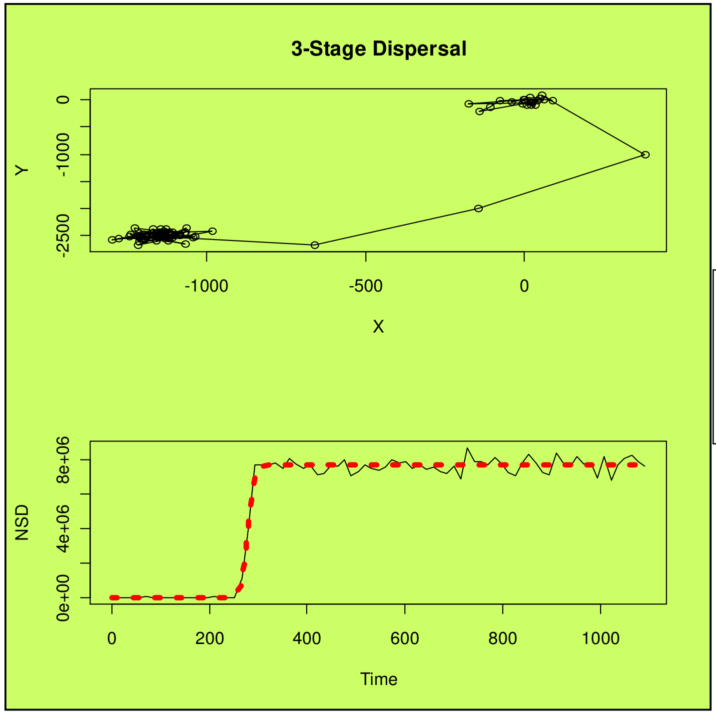
From Stationarity to Nomadism: The squared displacement approach



$$MSD = \frac{\phi_3}{1 + \exp\left[\frac{(\phi_4 - t)}{\phi_5}\right]}$$

Swansea University
Prifysgol Abertawe

Luca Börger (@lucaborger)

Movement Ecology Workshop
Margam FSC, 21 February 2018

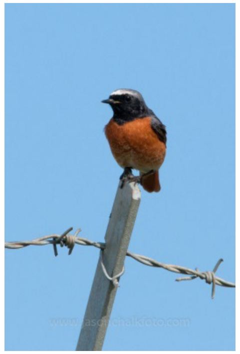
College of Science
Coleg Gwyddoniaeth

Movements
→ interesting, but difficult to study

"*Now we must consider in general the common reason for moving with any movement whatever*"
(Aristotle, De Motu Animalium, 4th century BC)

Question: what happens to migratory birds in winter?

1. Transmutation

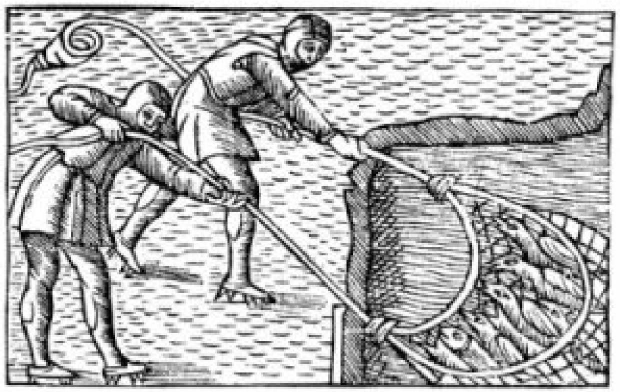


Redstart

Robin

2. 'Migration'

3. Hibernation



Plausible with some observations, but then taken as fact for centuries

Concept of intermittent movements

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

Phil. Trans. R. Soc. B (2010) **365**, 2267–2278
doi:10.1098/rstb.2010.0095

Review

Foraging theory upscaled: the behavioural ecology of herbivore movement

N. Owen-Smith[1,*], J. M. Fryxell[2] and E. H. Merrill[3]

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[2]*Department of Zoology, University of Guelph, 50 Stone Road E, Guelph, Ontario, Canada N1G 2W1*
[3]*Department of Biological Sciences, University of Edmonton, Edmonton, Alberta, Canada T6G 2E9*

We outline how principles of optimal foraging developed for diet and food patch selection might be applied to movement behaviour expressed over larger spatial and temporal scales. Our focus is on

- Foraging behaviour: multiscale hierarchical process
- Scales: food items….optimal annual routines

Fitness consequences environmental variation?
→ Behavioural responses large spatio-temporal scales
→ *intermittent locomotion across scales*

Multiple movement modes by large herbivores at multiple spatiotemporal scales

John M. Fryxell[a,1], Megan Hazell[a], Luca Börger[a], Ben D. Dalziel[a], Daniel T. Haydon[b], Juan M. Morales[c], Therese McIntosh[d], and Rick C. Rosatte[d]

[a]Department of Integrative Biology, University of Guelph, Guelph, ON, Canada N1G 2W1; [b]Department of Environmental and Evolutionary Biology, University of Glasgow, Glasgow G12 8QQ, United Kingdom; [c]Laboratorio ECOTONO, Universidad Nacional del Comahue, Quintral 1250, 8400 Bariloche, Argentina; and [d]Ontario Ministry of Resources, Trent University, DNA Building, 2140 East Bank Drive, Peterborough, ON, Canada K9J 7B8

Edited by Ran Nathan, The Hebrew University of Jerusalem, Jerusalem, Israel, and accepted by the Editorial Board July 14, 2008 (received for review February 22, 2008)

Movement Ecology Theory

Movement mode switches

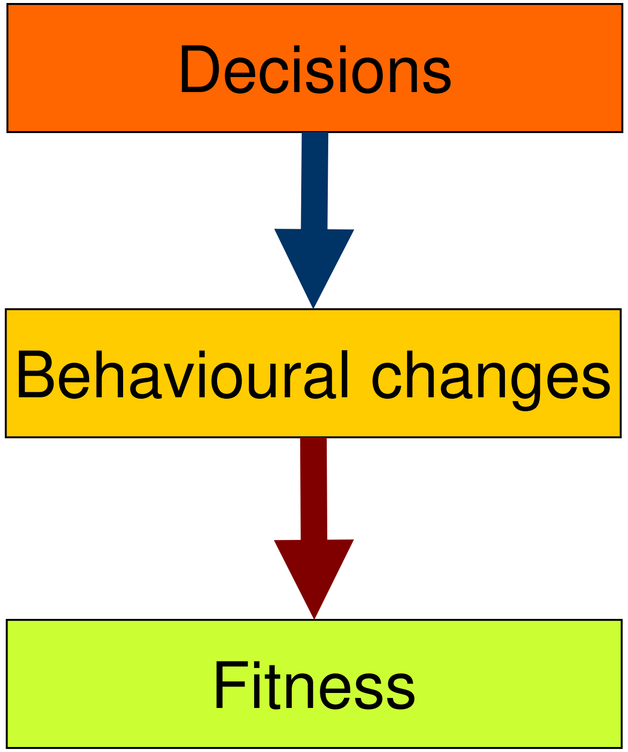
= ***f*** (Internal state + External environment | Movement & Navigation capacities)

Multiscale analysis: minutes-to-years; meters-to-100 km

→ Biphasic movement models

Multiphasic structure is fundamental to the movement patterns of elk at all temporal and spatial scales tested

Behavioural ecology of animal movements



Relevant spatio-temporal scales movement behaviour?

CHAPTER 8

Migration quantified: constructing models and linking them with data

Luca Börger, Jason Matthiopoulos, Ricardo M. Holdo, Juan M. Morales, Iain Couzin, and Edward McCauley

Oxford U. Press (2011)

→ to approach migration quantitatively, it is necessary to place it in the wider context of animal movement models (conceptual as well as mathematical)

Migration: inferential approaches

→ translate contrasting, verbal hypotheses into animal movement models
→ fit models to movement data
→ evaluate model fit

… what is 'migration'?

- any type of movement (Baker 1978)
- seasonal resource tracking movements (Fryxell 1991)
- periodic vertical diel movements of invertebrate zooplankton (surface/deep water; Hansson & Hylander 2009)
- One-way movements insect generations -> multigenerational pattern Holland (2006)

Borger et al. (2011) Oxford Univ. Press

Space use strategies & Migration

Classification difficulties usually indicate that the phenomena of interest are part of a continuum. This need not preclude a discrete classification of movement as long as we are prepared for the occurrence of non-archetypal movement patterns.

(Borger et al. 2011 Oxford. Univ. Press)

Intimate connections between sedentarism, dispersal, and migration

(Mayr and Meise 1930)

Time scale:

"In many cases, the daily movements of animals represent in miniature movements similar to migration, and require similar mechanisms of operation."

(Woodbury 1941)

including nomadism leads to a better conceptual understanding

(Borger et al. 2011 Oxford. Univ. Press)

(Muller & Fagan 2008)

Migration: inferential approaches

* consider migration in the wider context of animal movement models,

* translate specific questions and hypotheses about migration into appropriate movement models

* facilitates the choice of the most appropriate inferential approach.

Interpretation of results determined by ecological context/questions

Borger et al. (2011) Oxford Univ. Press

Theory of random walks and diffusion
why so important for animal movements?

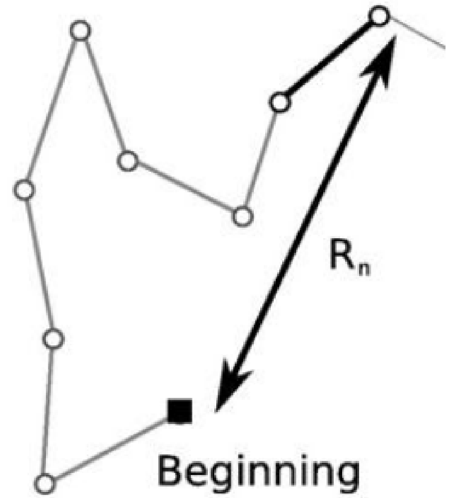
Remember:

1. Theory/Hypothesis
2. Compute the consequences
3. Compare to nature
4. Reject if not supported (!)

* Which behaviours/biological mechanisms need to be included to recreate the observed patterns?

* If multiple mechanisms are equally supported, which data will I need to distinguish between the competing hypotheses?

Squared displacement modelling approach



Time: continuous

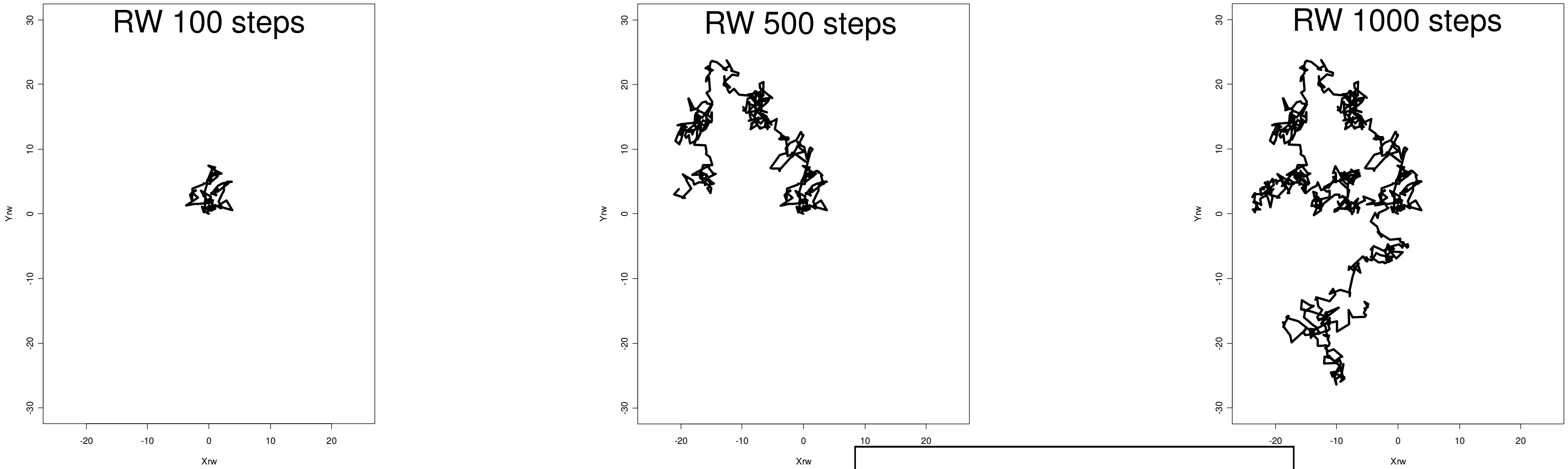
CHAPTER 17

Quantifying individual differences in dispersal using net squared displacement

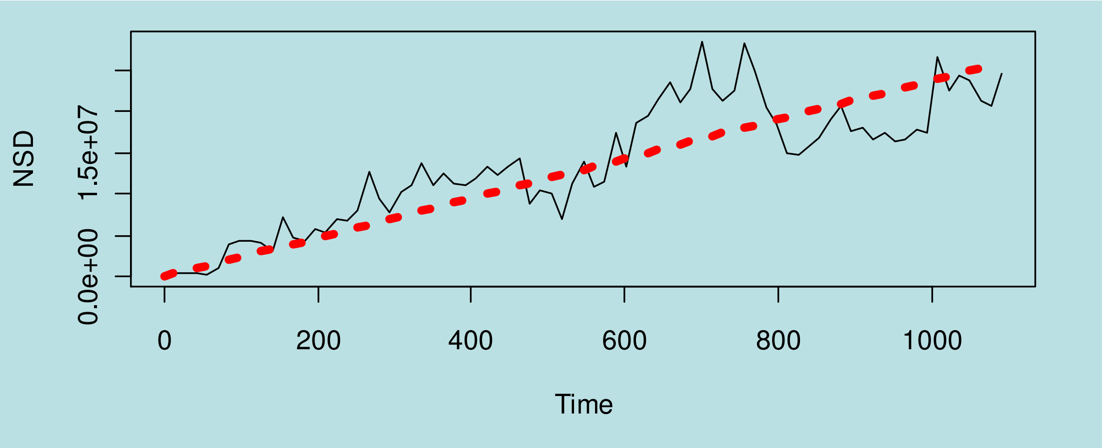
Luca Börger and John Fryxell

Oxford U. Press (2012)

Theory of random walks and diffusion
→ *Nomadism*

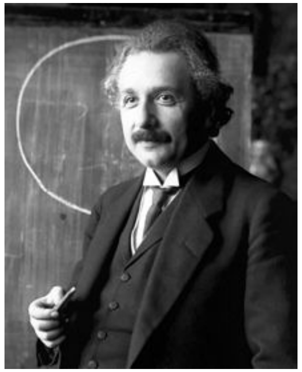


$$MSD = Dt^{\alpha}$$

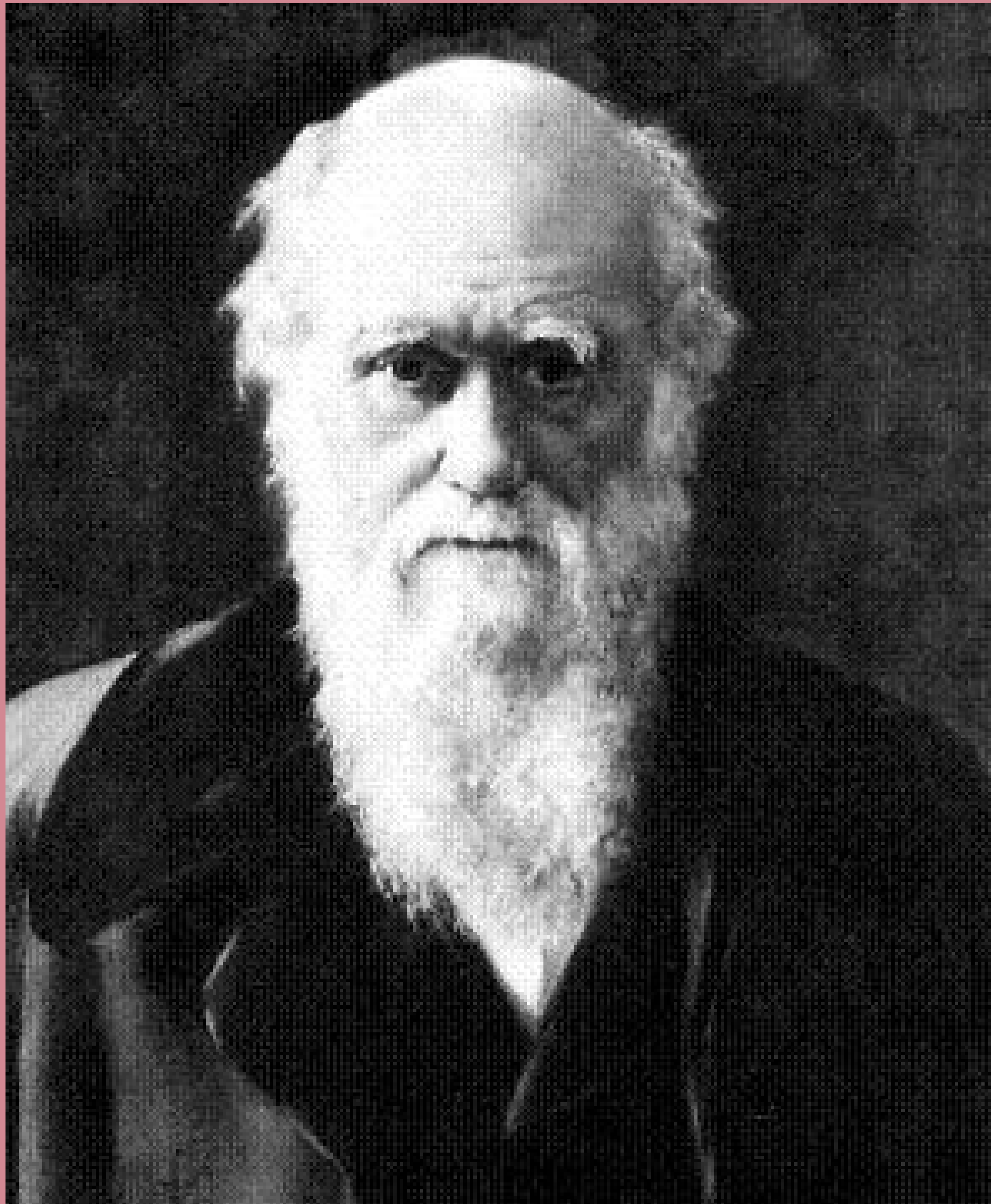


(α = 1)

MSD = 4Dt



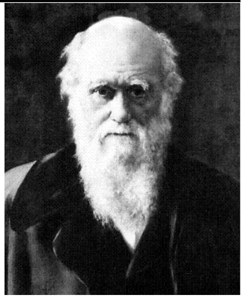
Einstein (1905) Annal. Phys.



