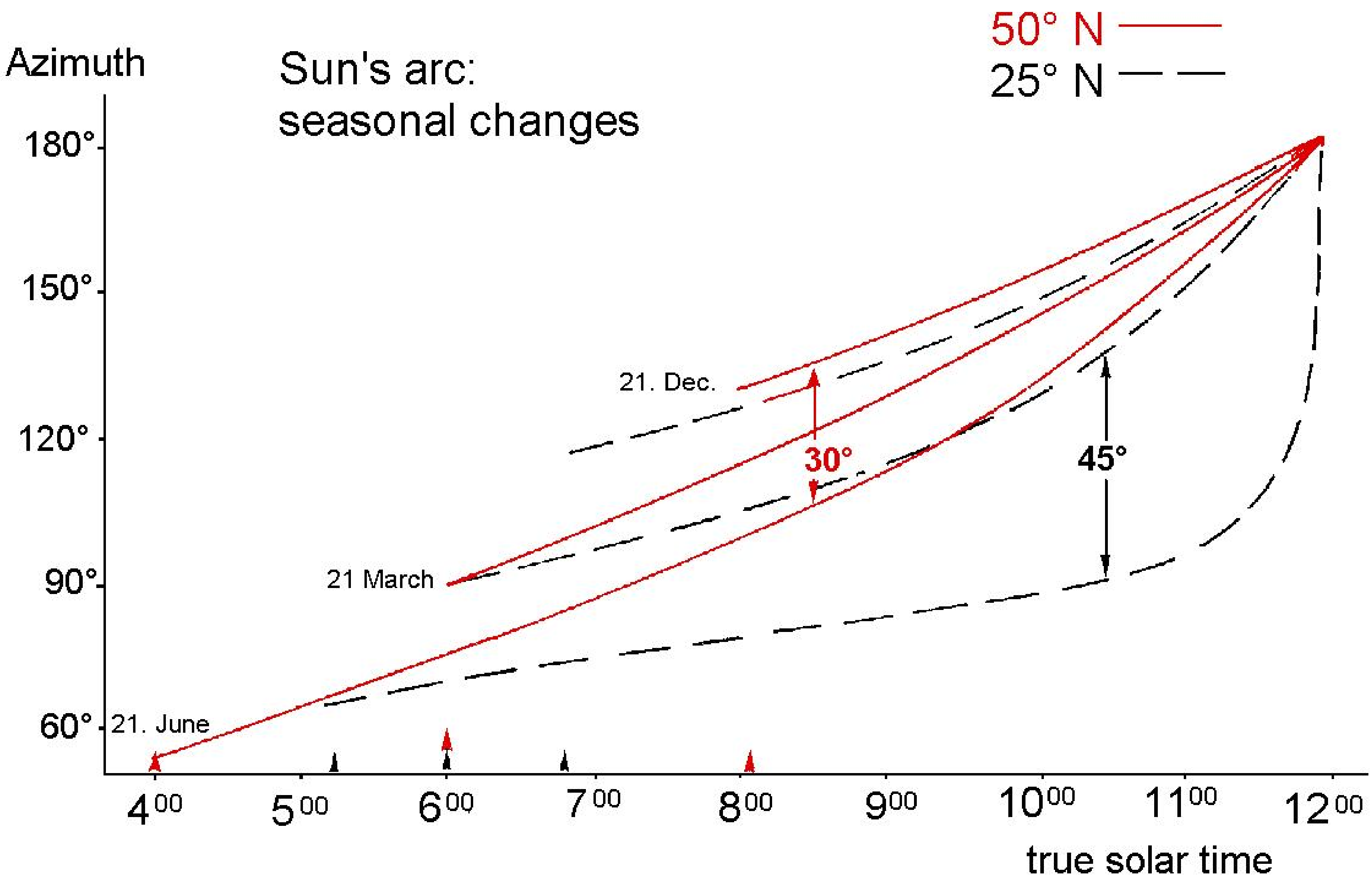
Demonstrating sun compass in pigeons



Sun's arc changes during the day



Sun’s arc changes during the year



Sun compass in pigeons is Learned

Establishing the sun compass in young homing pigeons:

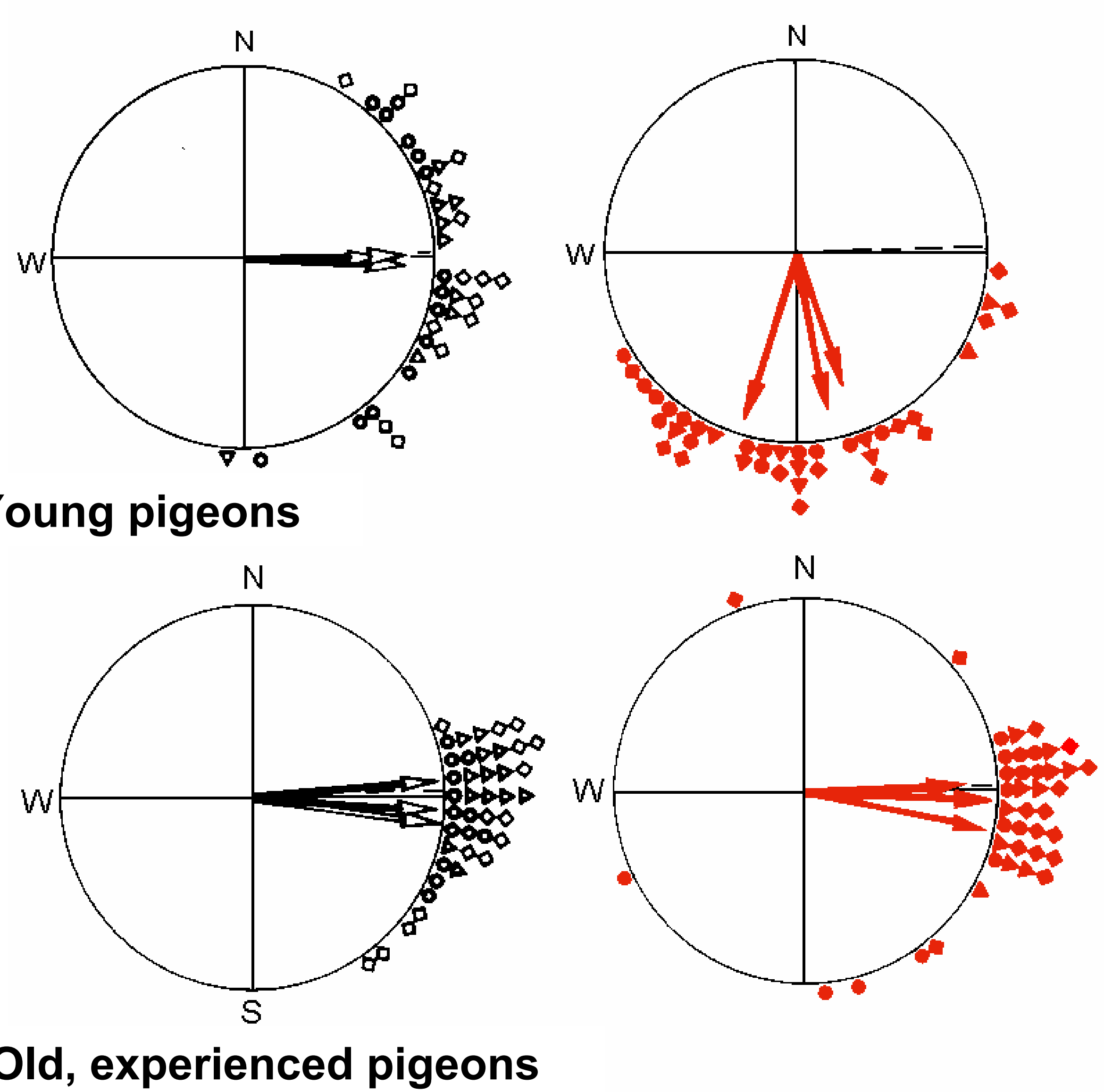
(1) Takes place spontaneously in the 3‘rd month of life and can be advanced by early flying experience.

(2) The pigeons must observe large portions of the sun's arc at different times of the day to be able to use the sun compass during the entire day.

(3) The geomagnetic field serves as reference system to assess the changes in sun azimuth.

Sun compass in pigeons is Learned

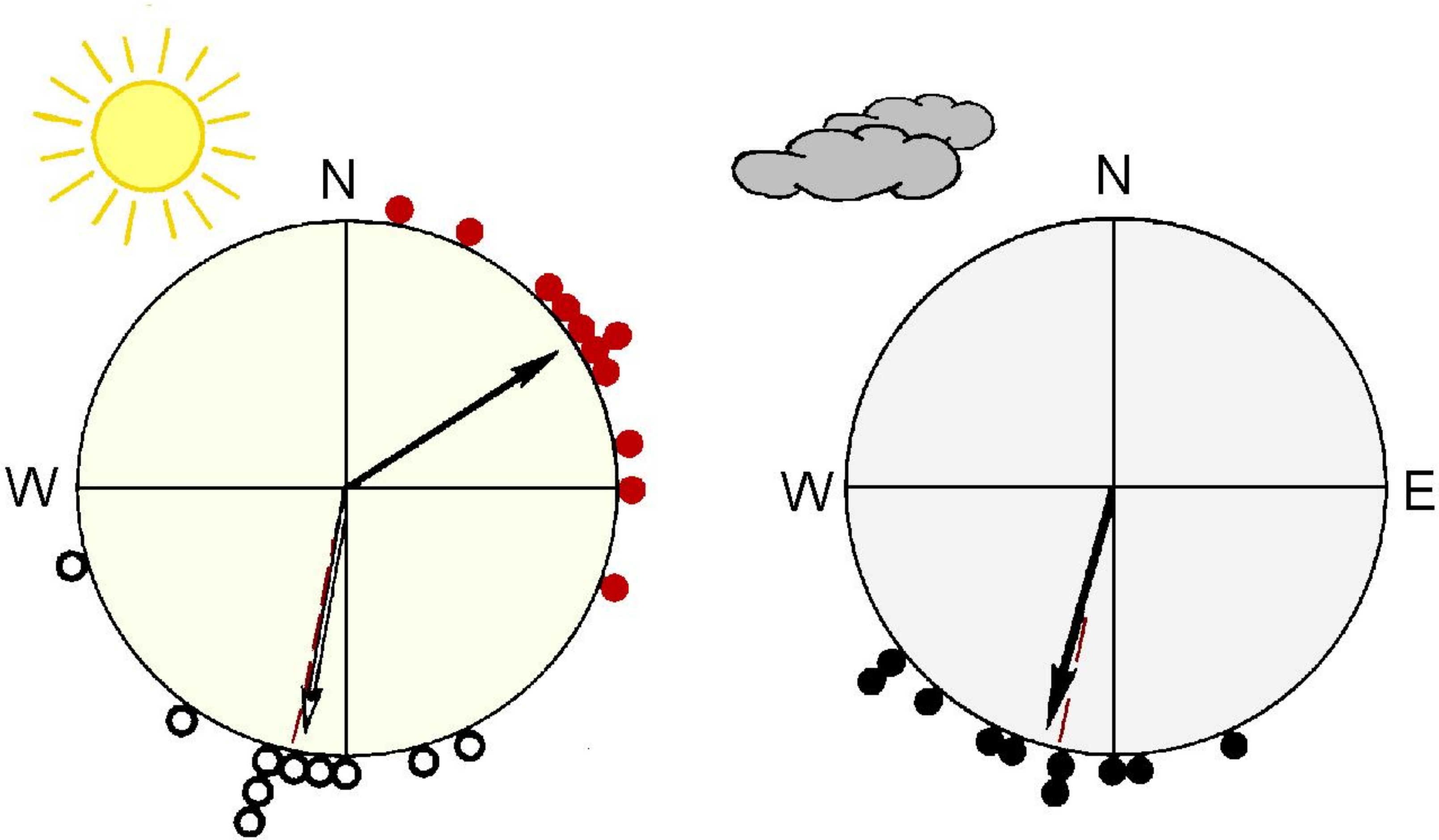
After observing the sun in an altered magnetic field for 10 days:



The magnetic field serves as reference for learning the sun compass

Indicates a sensitive phase (critial period)

Sun compass seems to dominate over magnetic compass in pigeons



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**
- Summary

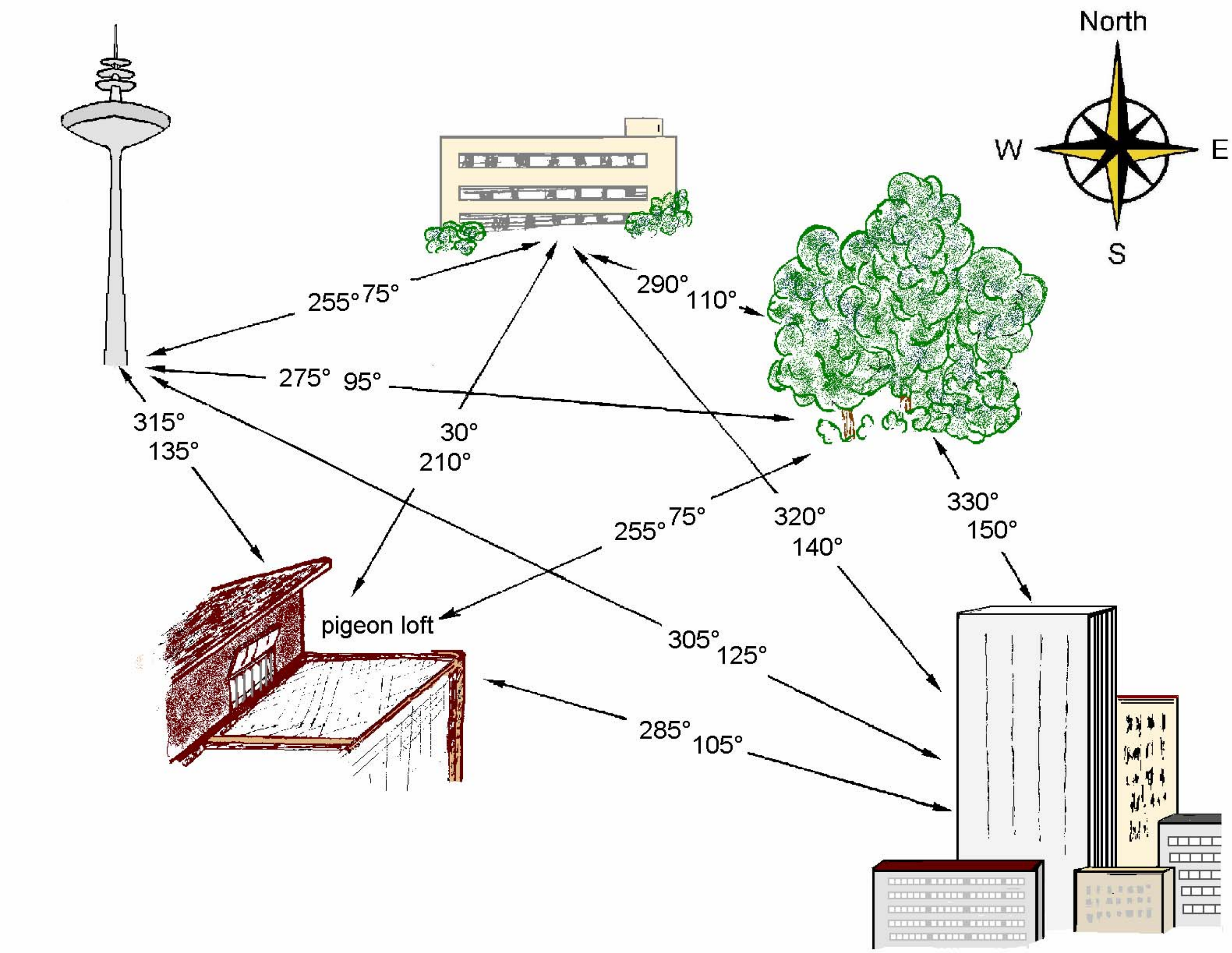
- *Next week: Brain mechanisms of navigation*