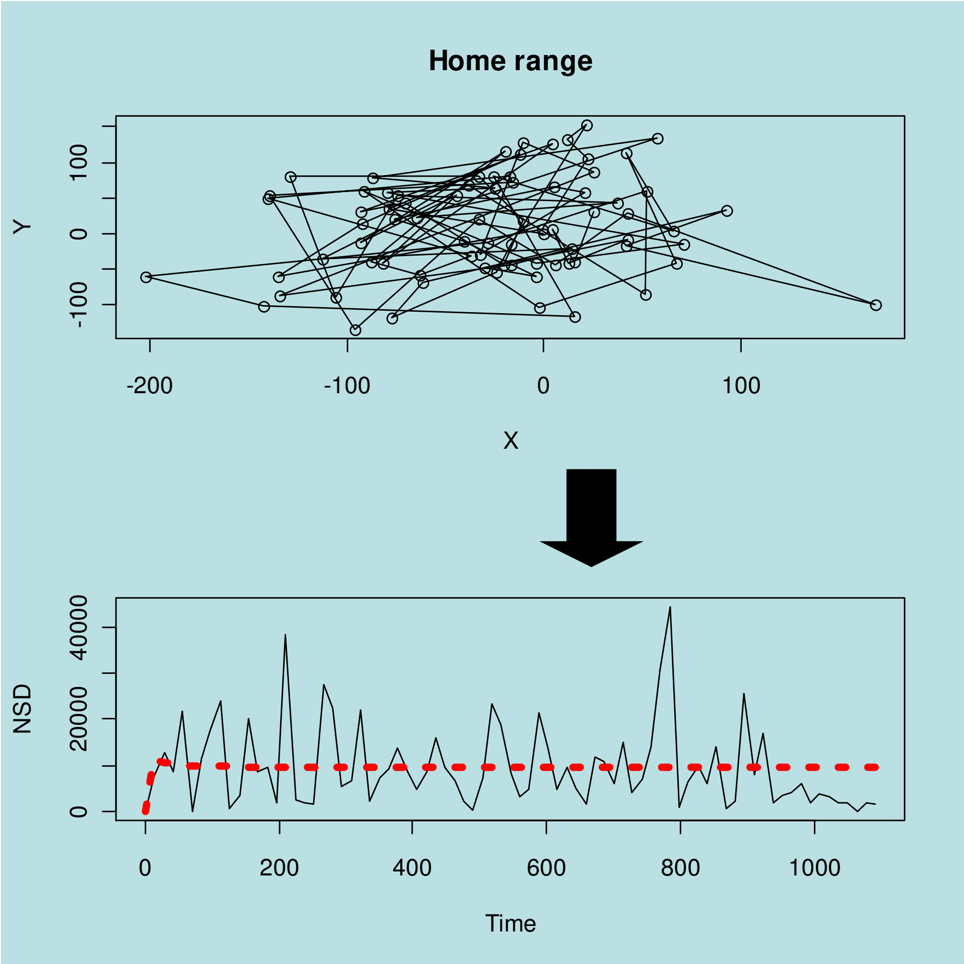
Observe …

Sedentarism (Home ranges)

"... most animals and plants keep to their proper homes, and do not needlessly wander about…"



Charles Darwin (1872) The origin of species 6th ed.



$$MSD = \phi_1 \left[1 - \exp(\phi_2 t) \right]$$

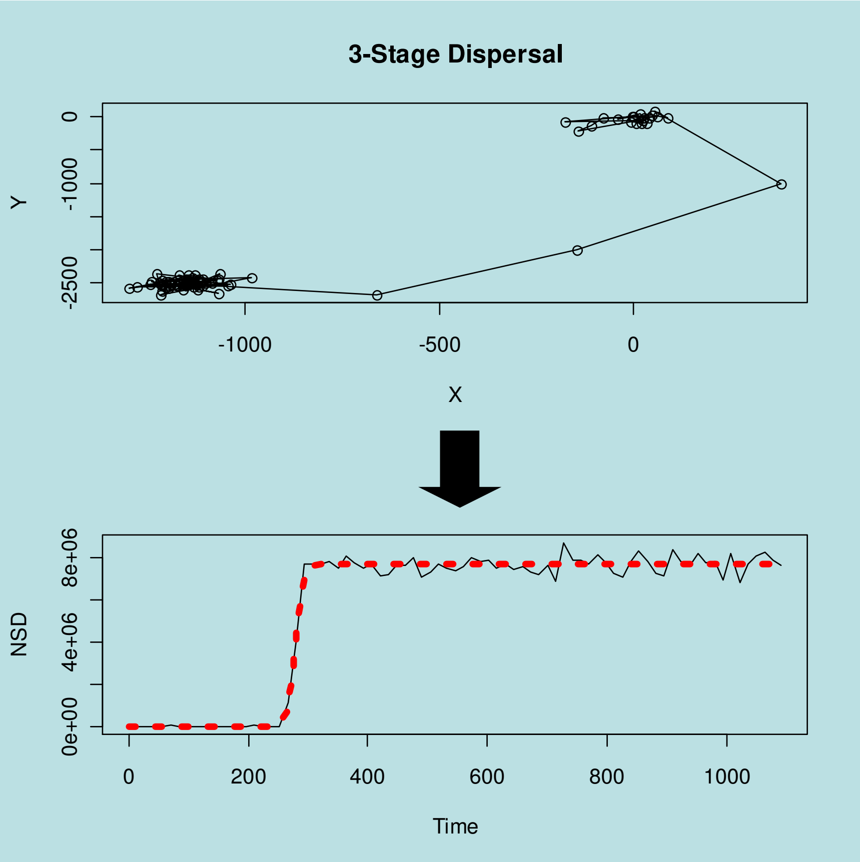
Moorcroft & Lewis (2006) Princeton U. Press
Borger et al. 2008 Ecol. Lett.
Borger & Fryxell (2012) Oxford University Press

Dispersal

But often animals search for a new home…

"Allen Tieren scheint der Trieb angeboren, ... das Verbreitungsgebiet ihrer Art zu erweitern …„

Kobelt (1902)



one-way movement without return

non-random **3-stage** process

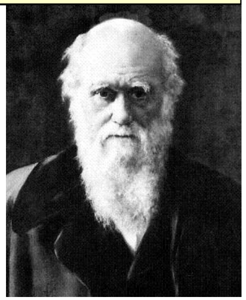
Clobert et al. (2009) Ecol. Lett.
Clobert et al. (2012) Oxford U. Press

$$MSD = \frac{\phi_3}{1 + \exp\left[\frac{(\phi_4 - t)}{\phi_5}\right]}$$

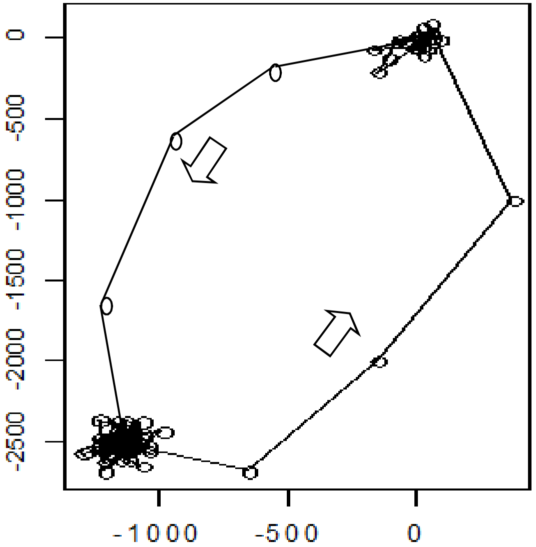
Borger & Fryxell (2012) Oxford University Press

Migration

"... most animals and plants keep to their proper homes,
and do not needlessly wander about…
**we see this also with migratory birds,
which almost always come back to their home**"

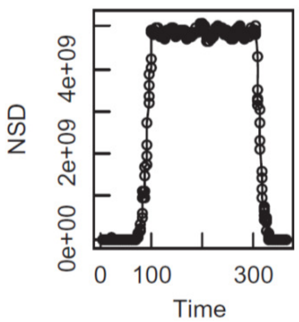


Charles Darwin (1872) The origin of species 6th ed.



- directed, oriented movements
  - two-way return movements
    - spatial coupling of distant areas

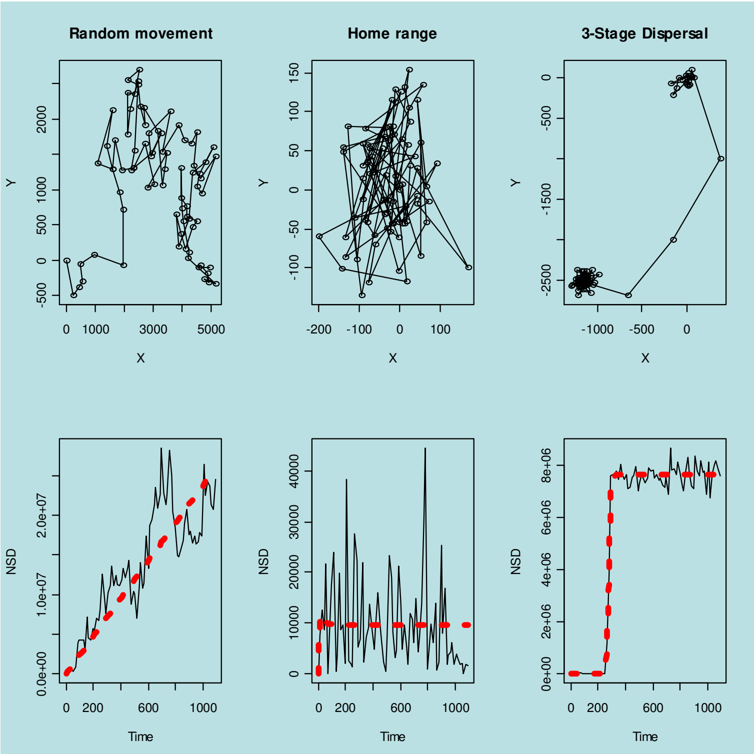
NSD of migration



$$\textbf{MSD} = \frac{\delta_s}{1+\exp\left(\frac{\theta_s - t}{\varphi_s}\right)} + \frac{-\delta_a}{1+\exp\left(\frac{\theta_a - t}{\varphi_a}\right)}$$

Borger et al. (2011) Oxford University Press
Bunnefeld, Borger et al. (2011) J. Anim. Ecol.
Borger & Fryxell (2012) Oxford University Press

Capturing the functional form of movement patterns with nonlinear models



Nonlinear Models

$$MSD = Dt^{\alpha}$$

$$MSD = \phi_1\left[1-\exp(\phi_2 t)\right]$$

$$MSD = \frac{\phi_3}{1+\exp\left[\frac{(\phi_4 - t)}{\phi_5}\right]}$$

$$MSD = \frac{\delta_s}{1+\exp\left(\frac{\theta_s - t}{\varphi_s}\right)} + \frac{-\delta_a}{1+\exp\left(\frac{\theta_a - t}{\varphi_a}\right)}$$

Hierarchical Modelling Framework

Borger & Fryxell (2012) Oxford University Press

Evaluate support from the data at individual level

Correspondence criterion

$$CC_i = 1 - \frac{\sum_{j=1}^{n_i}\left(y_{ij} - \hat{y}_{ij}\right)^2}{\sum_{j=1}^{n_i}\left(y_{ij} - \bar{y}\right)^2 + \sum_{j=1}^{n_i}\left(\hat{y}_{ij} - \bar{\hat{y}}\right)^2 + n_i\left(\bar{y} - \bar{\hat{y}}\right)^2} \qquad (-1 \leq \mathrm{CC} \geq 1)$$

Huang et al. (2009) Can. J. For. Res.
Borger & Fryxell (2012) Oxford Univ. Press

Does this really work?
→ Simulation study

Individuals (N = 140 each) moving according to different movement rules:

Pre-dispersal phase: 30 – 515 days
Dispersal phase: 30 – 90 days

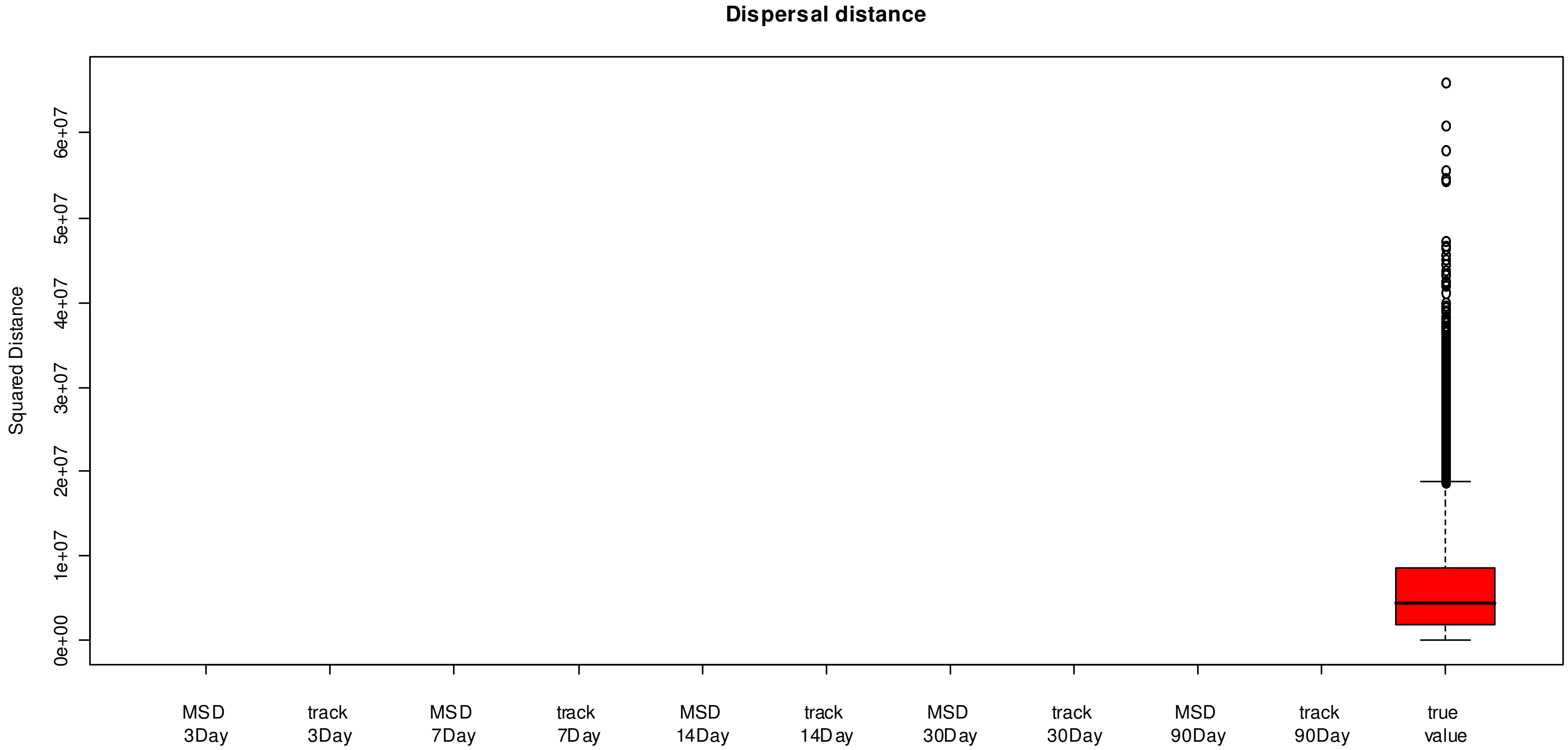
repeat 100 times

(i) Identify dispersal
(ii) Estimate correct parameters (distance, timing)
(iii) Sampling effect:

- MSD vs NSD
    - 3 days – 7 days – 14 days
    - 30 days – 90 days

Does this really work?
→ Dispersal distance

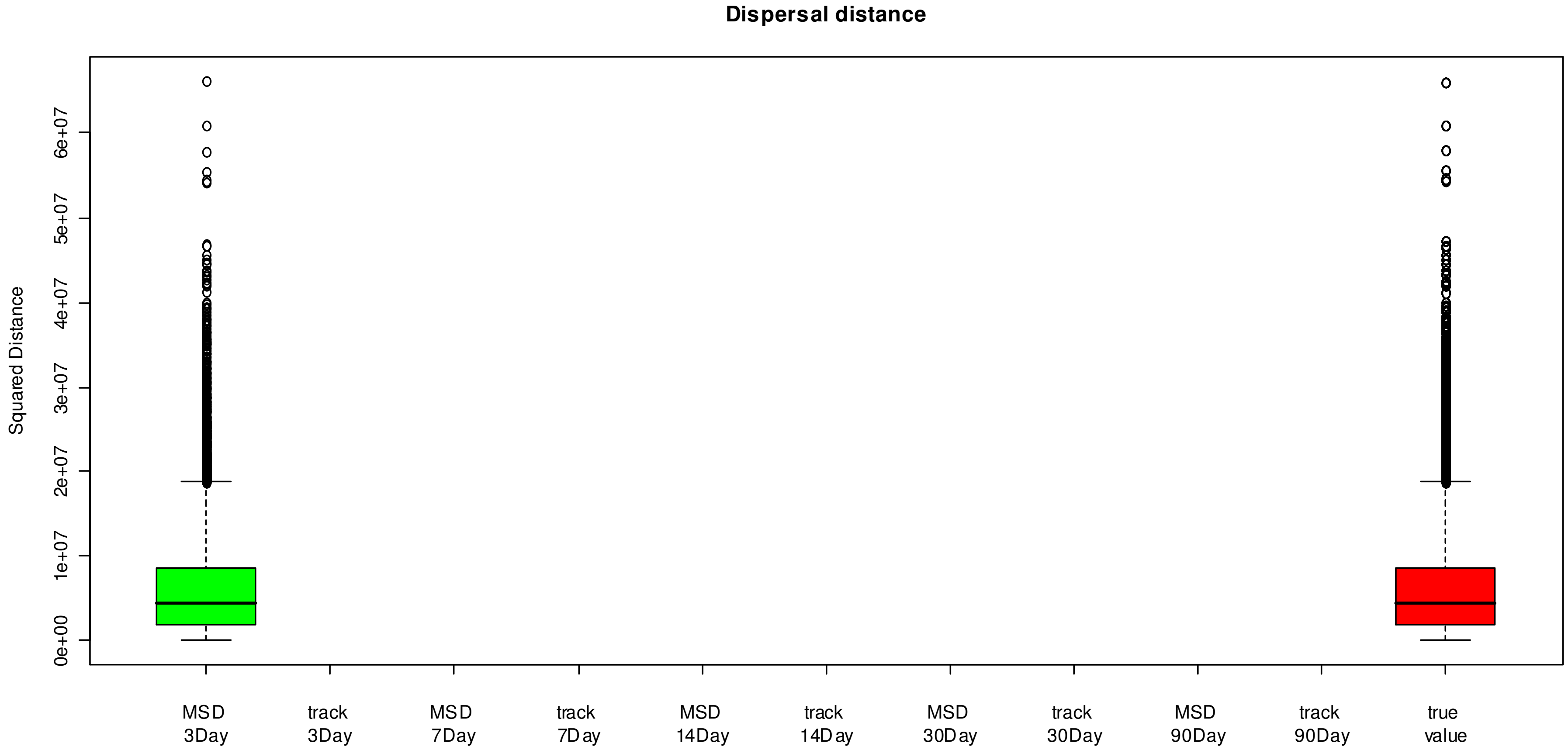
Simulate dispersal paths



Borger & Fryxell (2012) Oxford University Press

Does this really work?
→ Dispersal distance

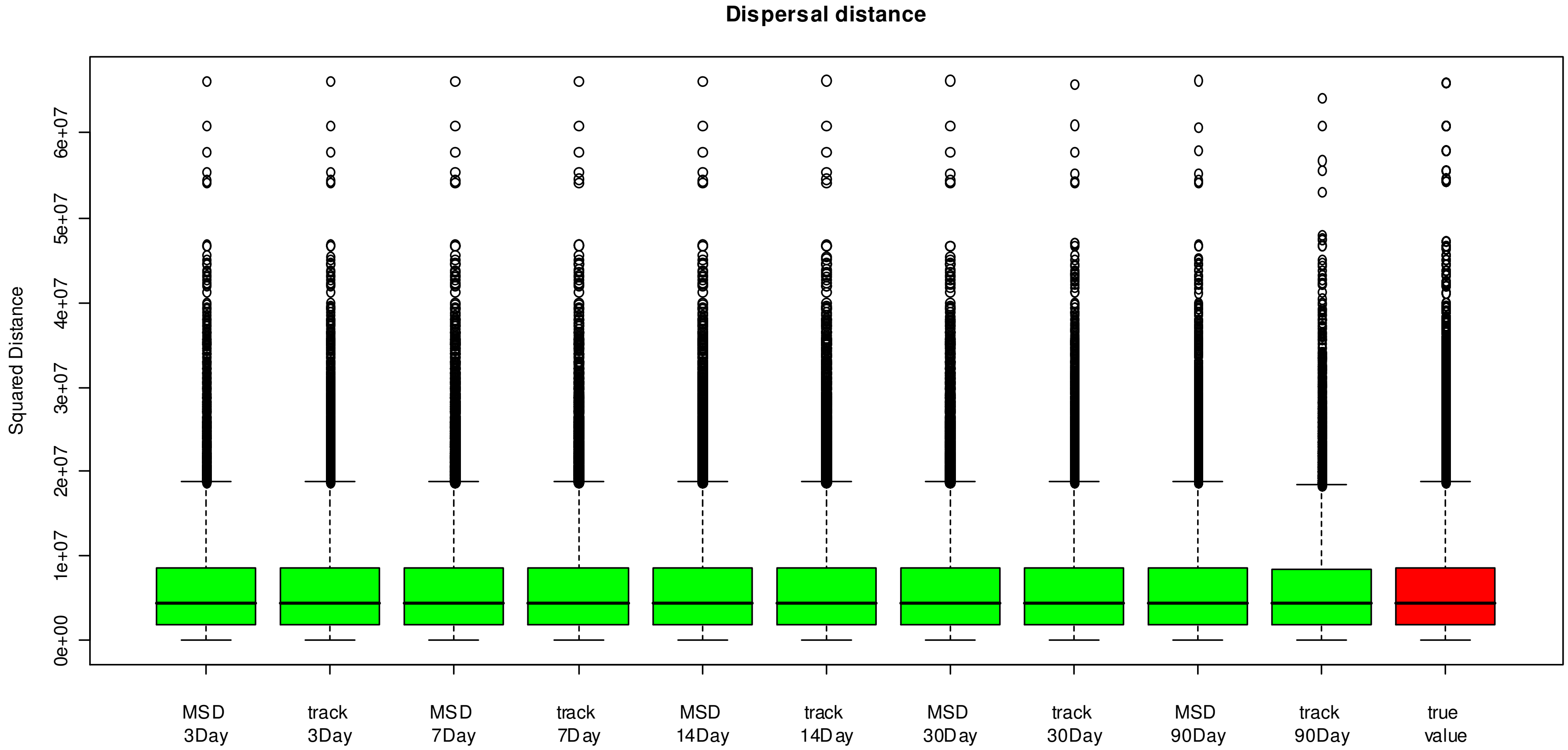
Simulate dispersal paths



Borger & Fryxell (2012) Oxford University Press

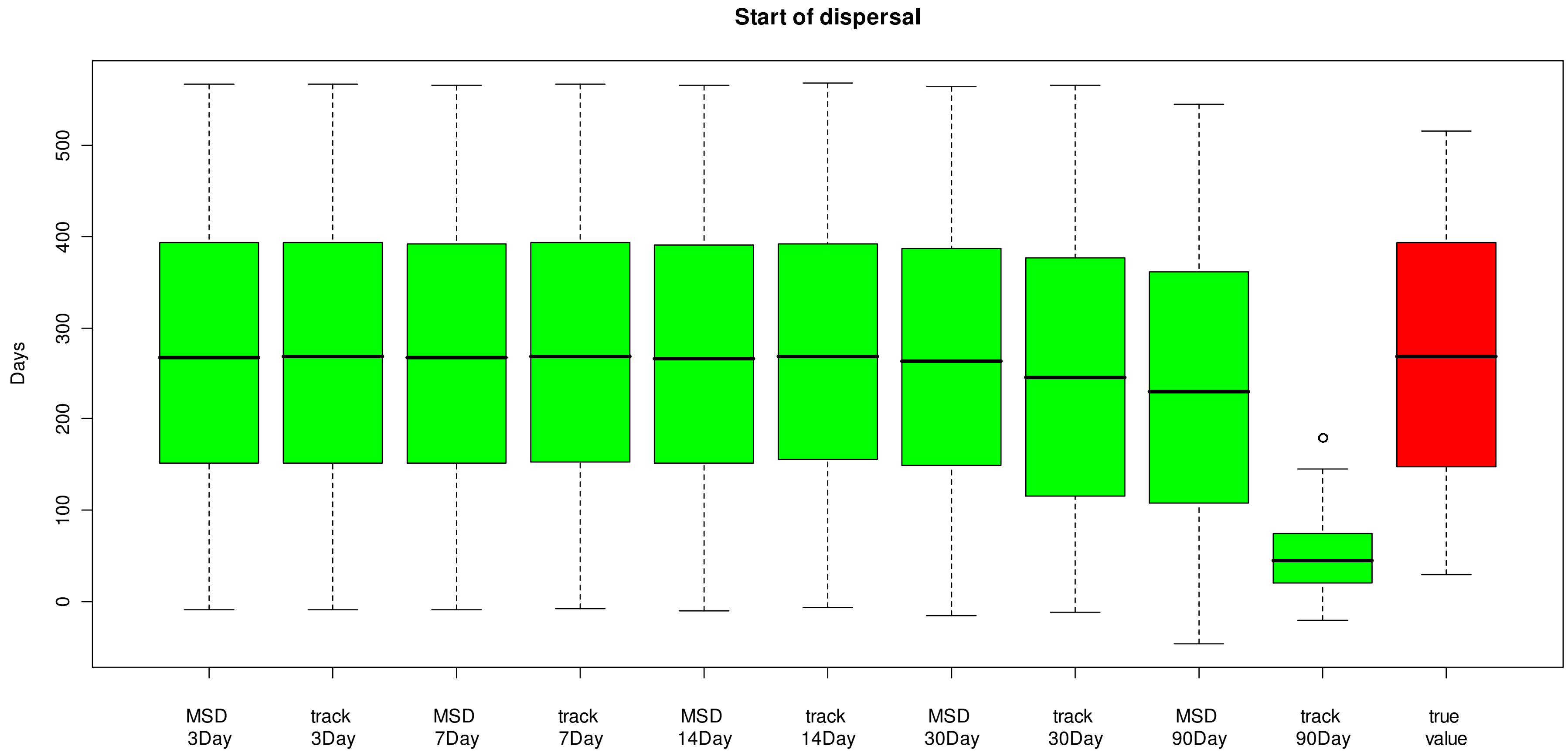
Does this really work?
→ Dispersal distance