Map mechanisms

Three main map mechanisms:

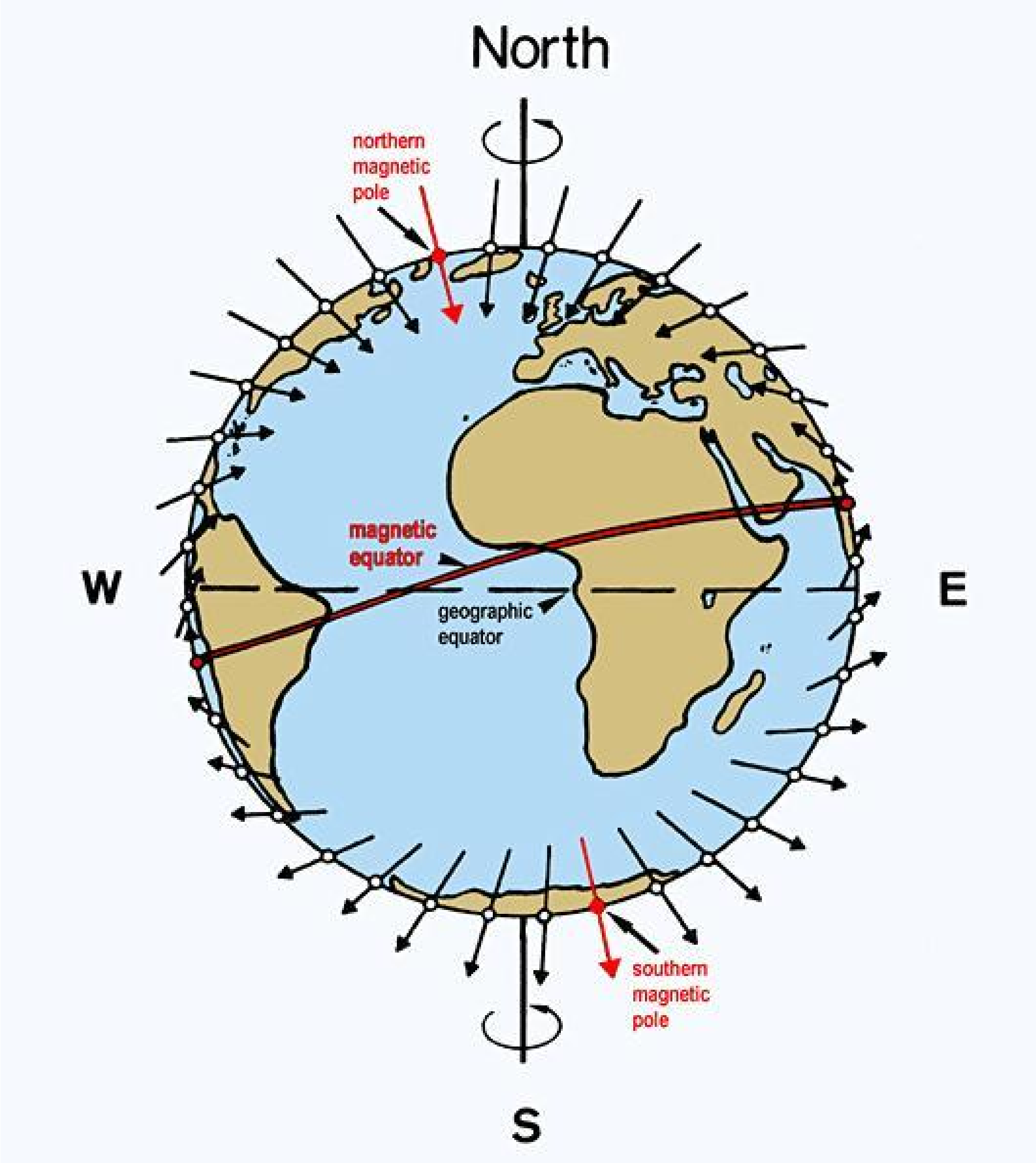
- ‘Mosaic map’ based on landmarks
- Magnetic map
- Olfactory bi-gradient map