Simulate dispersal paths

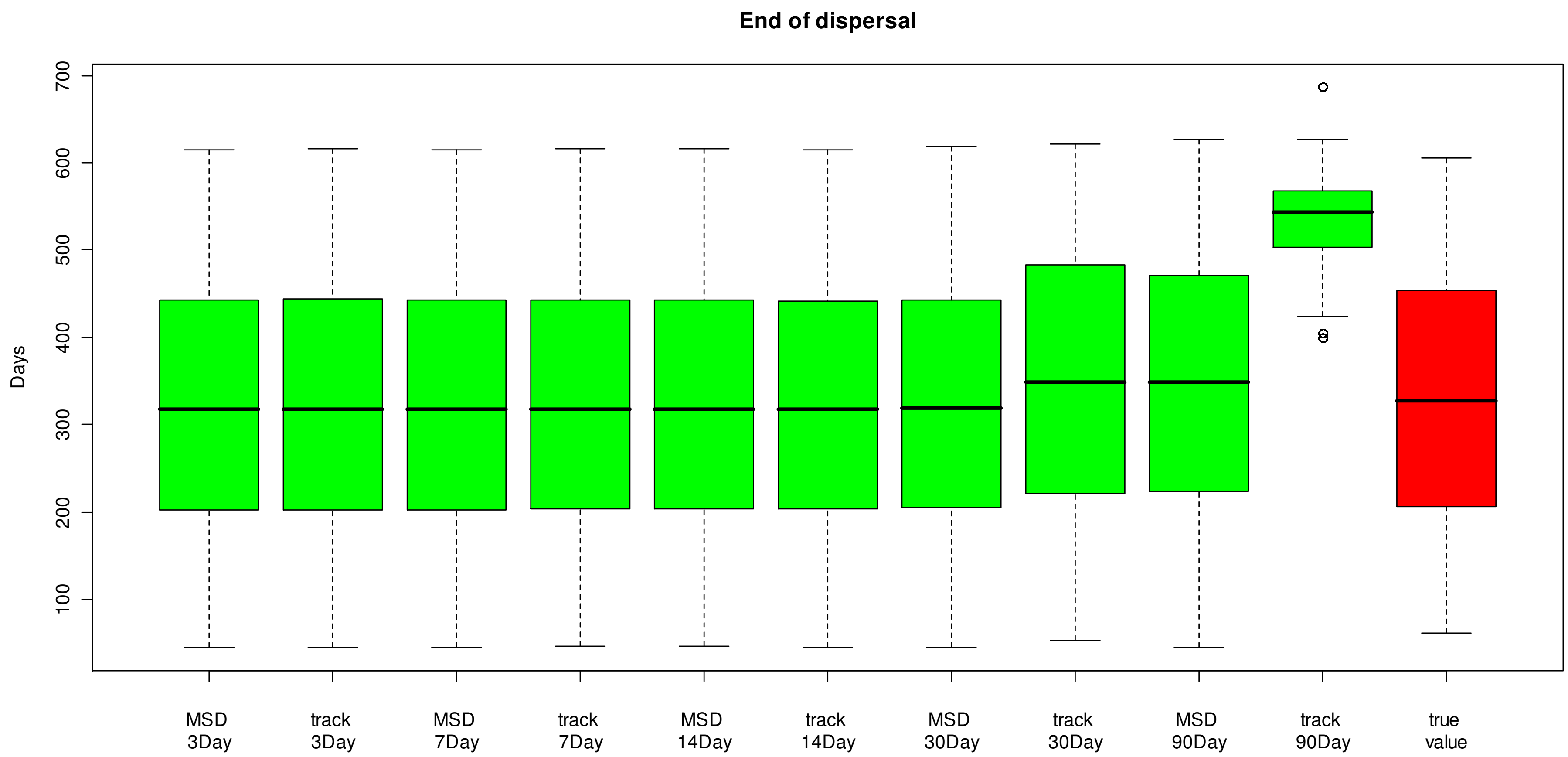


Borger & Fryxell (2012) Oxford University Press

Does this really work?
→ Departure



Does this really work?
→ Settlement



Does this really work?
→ Heterogeneous movement modes

Simulate different modes

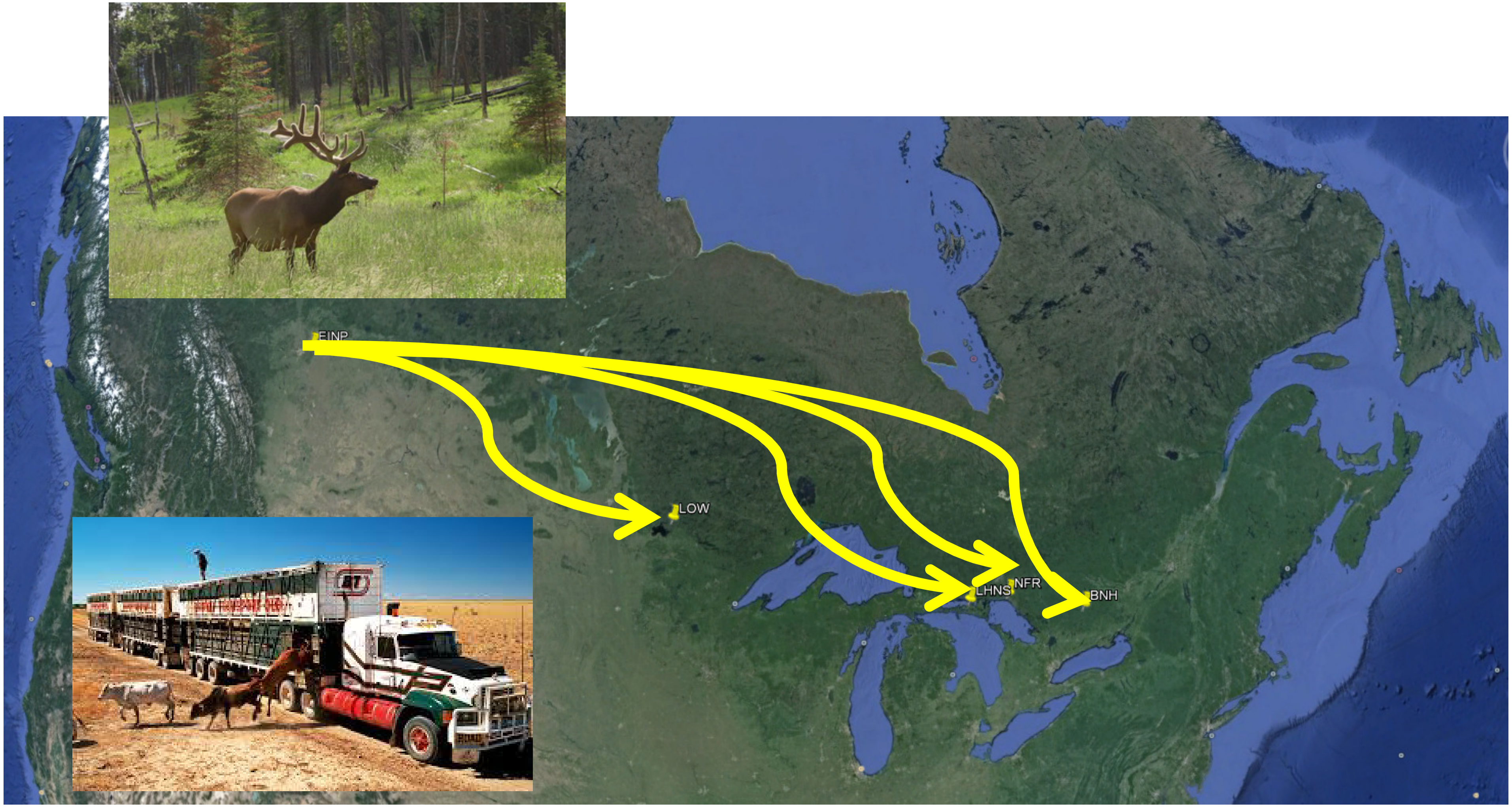
- **20 individuals HR behaviour**
- **20 nomadic (CRW)**
- **→ 100 dispersers**

- **repeat 100 times**

- **88% mean classification success (up to 100%)**

Borger & Fryxell (2012) Oxford University Press

Ontario Elk Restoration Initiative



443 elks released; 416 radiocollared

release age: 0 – 15+ years

Ontario Elk Reintroduction

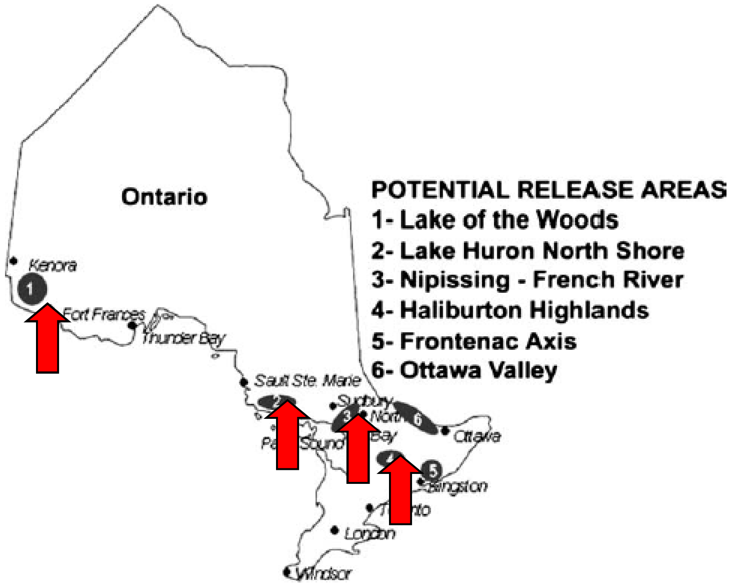


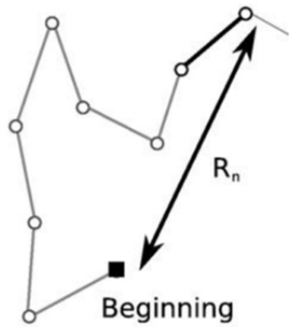
Figure 1. Potential elk release areas in Ontario.

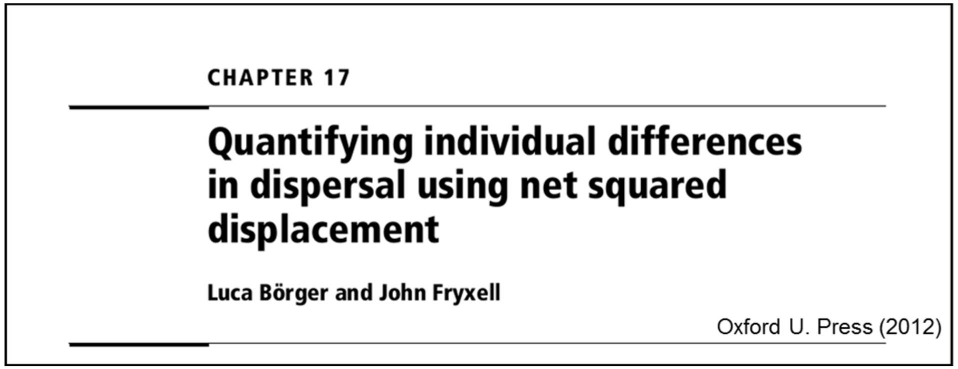
Rick Rosatte (Trent Univ.)

Josef Hamr (Cambrian College)

Mark Ryckman (Manitoba Cons.)

John Fryxell (U. of Guelph)





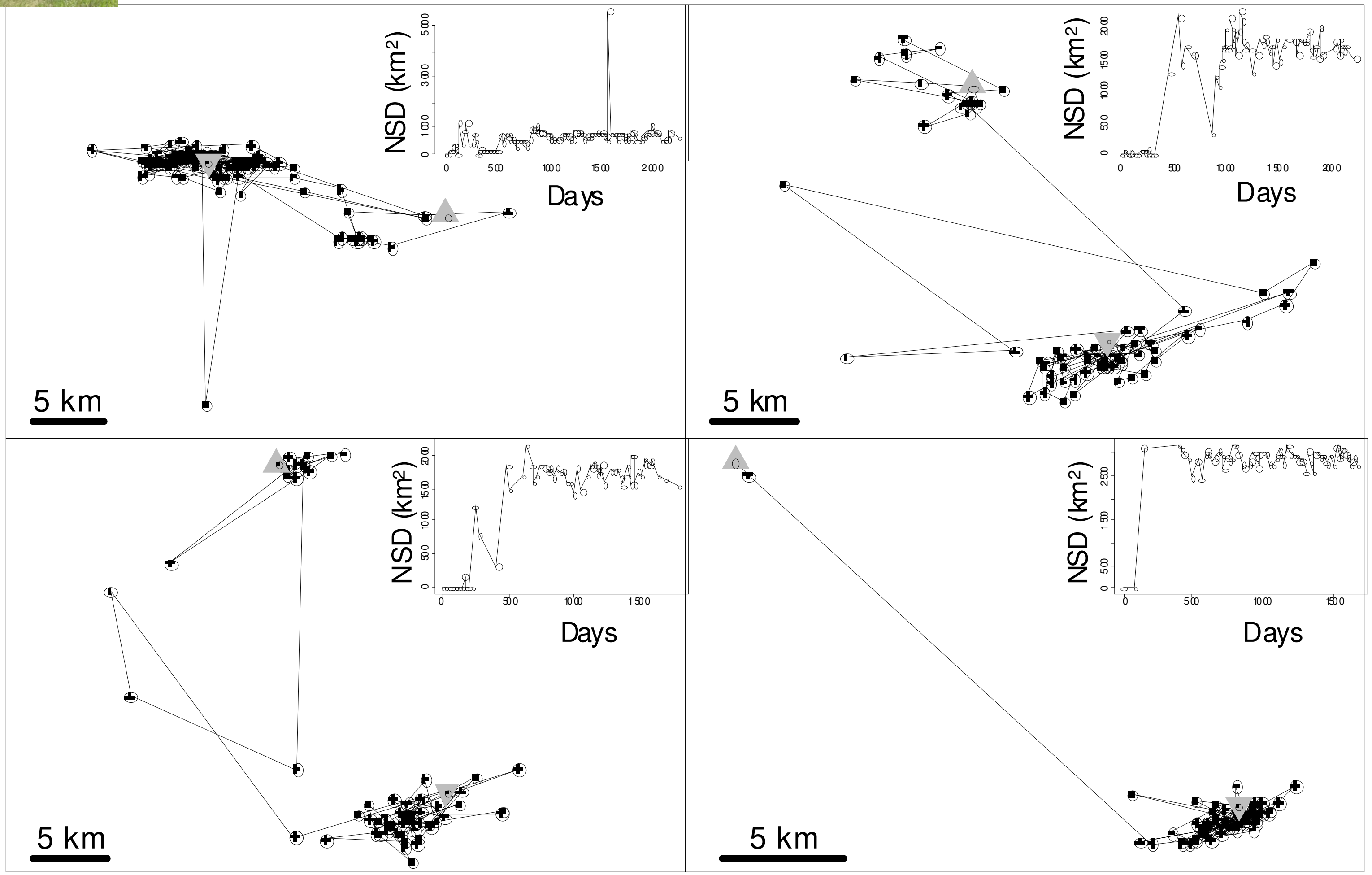
CHAPTER 17

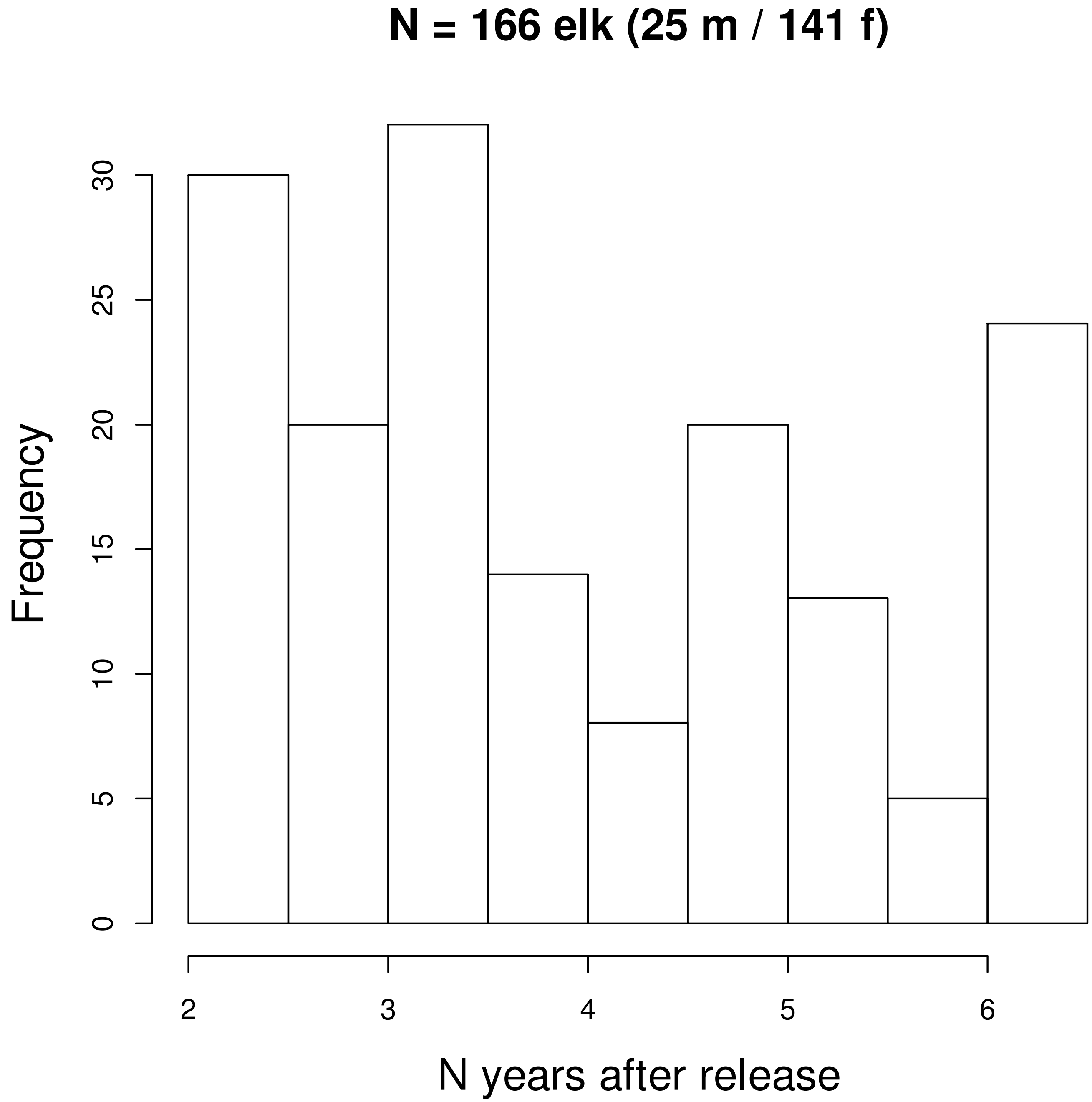
Quantifying individual differences in dispersal using net squared displacement

Luca Börger and John Fryxell

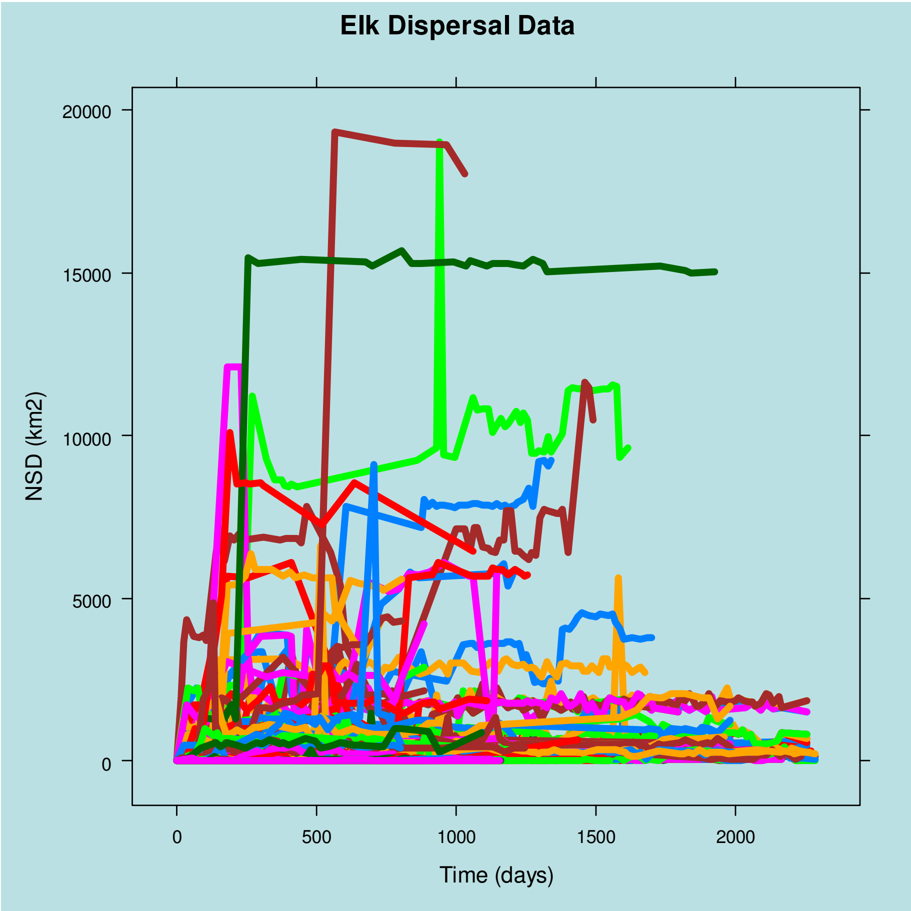
Oxford U. Press (2012)

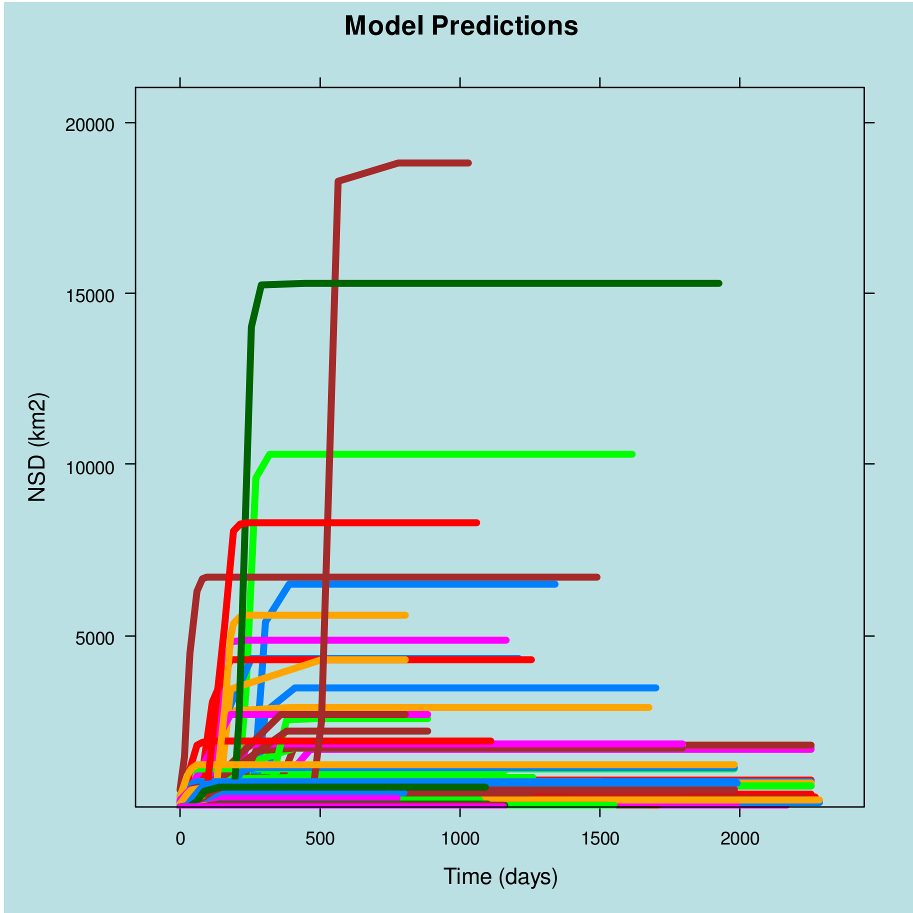
Example: four female elk movement paths and NSD



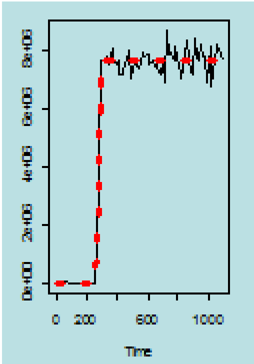

N = 166 elk (25 m / 141 f)
Frequency
0
5
10
15
20
25
30
2
3
4
5
6
N years after release

Individual variation in dispersal

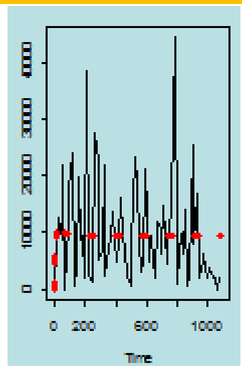


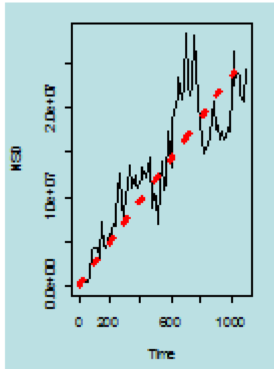


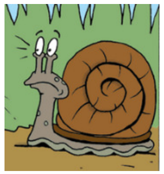
Movement modes – classification results



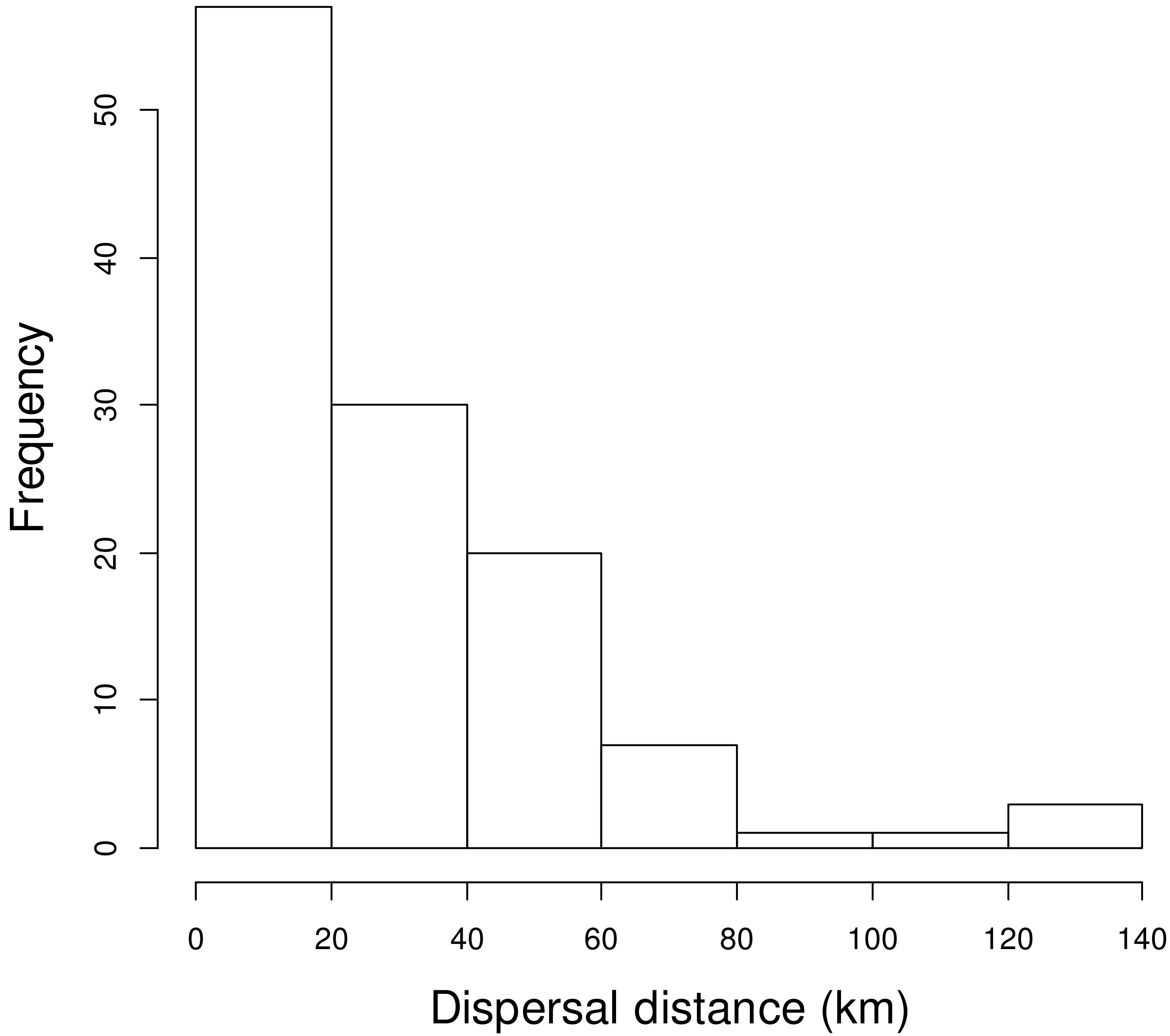
	Dispersed	Sedentary	not settled
female	108	9	23
male	11	3	12