The concept of ‘Mosaic Map’ based on familiar landmarks

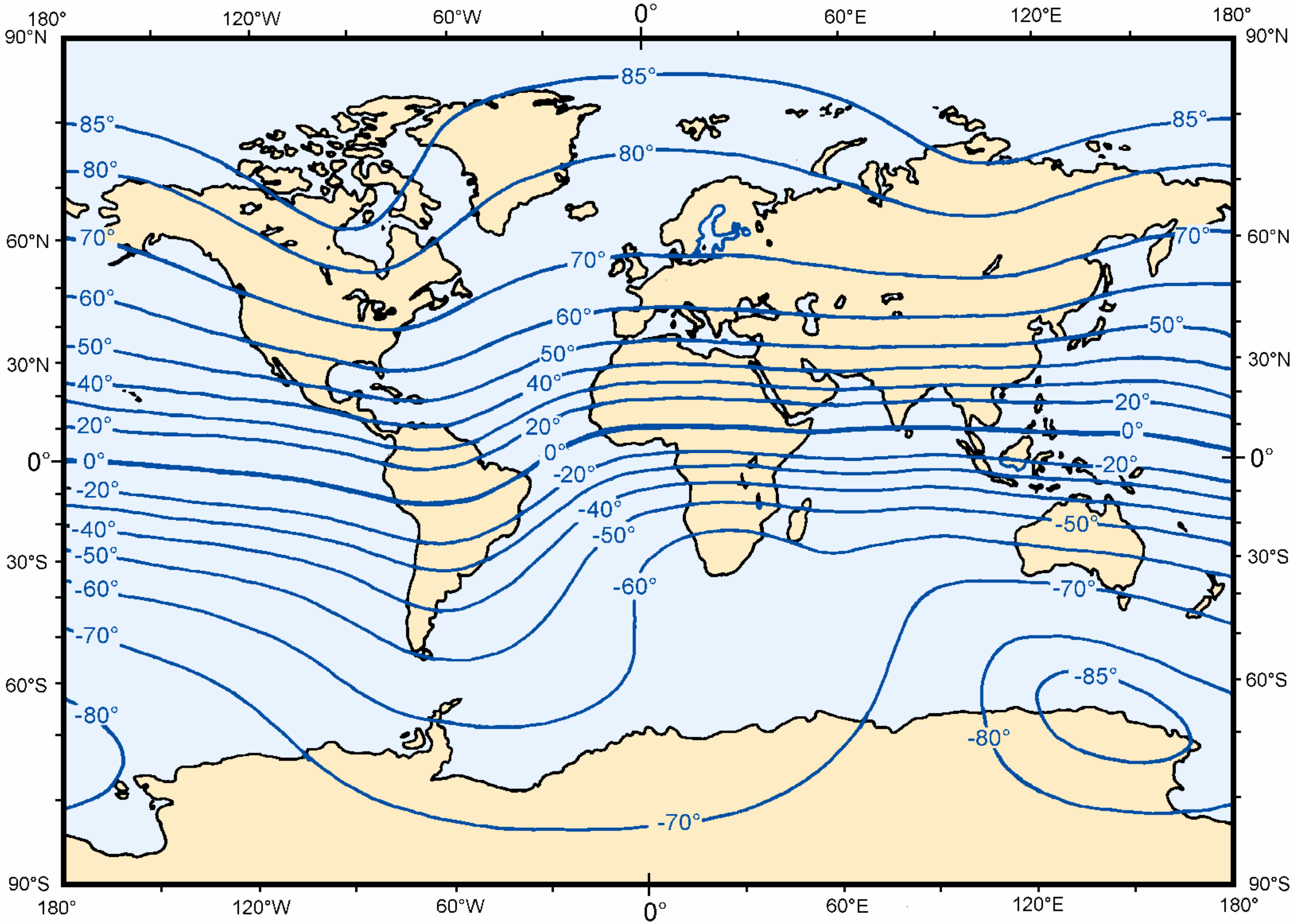


This „Mosaic Map“ concept is very <u>similar to how we think a rat navigates in a watermaze</u> in the lab: By triangulating itself relative to distal landmarks.

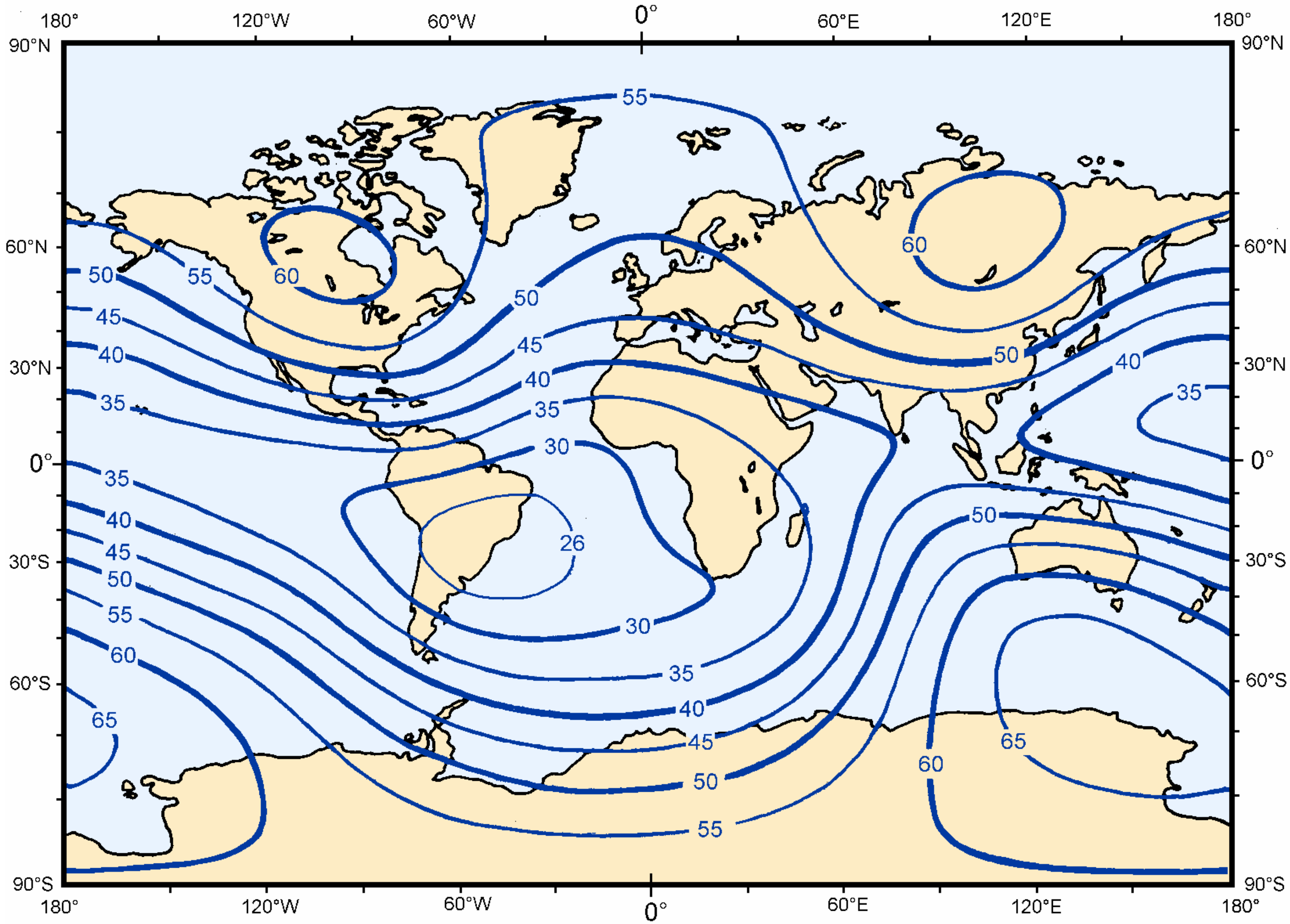
The magnetic field of the earth



Magnetic Inclination provides information about Latitude

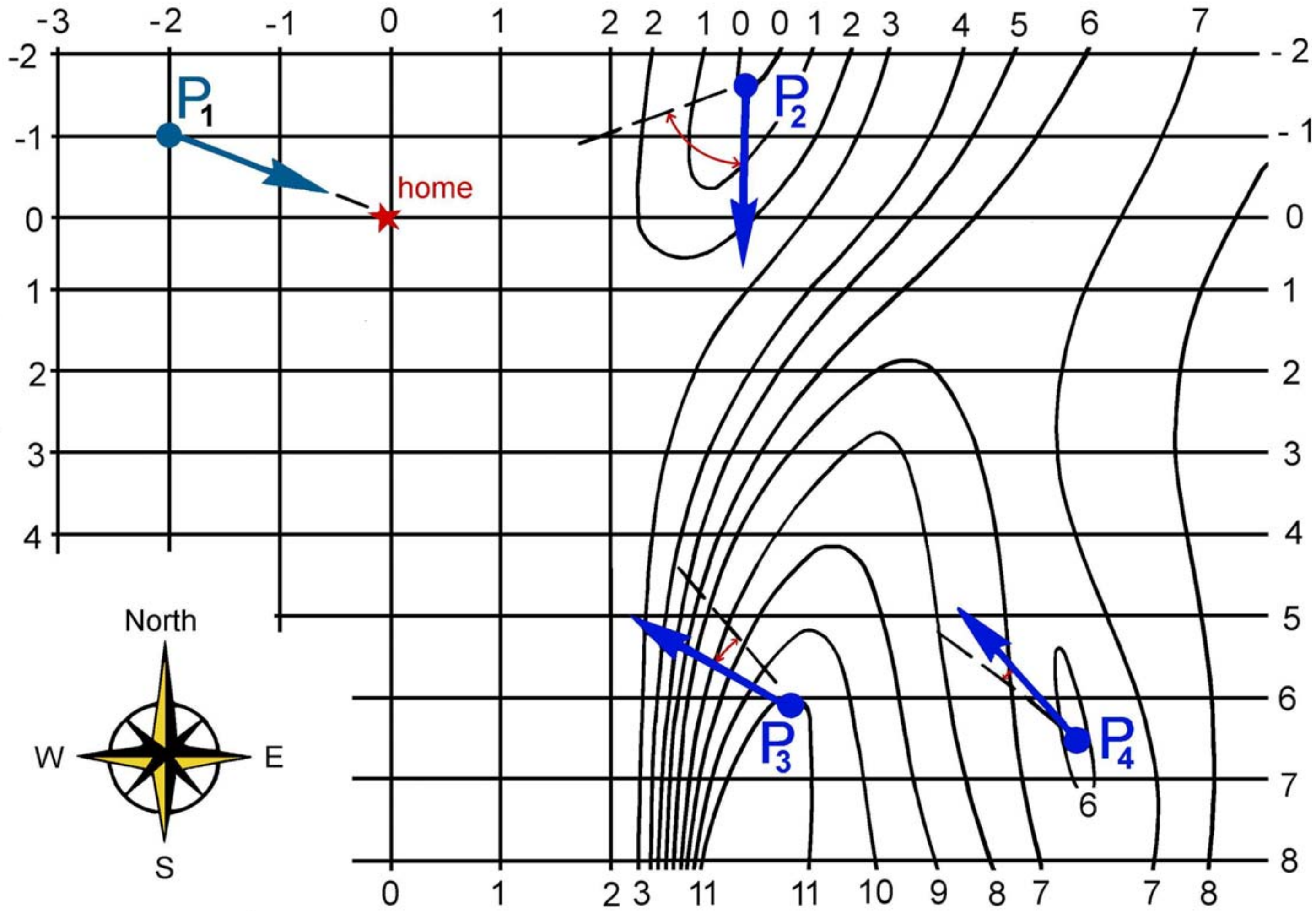