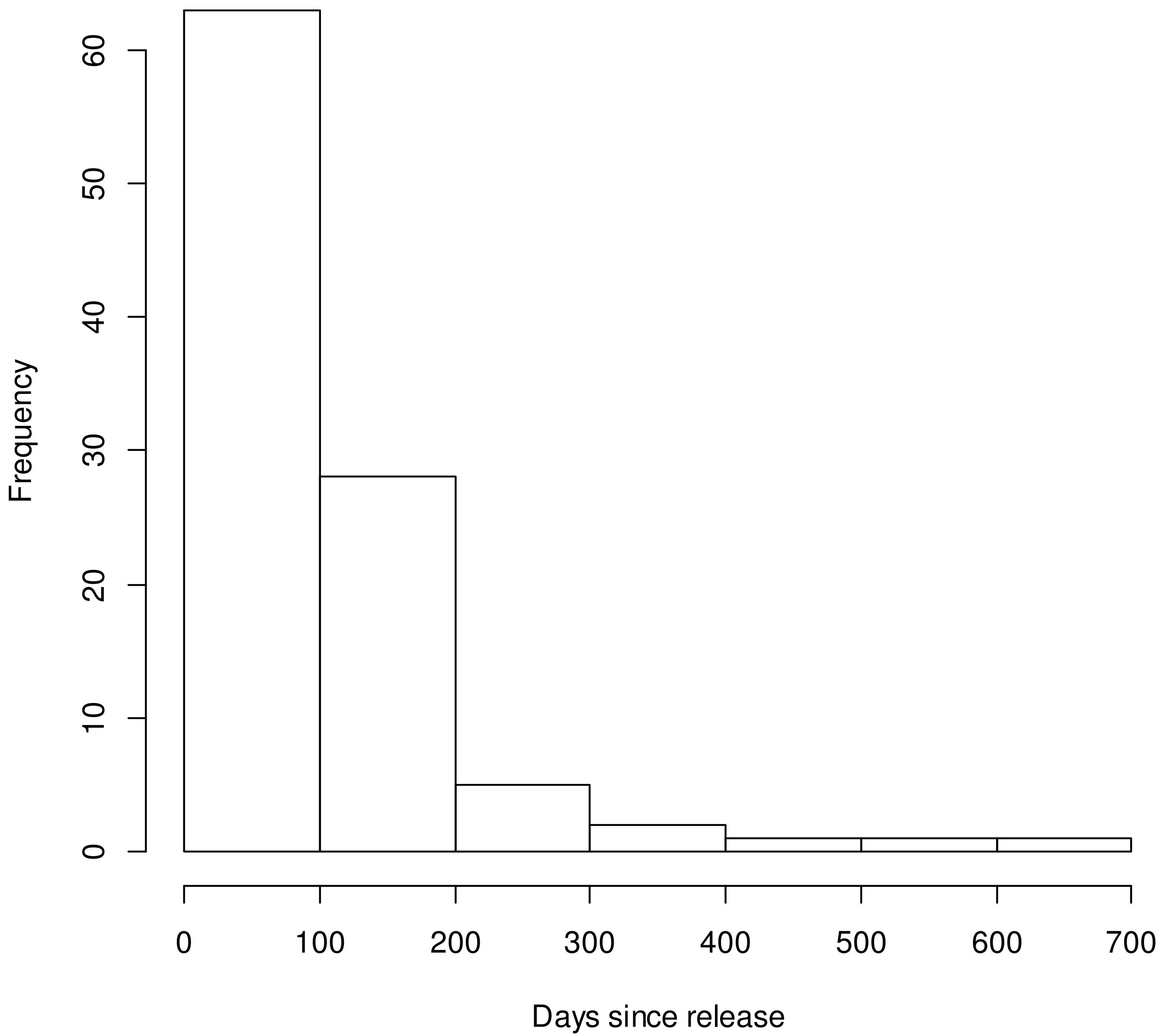




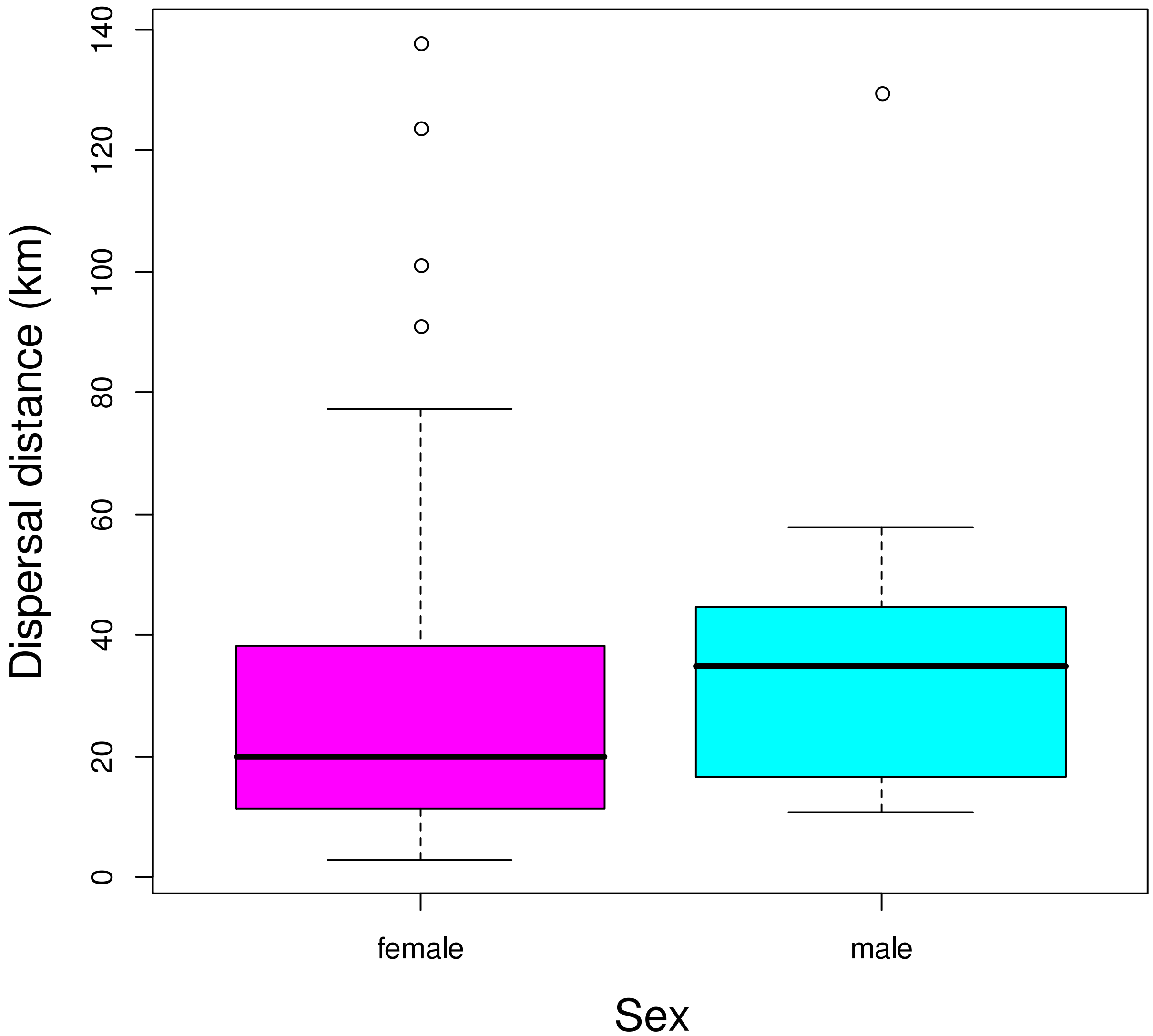
Distance of dispersal



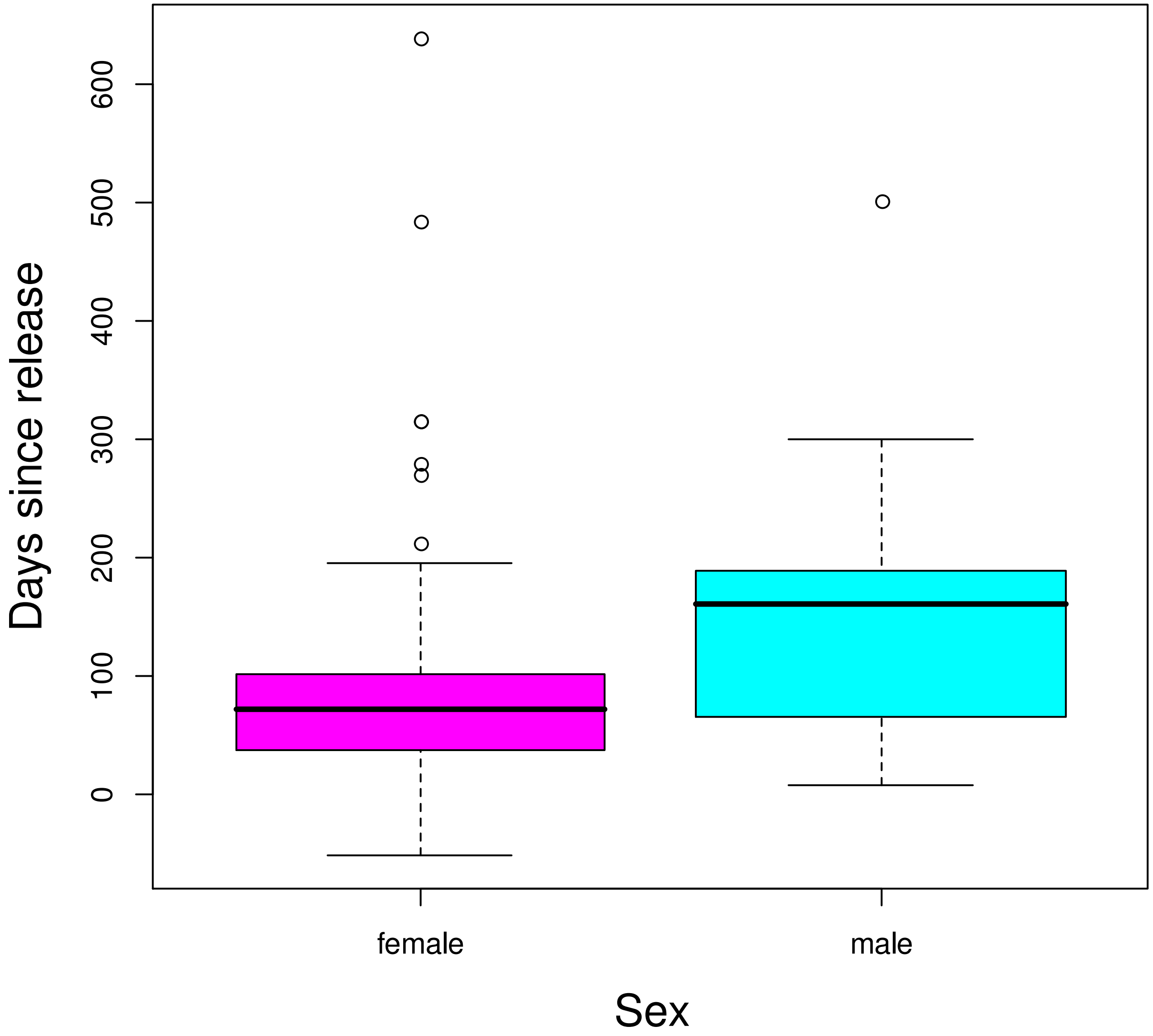
Start of dispersal



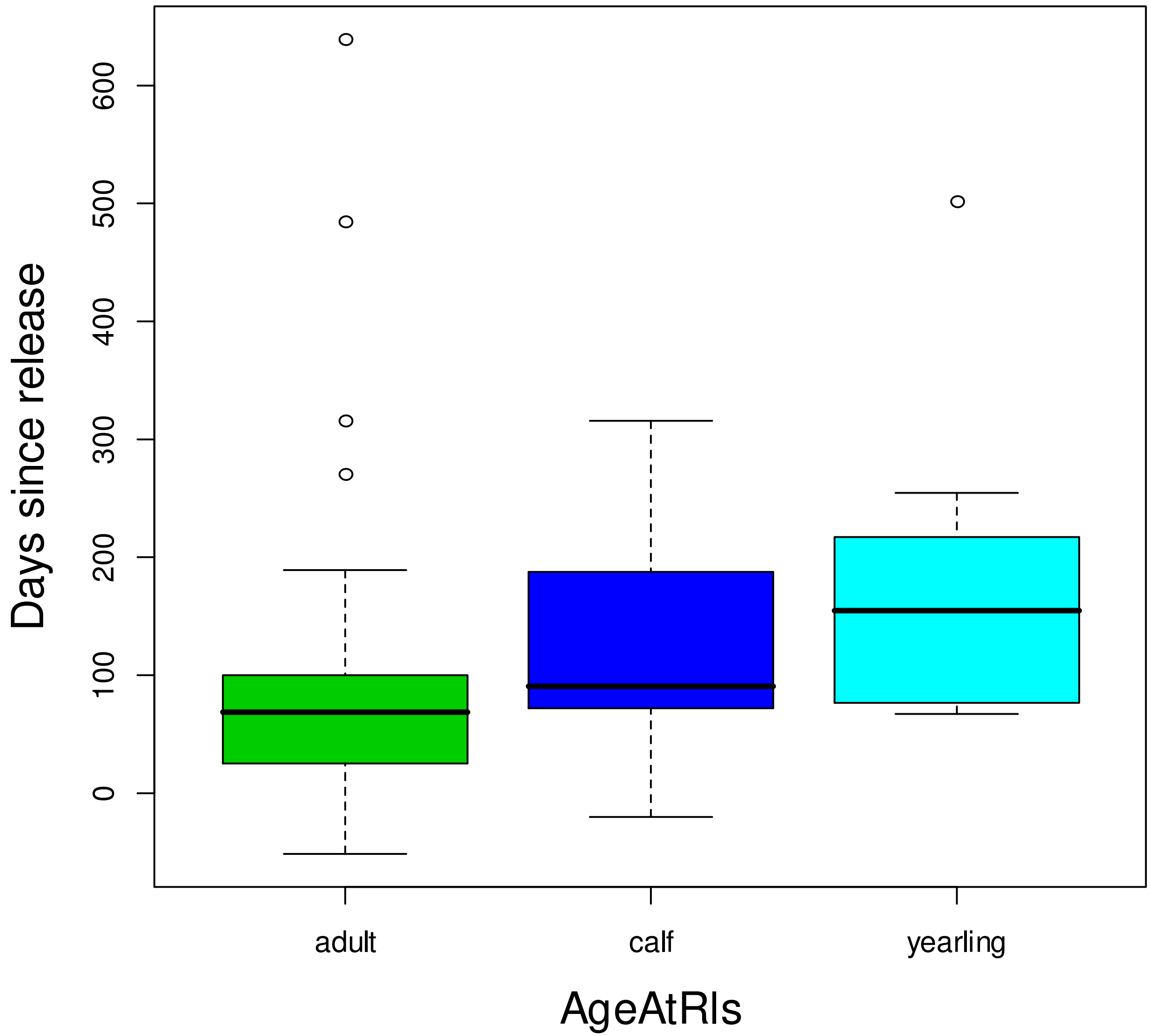
Sex differences - distance



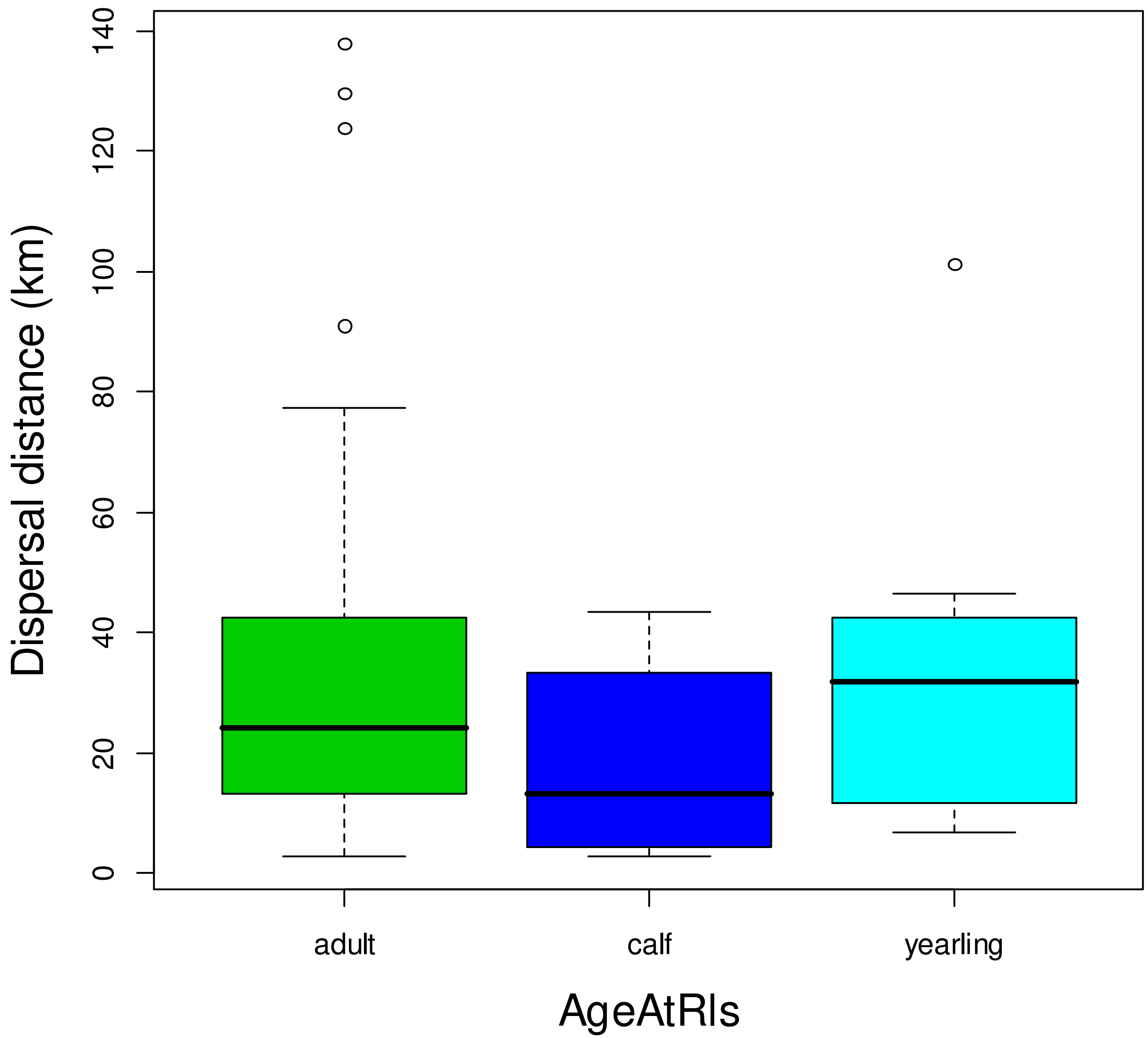
Sex differences - timing



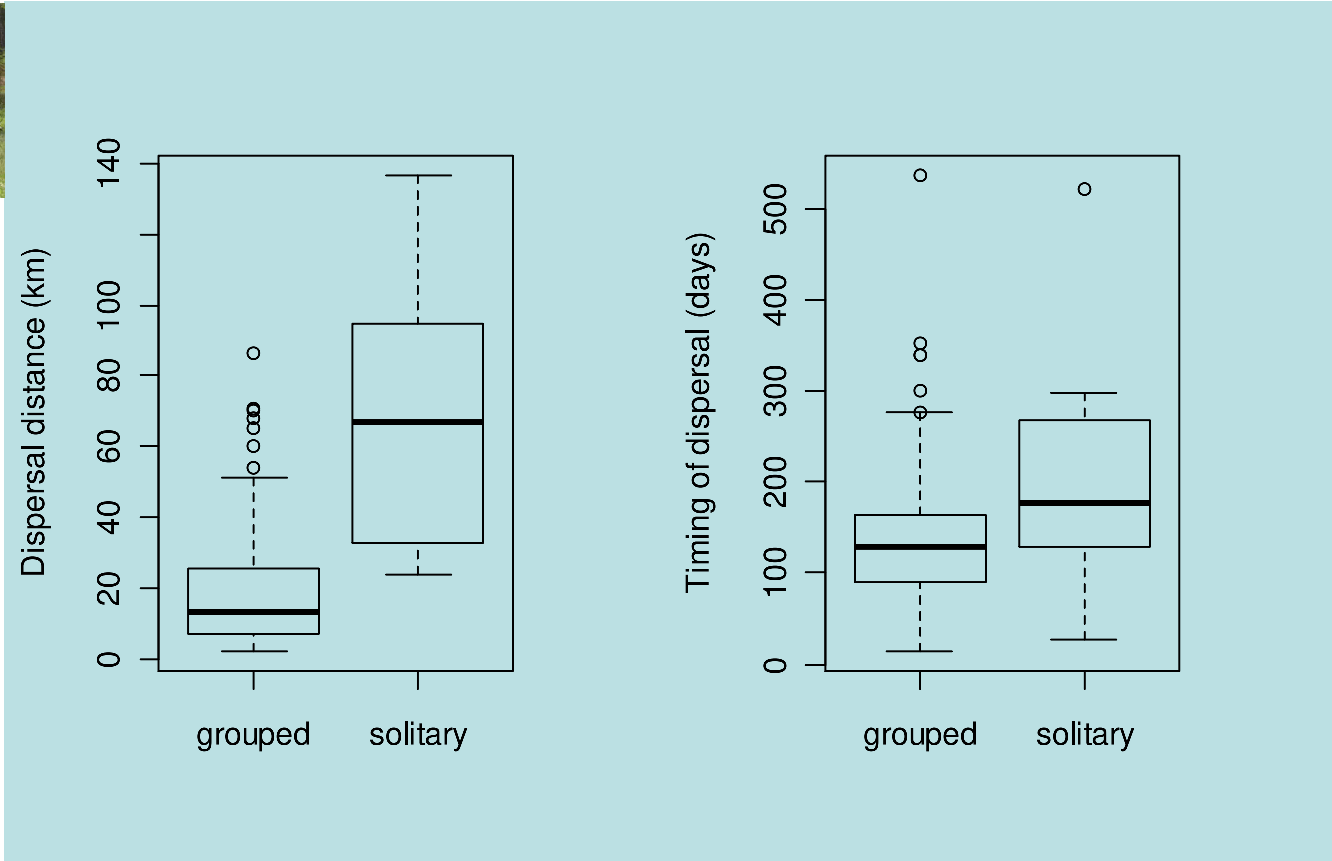
Age effects - timing



Age effects - distance



Determinants of individual variation in dispersal



Conspecifics: Distance (25km vs. 78km) + Timing (5 month vs. 8 month))

Release conditions: Timing (up to 2 months diff) + Speed

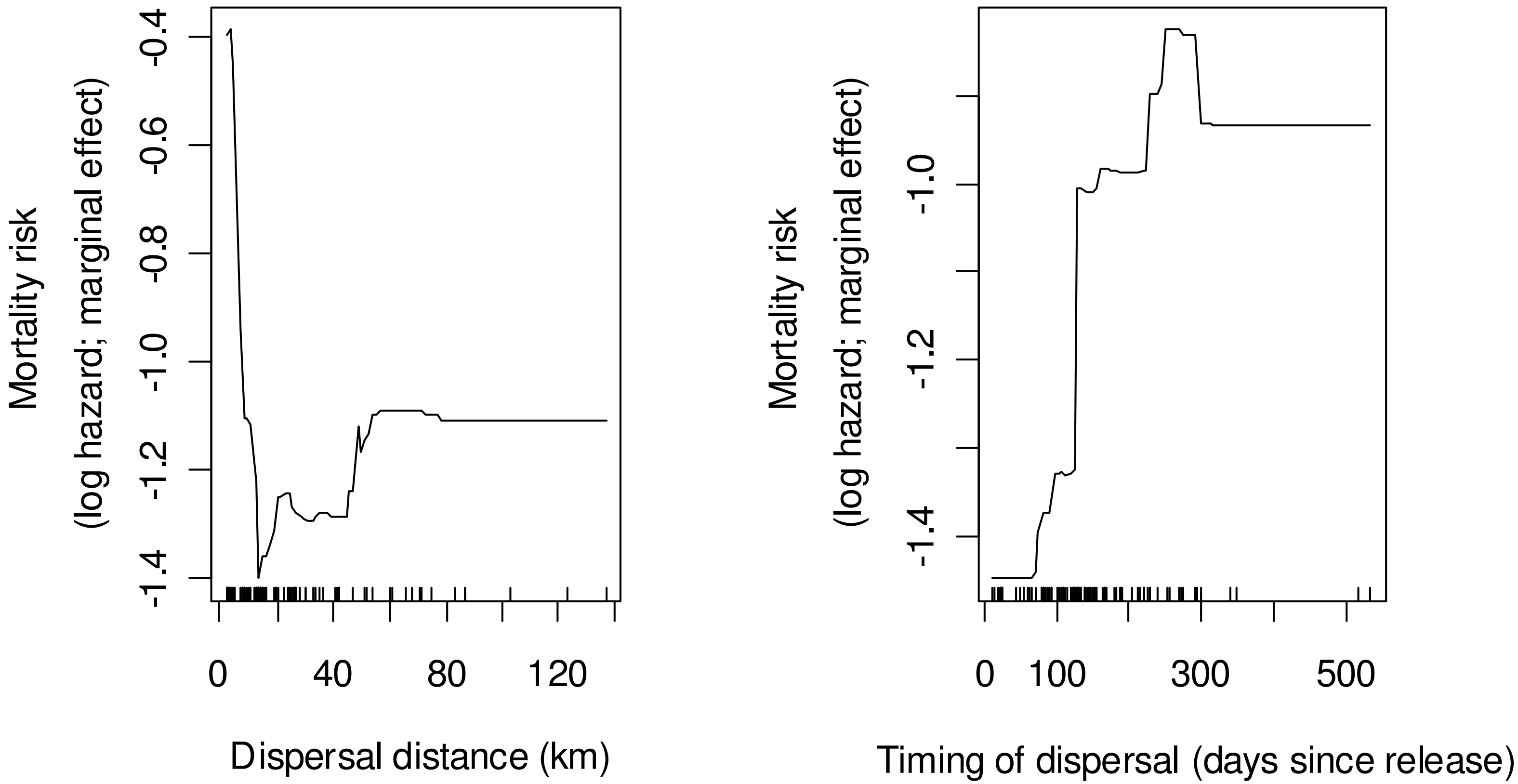
20% other individual differences

Survival consequences
2 – 7 yrs postrelease

41/142 radio-collared elk died
(tracked on average for four years post-release)

15 killed by wolves
5 drowned
7 were hit by a car/train/shot
5 died of infections/starvation
9 death causes unknown

Survival consequences
2 – 7 yrs postrelease
Distance & Timing Dispersal



Cox models, 19% and 12% relative contribution,

Additional 3% influence: higher marginal risk for solitary individuals

Survival consequences
2 – 7 yrs postrelease
Age

Cox models, 26% relative contribution,

Increasing with age at release

Survival consequences
2 – 7 yrs postrelease
Habitat

Proportion of forest: 19% relative contribution

Proportion of pastures: 7% relative contribution

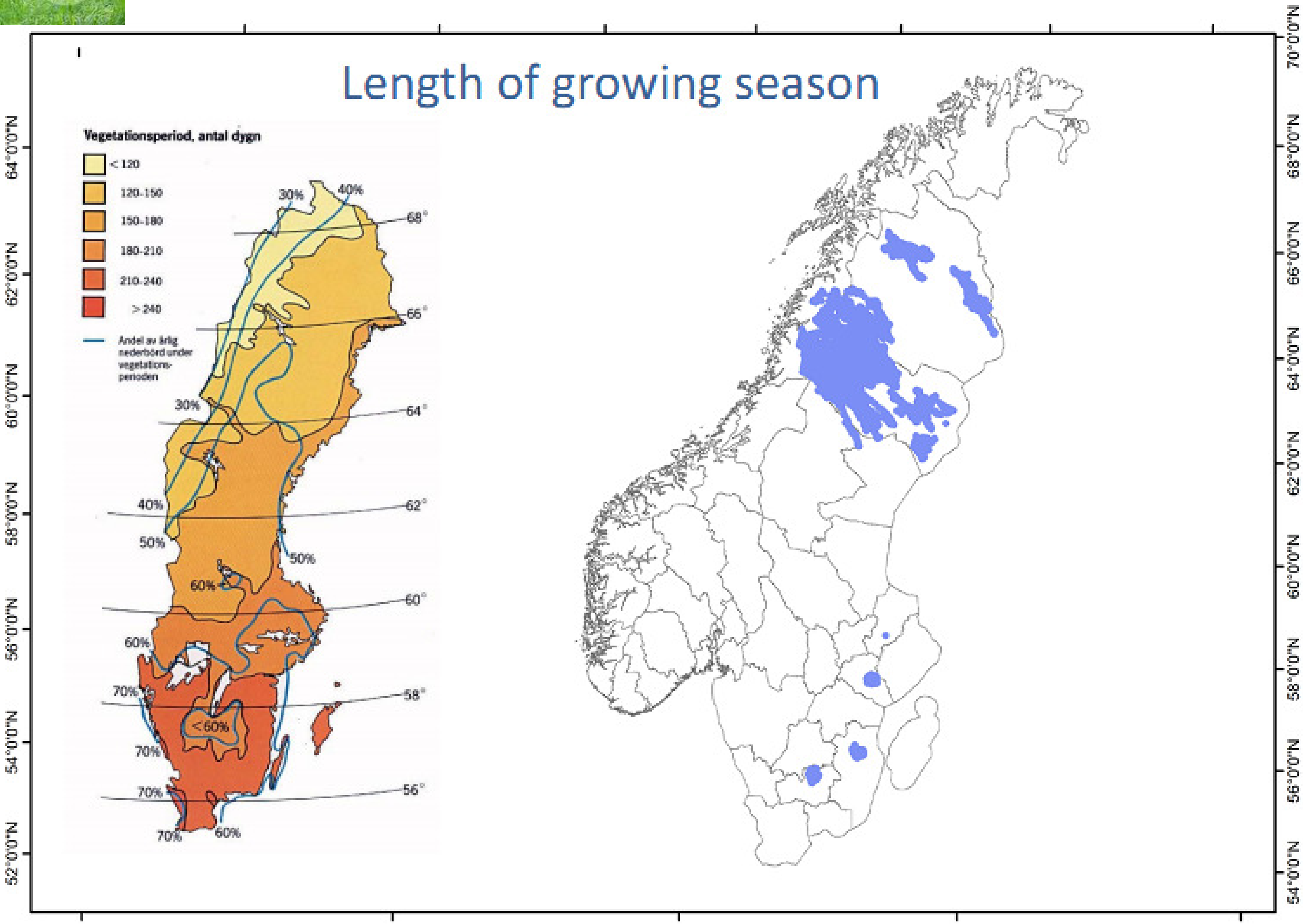
Survival consequences
2 – 7 yrs postrelease
Release area