Magnetic Intensity also provides information about Latitude



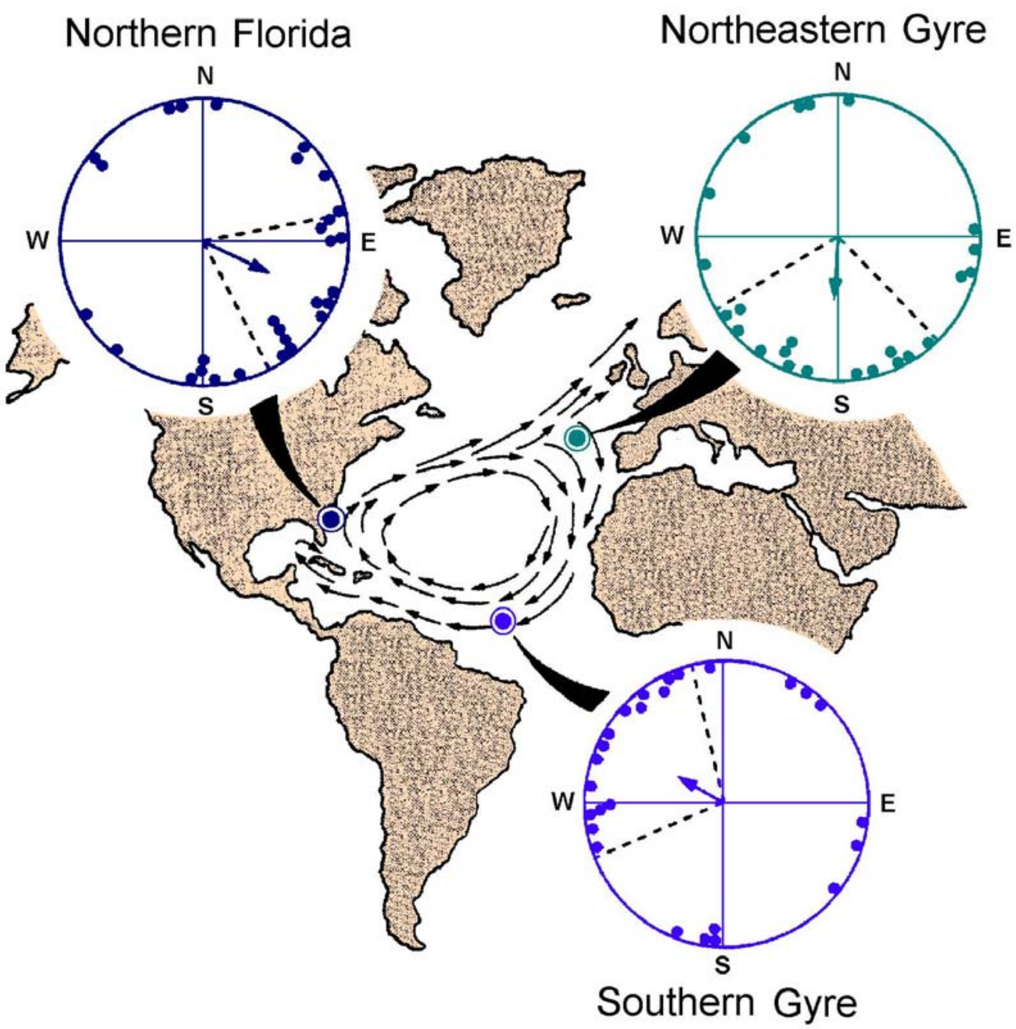
Field in micro-Tesla (μT)

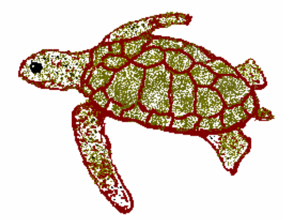
Magnetic Anomalies might provide local map information