Differences between study areas: 15% relative contribution

Climate (green-up); forest type; predator density; deer density; human density

Moose space use across Sweden

with Navinder Singh & Goran Erikson – SLU Umea

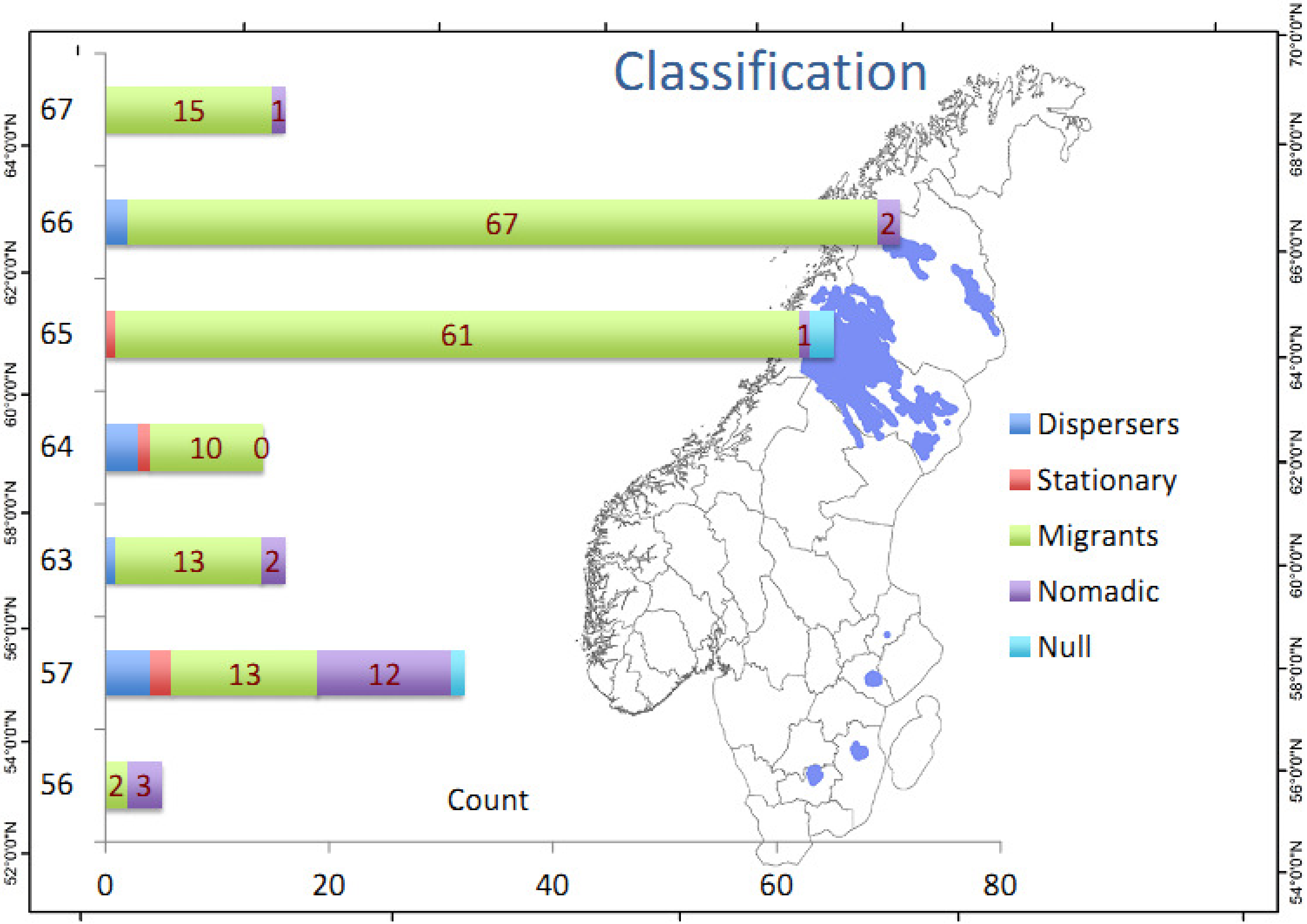


213 GPS-collared females – annual scale

> 1100 km latitudinal gradient

Singh, Borger et al. (2012) Ecological Applications

Moose space use across Sweden



Singh, Borger et al. (2012) Ecological Applications

Moose space use across Sweden

Decisions

↓

Behavioural changes

? 'drivers'

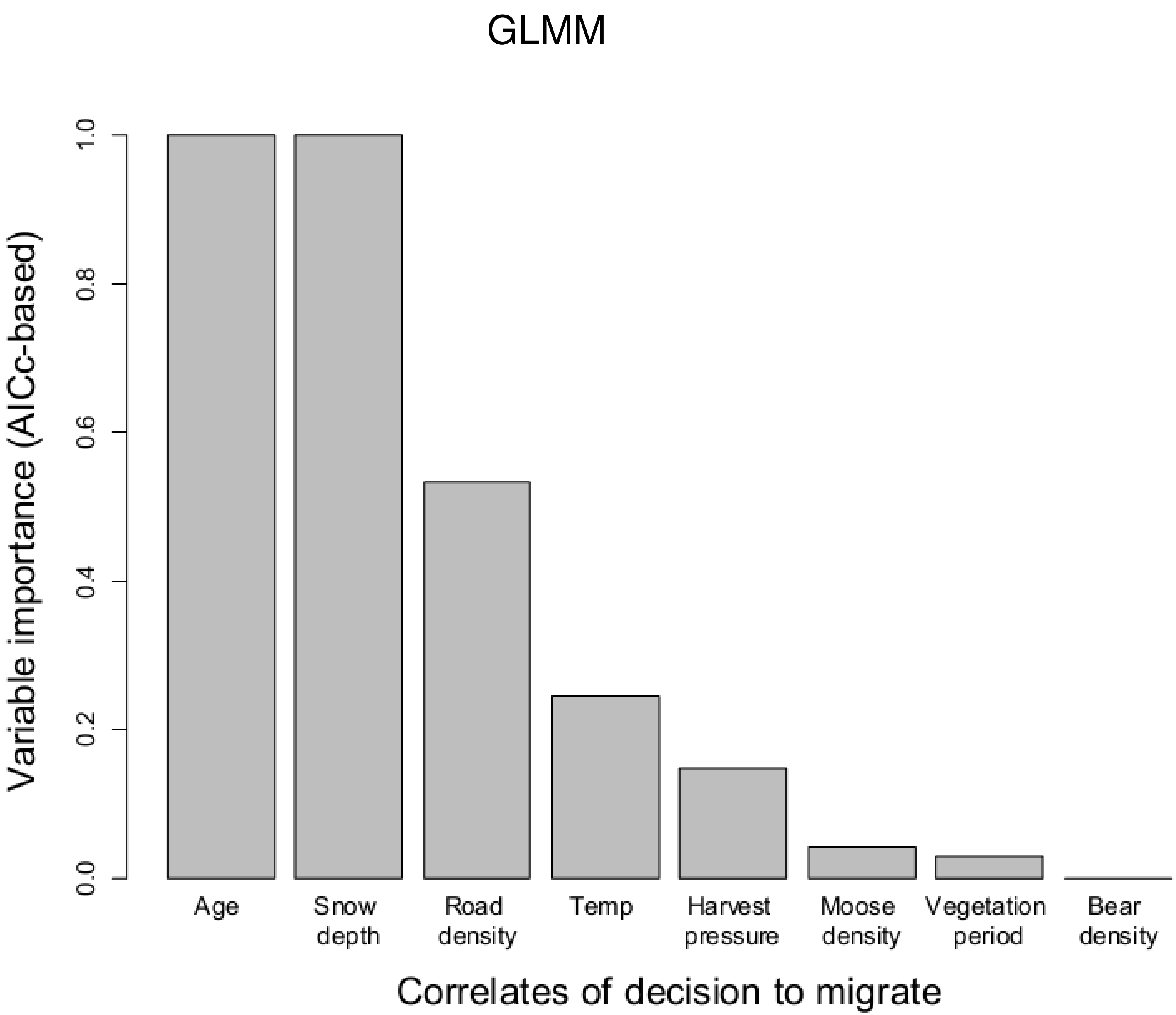
Migratory mode ~ Snow depth,

Age,

Roads, Productivity (annual Temp), Vegetation,

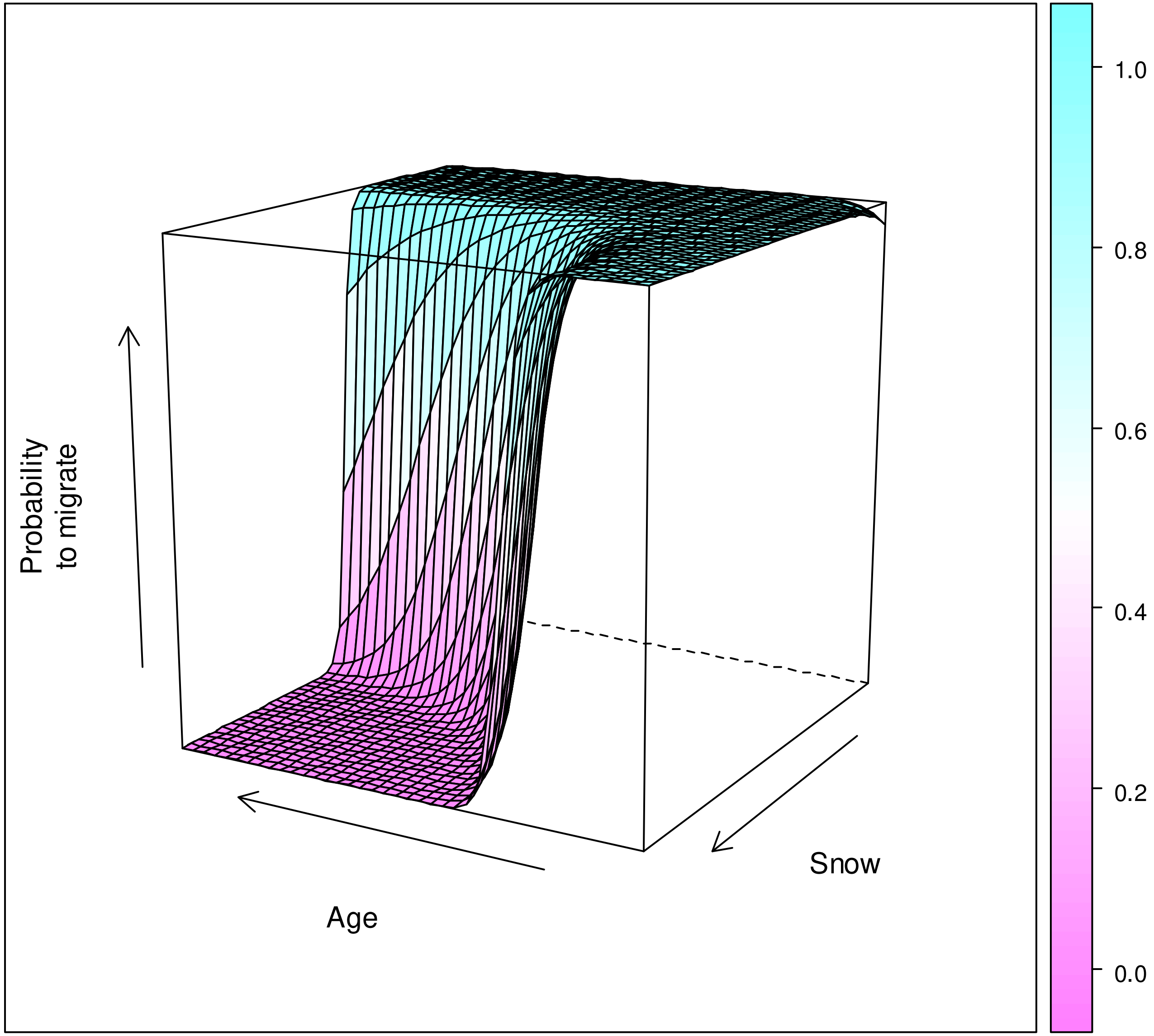
Harvest, Predators, Conspecifics

Singh, Borger et al. (2012) Ecological Applications

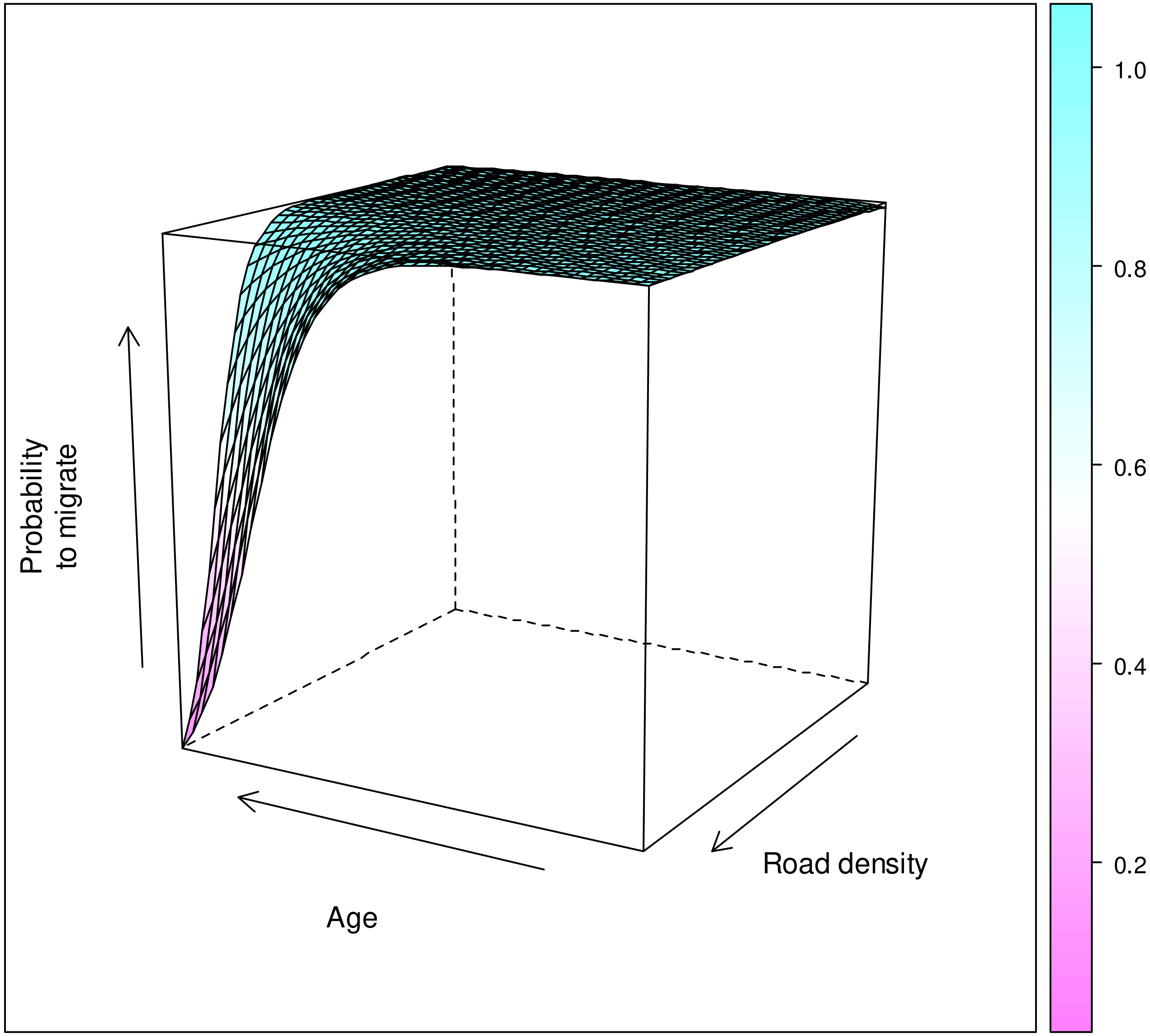


Singh, Borger et al. (2012) Ecological Applications

Moose space use across Sweden

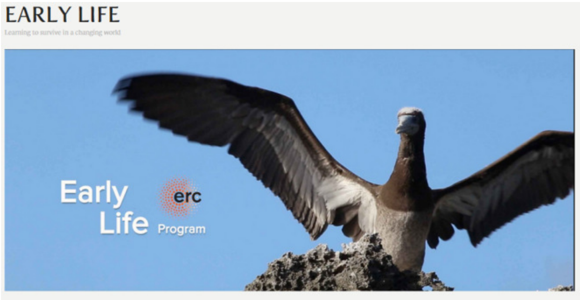


Singh, Borger et al. (2012) Ecological Applications

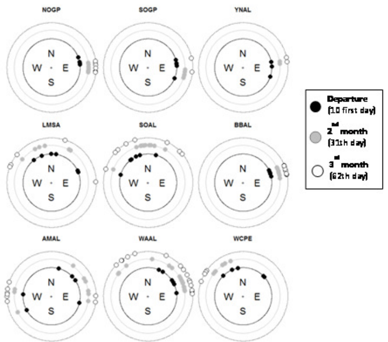


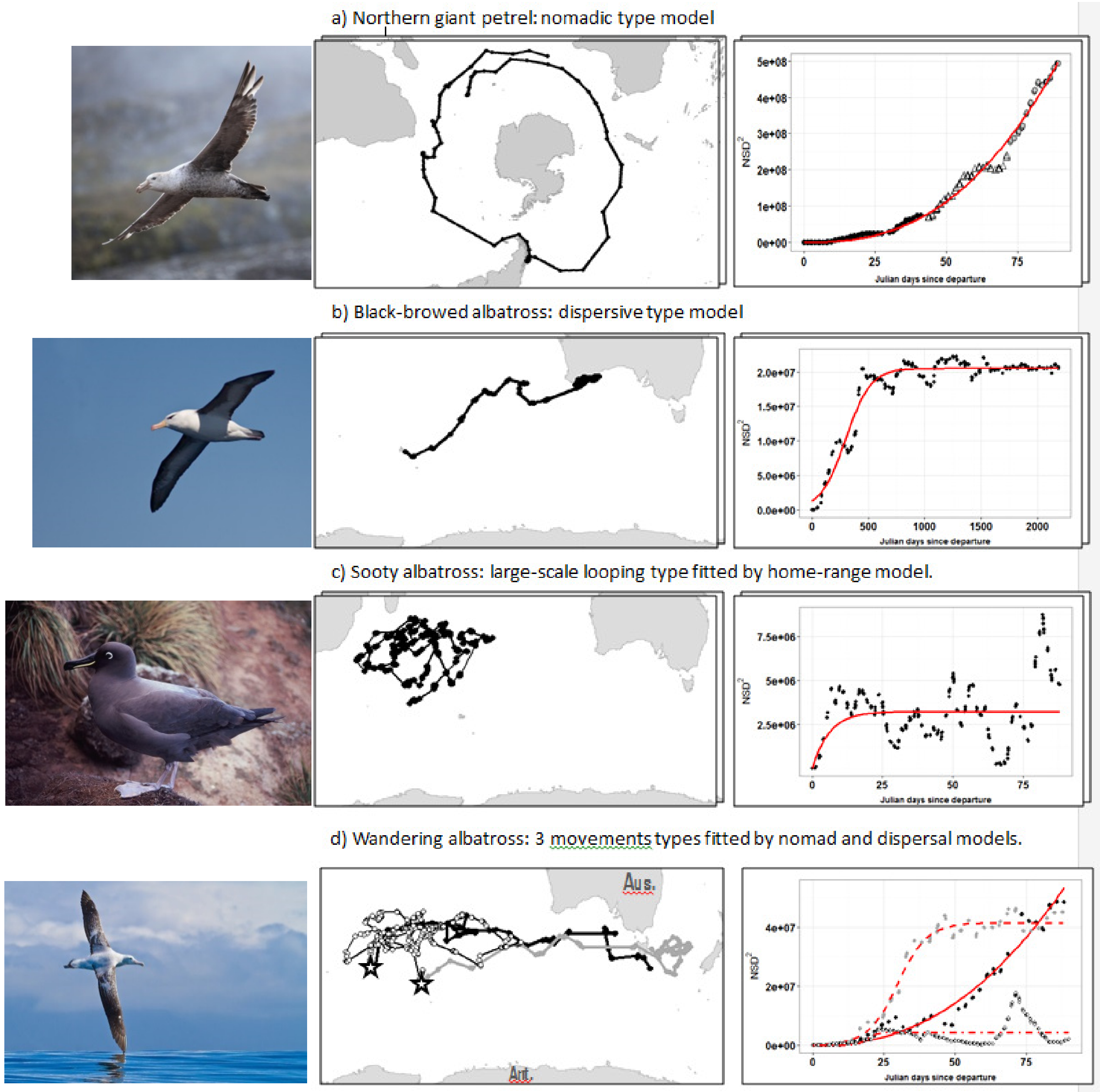
Singh, Borger et al. (2012) Ecological Applications

How do naïve juveniles navigate the environment?