Evidence for usage of magnetic map information in sea turtles

Trigger effect in young marine turtles, *Caretta caretta*



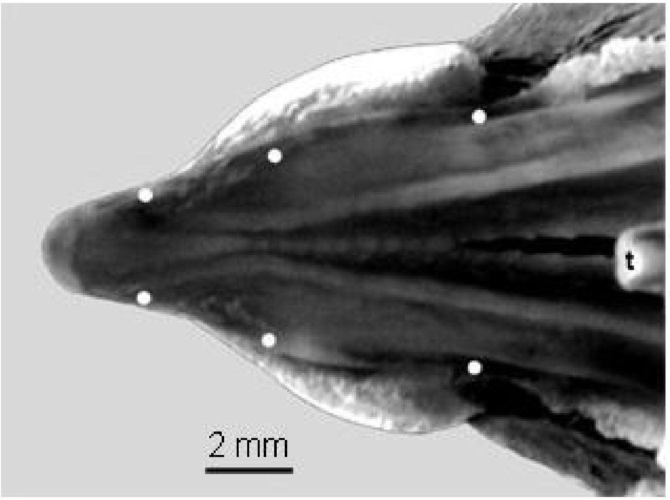


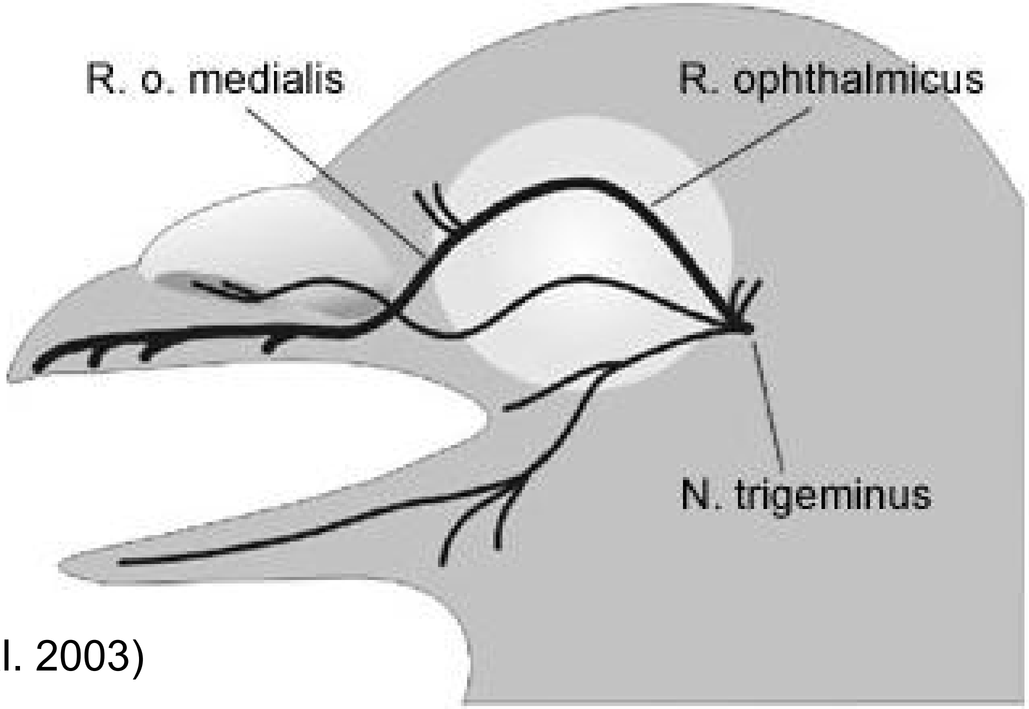
The magnetic conditions in specific areas elicit different directional tendencies

(Lohmann & Lohmann 2002)

Mechanism for sensing magnetic intensity in birds

Magnetite is found in the upper beak of birds:





(from Fleißner et al. 2003)

Caveat: Raging arguments for years between proponents of magnetic map and proponents of olfactory map: The key reason that these arguments rage is that both the nostril and the upper beak are innervated by the same nerve, so invasive experiments that are done to show causality (and many such experiments have been done) are very difficult to interpret unequivocally as supporting one sensory system or another.

Current hypothesis: Magnetic compass in bird's eye ; magnetometer in the beak – involved in map navigation

	Compass	Map
Parameter of the geomagnetic field:	**magnetic vector**	**intensity gradient**
Function in avian navigation:	**directional orientation**	**determining position, serving as 'trigger'**
Primary process based on:	**radical pair mechanism in photopigments**	**iron oxid particles**
Location of receptors:	**retina of the right eye**	**upper beak**
Nerve structures involved:	**optic nerve, nBOR, *tectum opticum***	**ophthalmic nerve, trigeminal ganglion**

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Summary: Take home messages

- Animal navigation is complex and rich, and relies on <u>multiple cues</u>:
  - Need to find animal models that allow isolating certain cues or strategies (e.g. path integration in the desert ant)
  - *Warning*: When studying navigation and spatial memory in the lab, always be very careful and suspicious: Perhaps the animal is using another cue, not what you are thinking? Perhaps your animal is ‘cheating’ you? Perhaps you are cheating yourself? ...

- The same warning goes for all of animal behavior: When studying a certain behavioral phenomenon, be very careful and make sure you ruled out the possibility that the animal is using an alternative behavioral strategy.
  - <u>**The good news are:**</u> It’s possible to do it ; but you have to be careful !