6 Albatross species
2 giant petrel species
1 petrel species
98 Argos-tracked 3 months

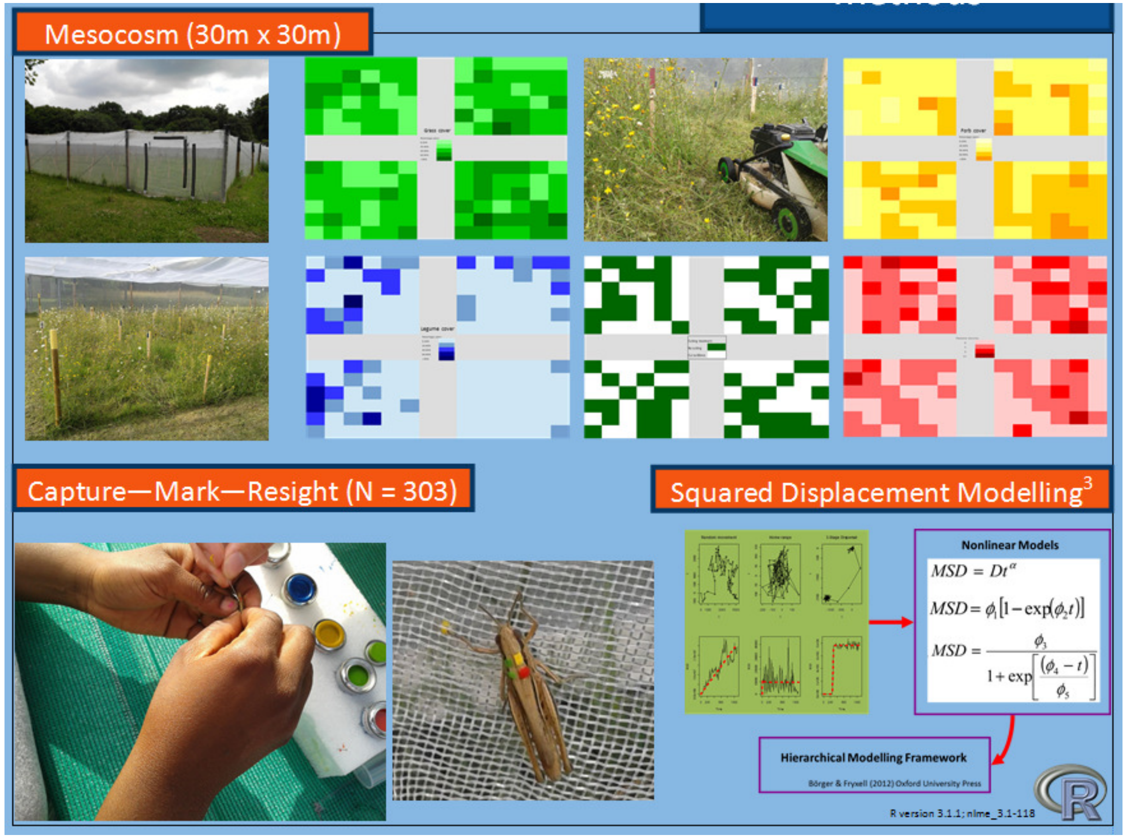




De Grissac et al. (in review)

Personality and Functional Traits Determining Grasshopper Dispersal

Fisayo Adeniran, Richard Pannell, Gross, N., Badenhausser I. Börger, L.



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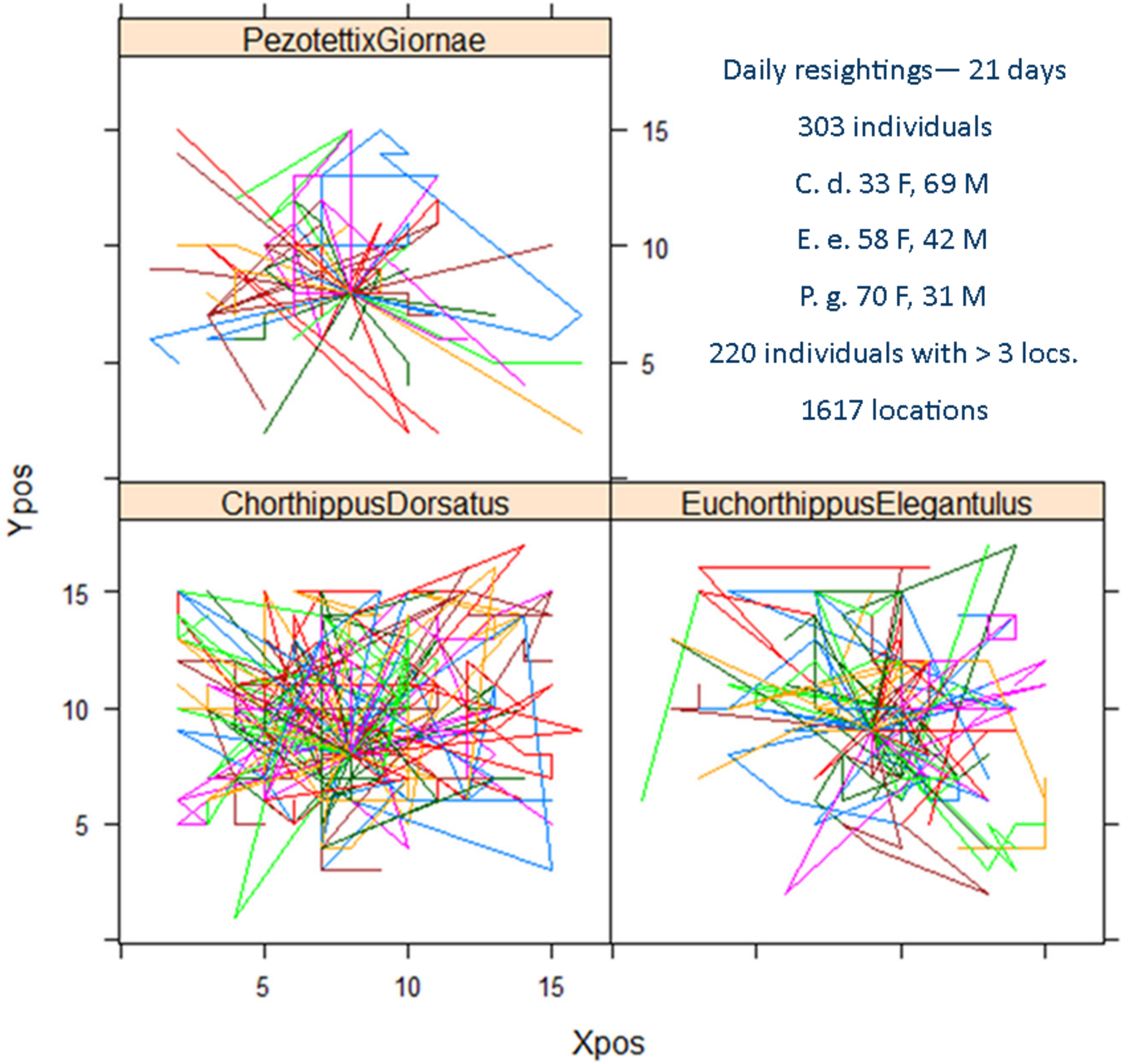

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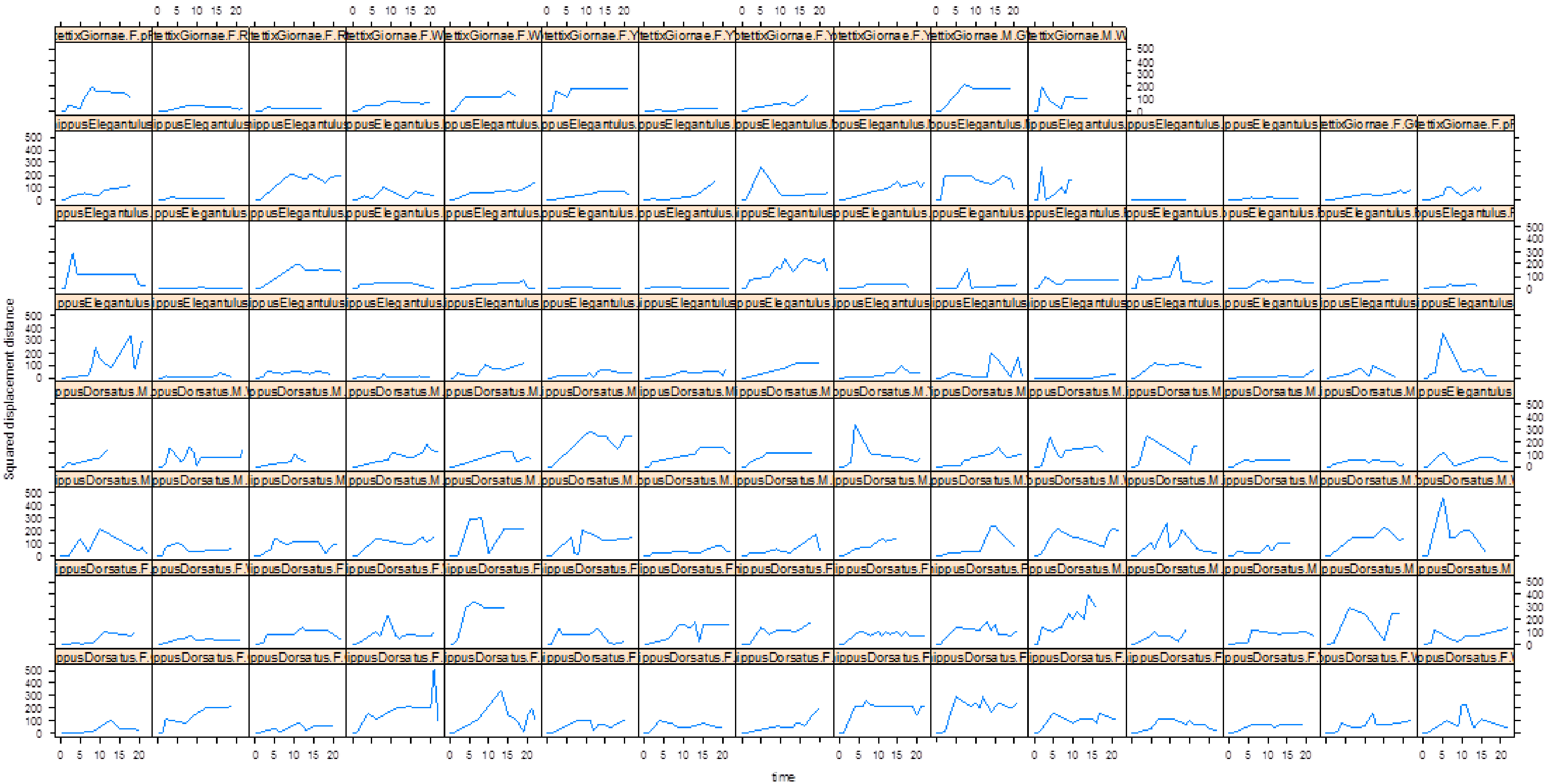


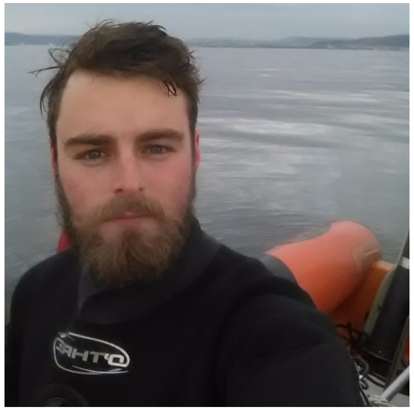
Grey seal pup dispersal patterns and marine energy installations in Wales

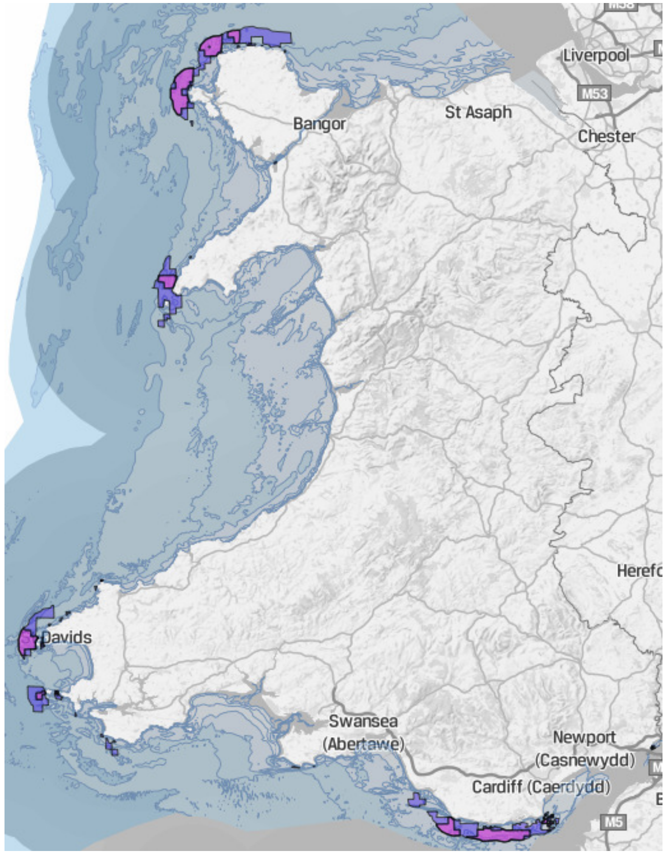
William Kay[1], James Bull[1], Tom Stringell[2], Luca Börger[1]

[1]Swansea Laboratory for Animal Movement, Biosciences, Swansea University, SA2 8PP

[2]Natural Resources Wales, Penrhos Rd, Bangor, Gwynedd, LL57 2DN.

@willmarine92





kess
Ysgoloriaethau Sgiliau Economi Gwybodaeth
Knowledge Economy Skills Scholarships

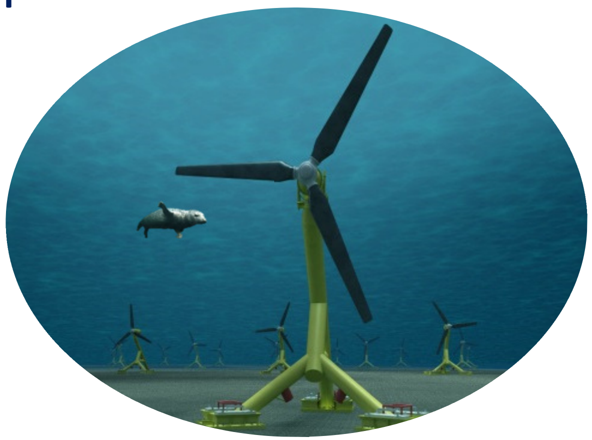
Prifysgol Abertawe
Swansea University

Cyfoeth Naturiol Cymru
Natural Resources Wales

This work has been supported by the European Social Fund (ESF) through the Welsh Government

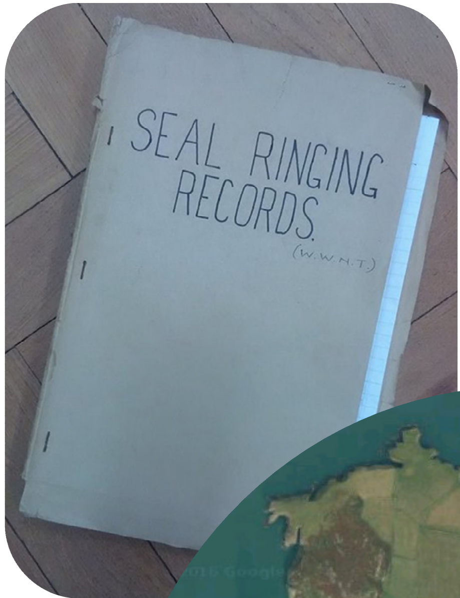
Knowledge gap – first months at sea

- Particularly marine predators
- Logistically challenging
- Difficult to observe
- Studies focused on adults
- Pups ~ 50 % of population

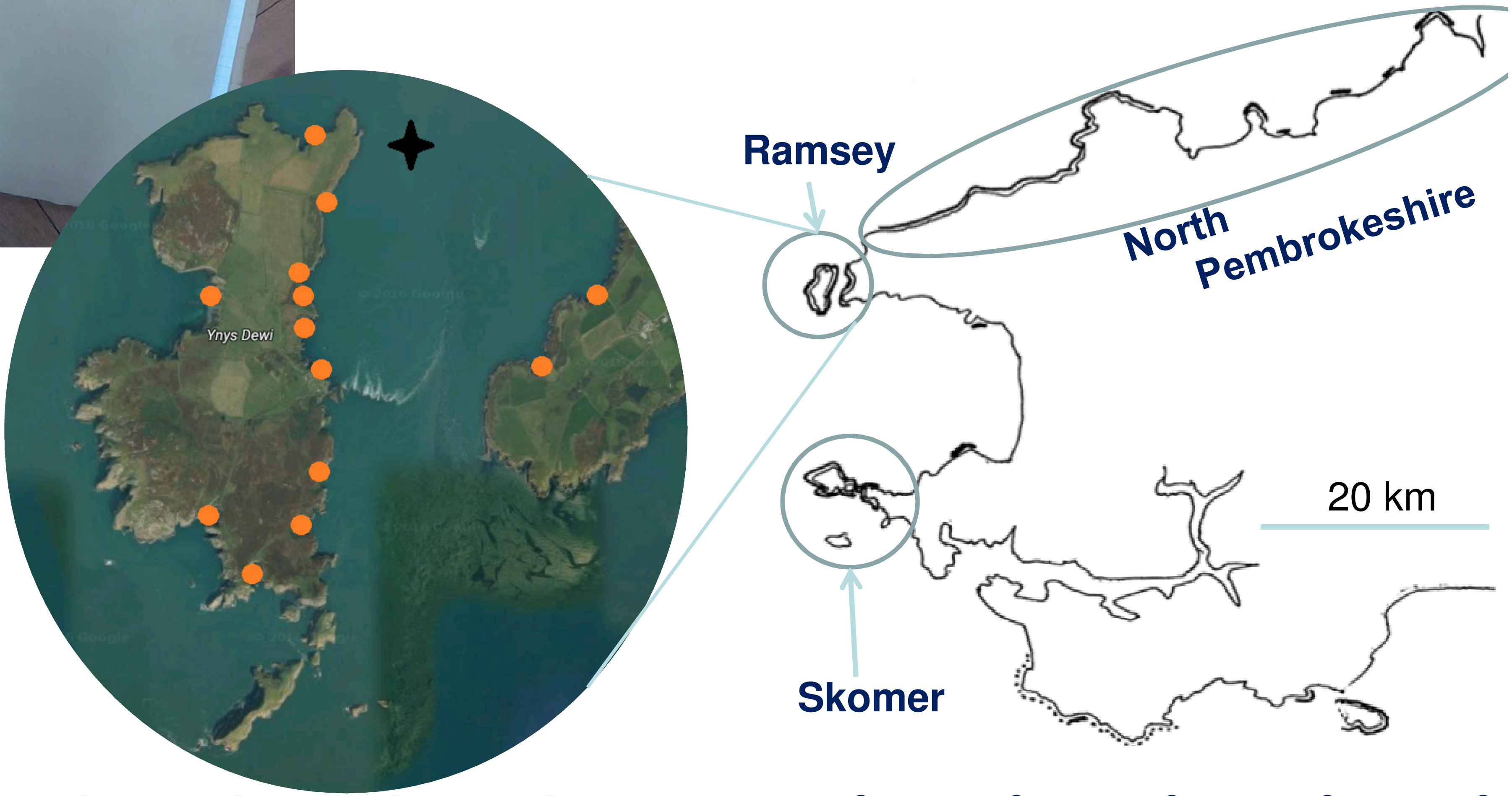


Ådahl *et al.*, 2006

Methods: Data

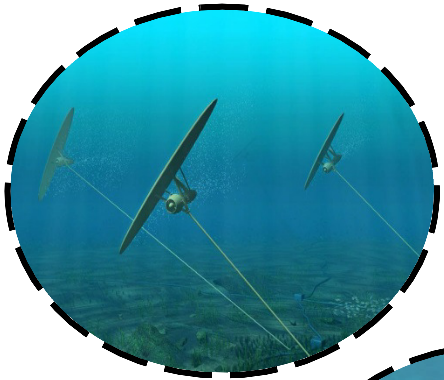


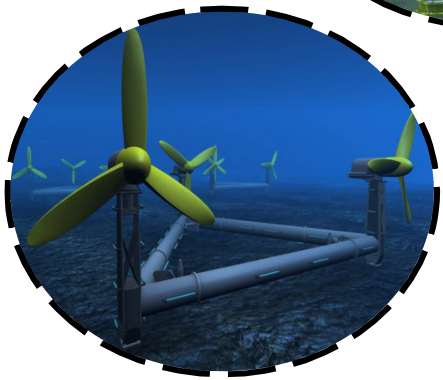
- 1954 – 1971 (19 years)
- 1368 marked - Individually marked and aged
- 256 resighted; 19 %
- 155 Ramsey, 63 Skomer, 32 NPembs
- 128 female; 121 male

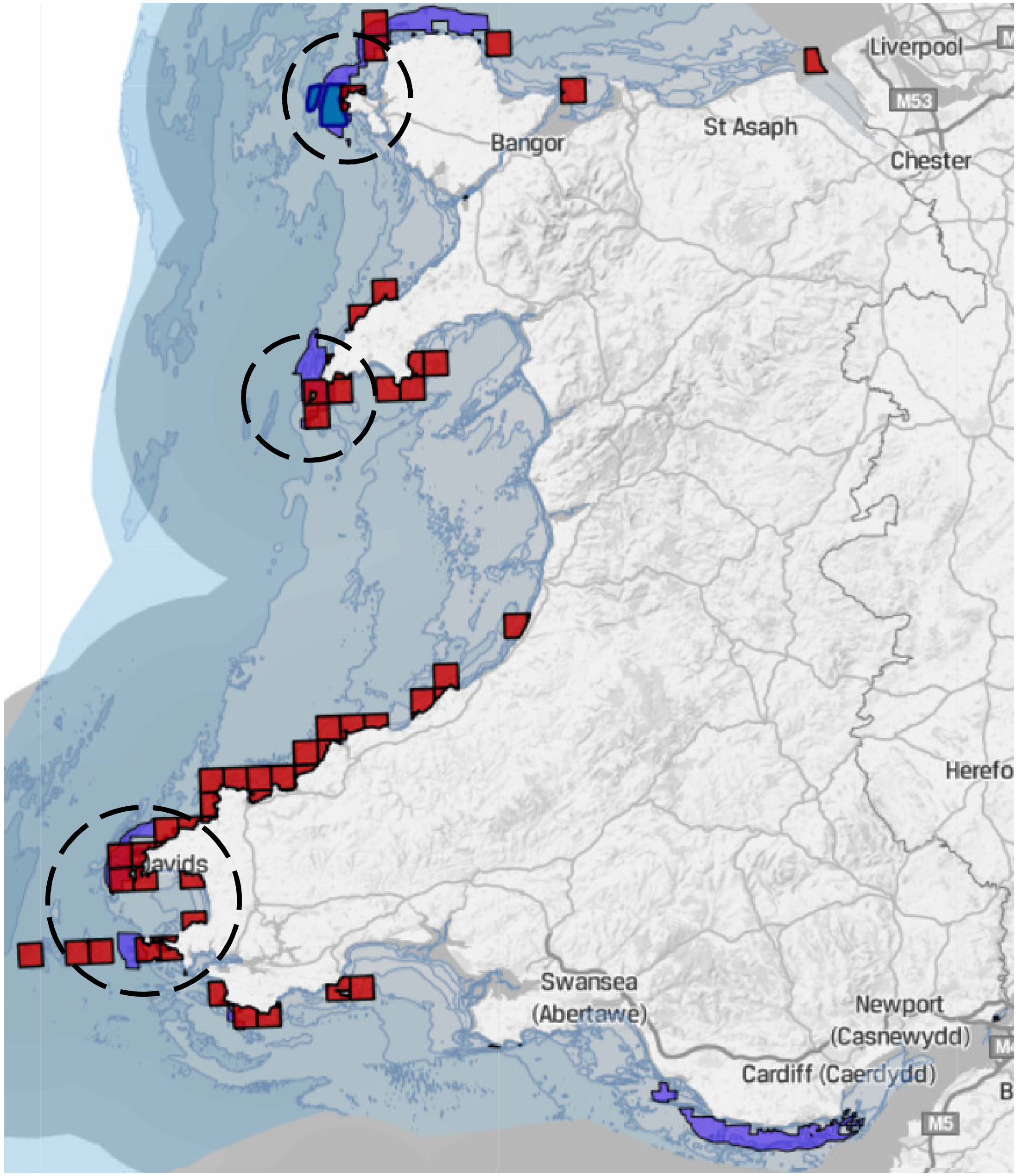


Introduction: Marine renewables in Wales

- Tidal resource areas
- Tidal energy installations
- Grey seal pup haul out

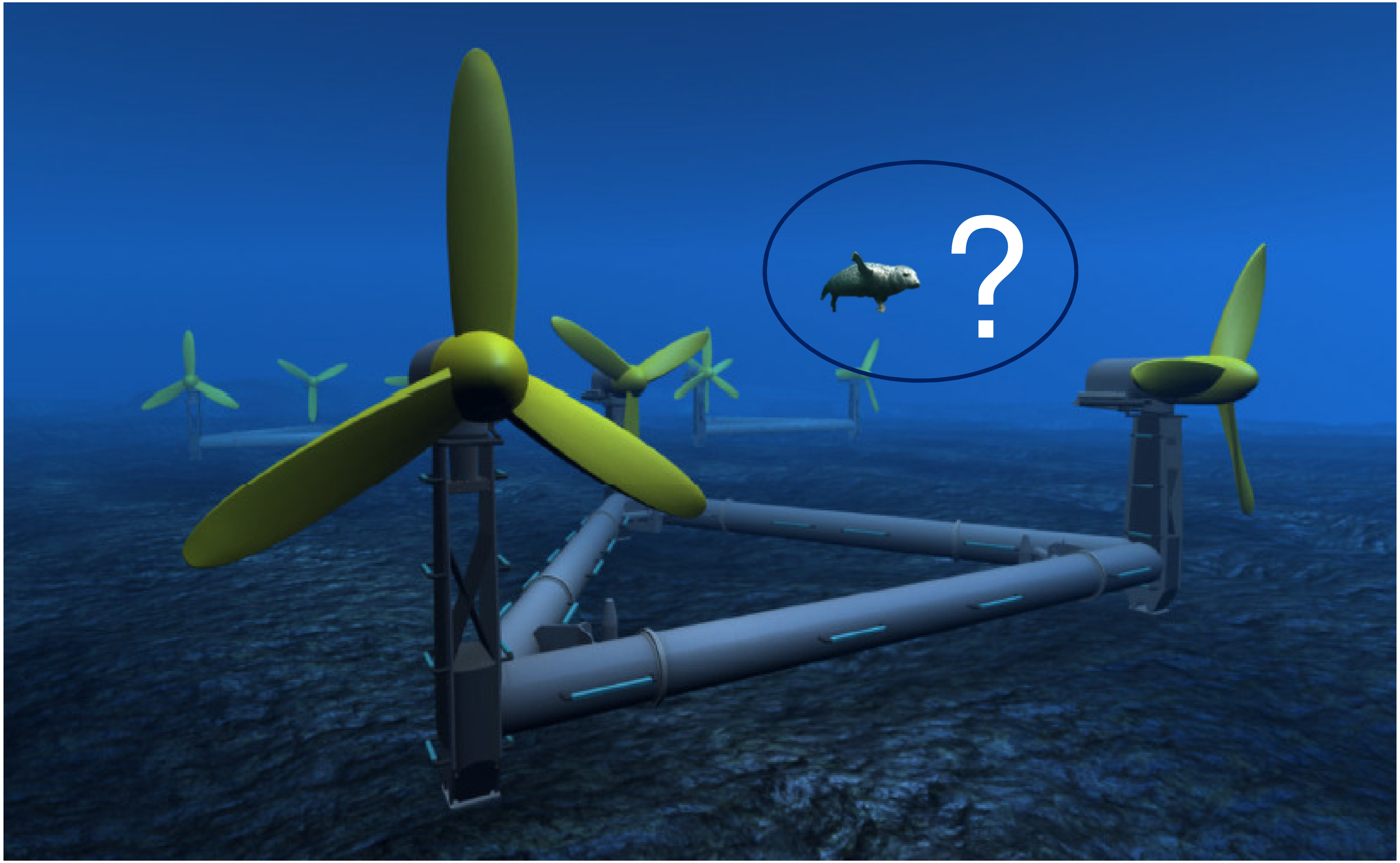




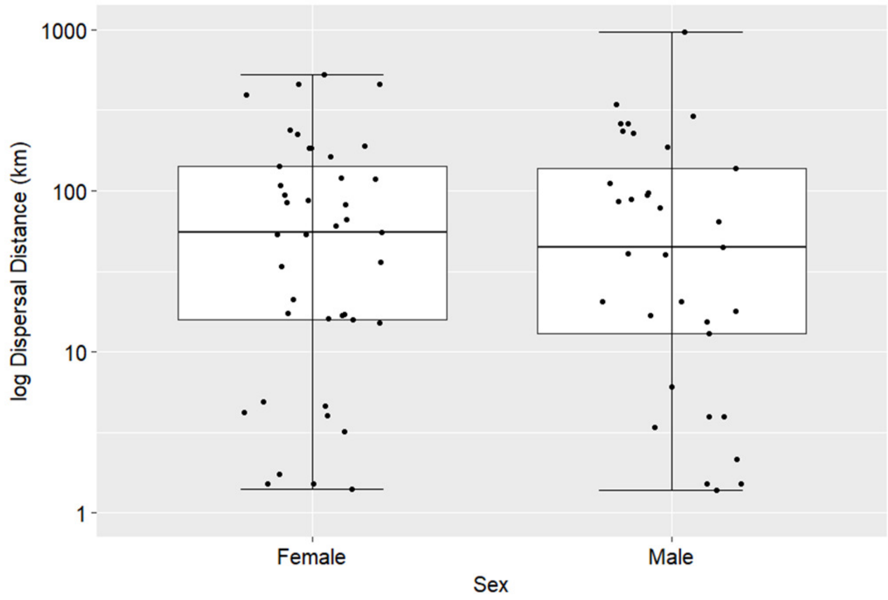


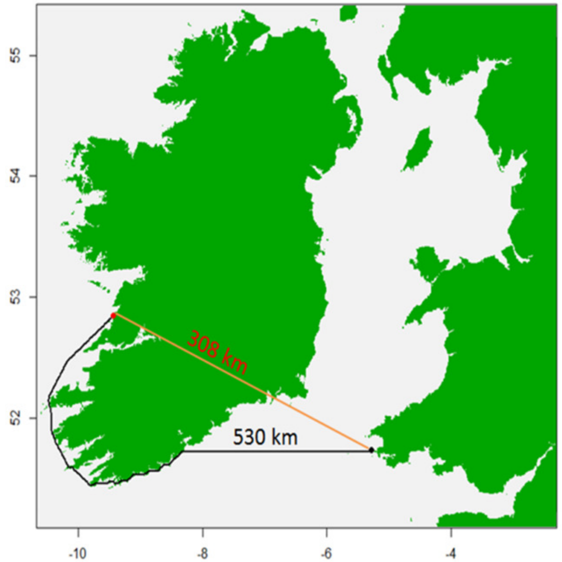
Introduction: Seals and marine renewables?

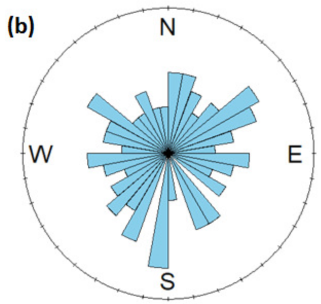
Marine mammals and **tidal turbines** – e.g. **collision risk** – **High priority** for consenting.

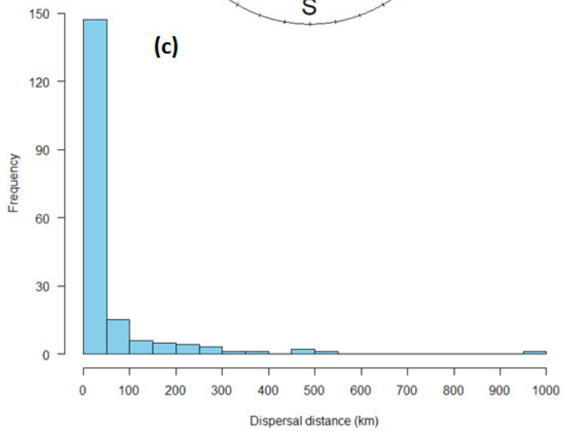


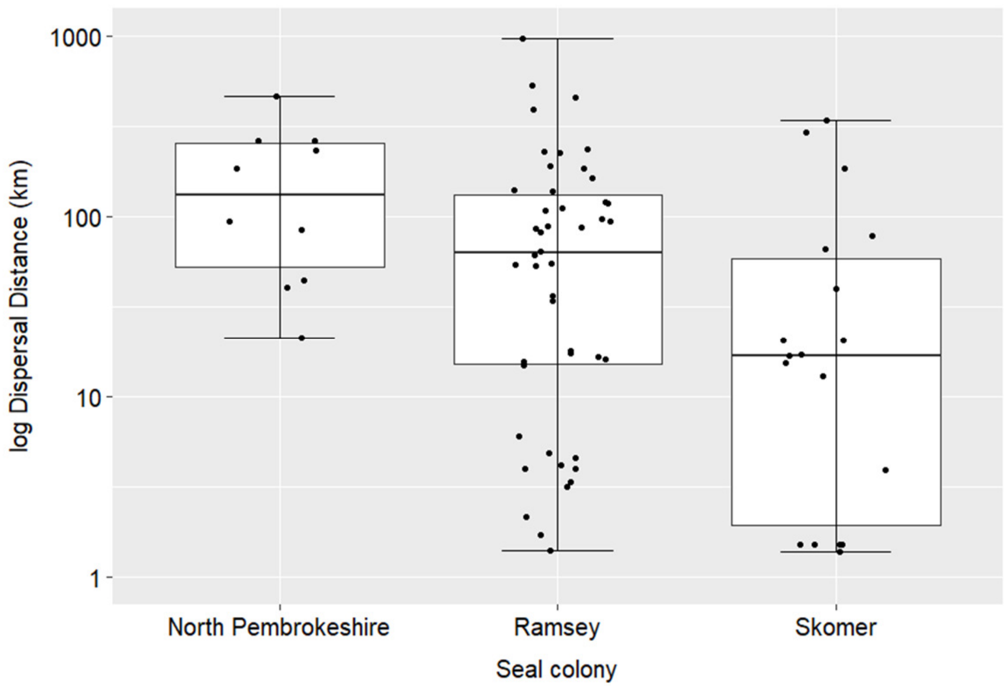
Results: Observed displacement









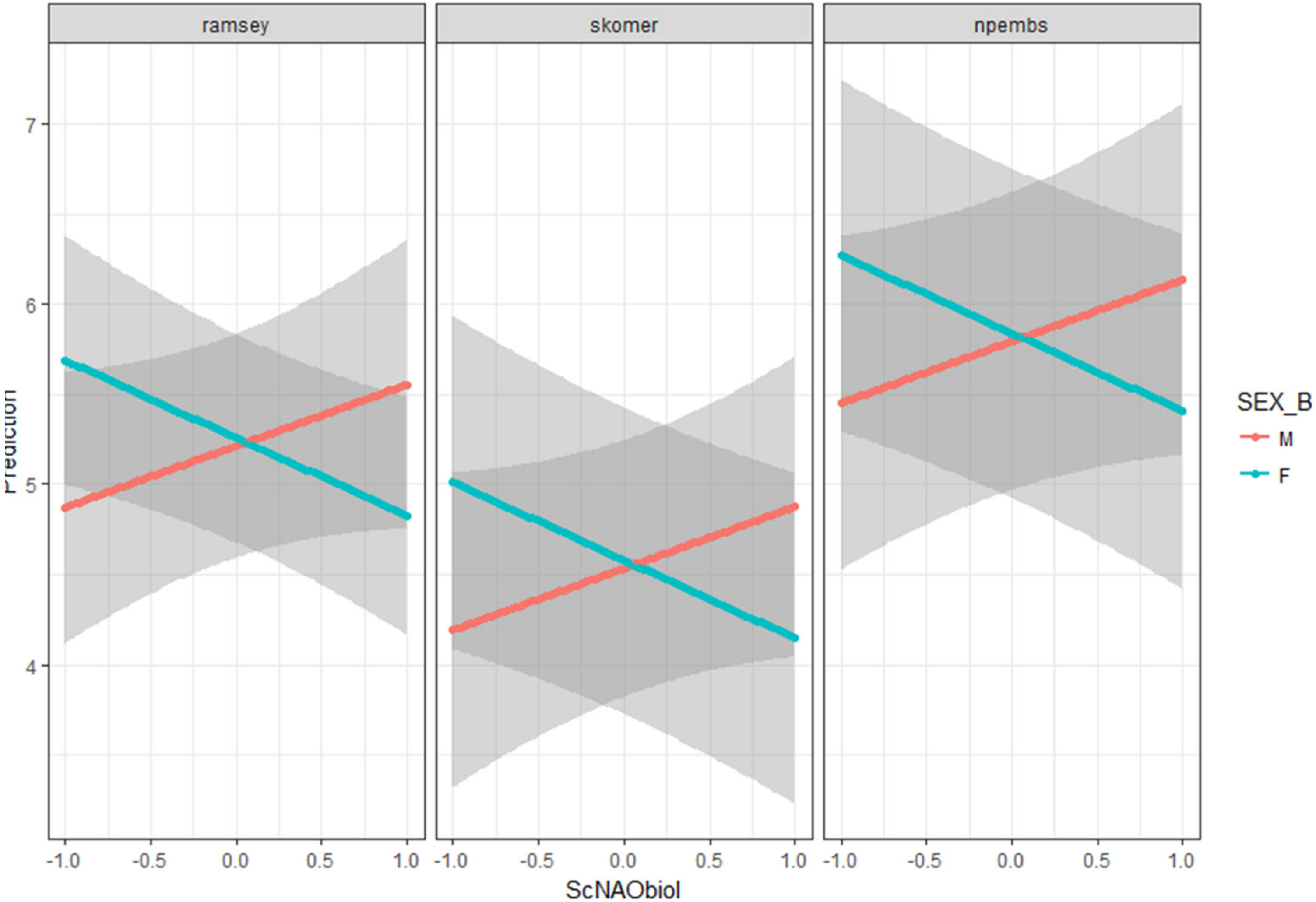


Results: Drivers of displacement

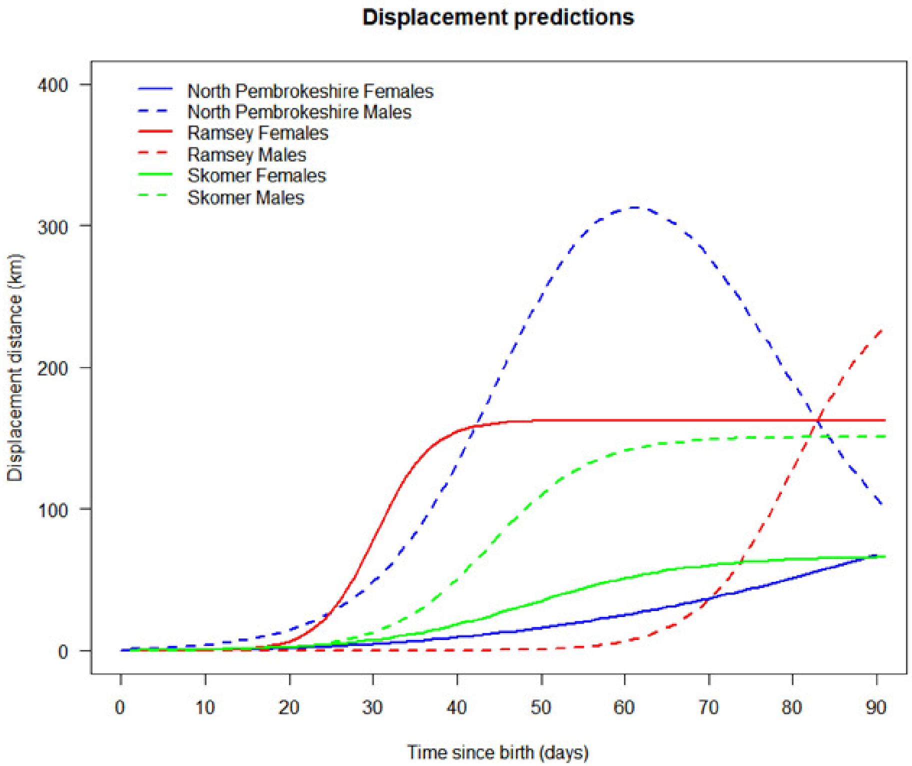
Displacement ~ TIME + COLONY + SEX * NAO

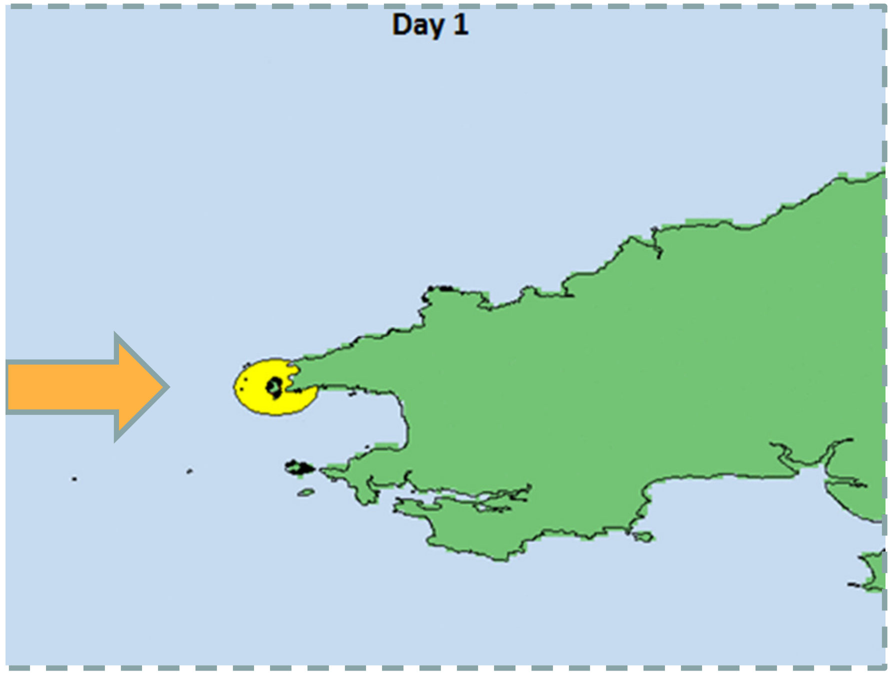
Best measure of NAO:
Biological (Sept - Aug) Annual Average

North Atlantic Oscillation ($P < 0.05$)
- Positive for males
- **Negative for females**



Results: Displacement curves/kernels





5 km buffer zone

Ramsey

Skomer

Combine displacement predictions with daily/weekly number pups born in the different colonies

→ Spatial overlap predictions with tidal turbines