Seasonal Sea Otters, Foraging Fur Seals and Whimsical Wolves
Analysis of individual animal movement on all kinds of scales

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Importance of Movement

Fundamental characteristic of all animals. Ecological processes
Foraging
Survival
Reproduction
Migration
Invasion
Dispersal
Aggregation
Measurable behavioral output
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- Measurable behavioral output
Conceptual model of Behavior
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**Environment (E_t):**
- Food presence,
- Predator presence,
- Temperature,
- Visibility,
- etc...

**State (X_t):**
- Location
- Satiation
- Desires
- Experience
- etc...
Conceptual model of Behavior

Environment ($E_i$):
- Food presence,
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BEHAVIOR

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Environment ($E_i$):
- Food presence,
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Movement ($\Delta X_i$):
- Angle
- Speed

State ($X_i$):
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Conceptual model of Behavior

\[ \Delta X_t = f(X_t, E_t) \]

**In Math:** \( \Delta X_t = f(X_t, E_t) \)

**In English:** Behavior \( f \) is a process which transforms the state of an organism \( X_t \) and the local environment \( E_t \) into Movement \( \Delta X_t \).
Track Data

- Treecreeper (Doerr 2004)
- Albatross (Fritz 2002)
- Iberian wolf (Bascompte 1997)
- Heterosigma (Bearon 2003)

- Daphnia Pulex (Uttieri 2005)
- Cebus monkey (Wentz 2003)
- Narwhal (Laidre 2004)
- Petrel (Fouchauld 2003)
Common, Inconvenient Features of Movement Data (CIF’s):

- Multi-dimensional (X,Y,Time)
- Not independent!
- Auto- and Cross-correlated
- Bonus Feature: Measurement error / irregular sampling.
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Extra Special Features of Movement Data: (ESF’s)

- Heterogeneous!
  - Population • Individual • Habitat • Time of Day/Year • etc.
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- Heterogeneous!
  - Population
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*But that’s OK! Because often this is what we want to learn!*
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  - etc.

  *But that’s OK! Because often this is what we want to learn!*

- No Consensus On Analysis In The Literature.

  *But that’s OK, too! Because every analysis is special!*
Northern Fur Seal (*Callorhinus ursinus*) and BCPA
Map of all foraging trips for F01
Orthogonal decomposition
Orthogonal decomposition

Persistence Velocity Component: \( V_p = V \cos(\theta) \)

- **mean** = speed + consistency of orientation
- **variance** = variability of behavior
- **auto-correlation** = movement changes with respect to sampling interval
Orthogonal decomposition

Orthogonal Component of Velocity: $V_t = V \sin(\theta)$

- **mean** = 0.
- **variance** = speed and sharpness of turns
- **auto-correlation** = turning radius.
Actual Data Decomposed (northern fur seal)

\[ V_p = V \cos(\theta) \]

\[ V_{\theta} = V \sin(\theta) \]

Normal Q–Q Plot
Theoretical Quantiles
Sample Quantiles
- Stationary
- Gaussian
- Modelable using standard time-series techniques
Stationary
- Gaussian
- Modelable using standard time-series techniques
• Stationary
• Gaussian
• Modelable using standard time-series techniques
Properties of AR(1)

\[ X_t = \rho (X_{t-1} - \mu) + \mu + \epsilon \]
\[ \epsilon \sim N(0, \sigma^2) \]
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\[ \hat{\rho}_\tau = 0.33 \]
Properties of AR(1)

\[
X_t = \rho (X_{t-1} - \mu) + \mu + \epsilon
\]
\[
\epsilon \sim N(0, \sigma^2)
\]
AR(1): Arbitrary Interval

\[ \hat{\rho}_c = 0.144 \]

\[
\begin{align*}
\mathbb{E}[X(t)] &= \mu \\
\text{Var}[X(t)] &= \sigma^2 \\
\text{Corr}[X(t), X(t - \tau)] &= \rho^\tau
\end{align*}
\]
AR(1): Arbitrary Interval

\[ f(X(t)|X(t - \tau)) \sim \text{Gaussian} \left[ \rho^\tau X(t - \tau), \sigma^2(1 - \rho^{2\tau}) \right] \]
Estimating $\rho$

Conditional Likelihood:

$$L(\rho|X, T) = \prod_{i=1}^{n} f(X_i|X_{i-1}, \tau_i, \rho),$$

then:

$$\hat{\rho} = \arg\max_{\rho} L(\rho|X, T)$$
Estimating $\rho$

Simulated Gappy Time Series

Log-likelihood profile

$\log$ Likelihood

$\rho$ estimate

$\log$ Likelihood
Structural shifts

\[ \Theta(t) = \begin{cases} 
\Theta_1 & \text{if } 0 < t \leq t_1 \\
\Theta_2 & \text{if } t_1 < t \leq T 
\end{cases} \]

\[ L(\Theta|X, T) = \prod_{i=1}^{n} f(X_i|X_{i-1}, \Theta_1) \prod_{j=n+1}^{N} f(X_j|X_{j-1}, \Theta_2) \]
Identifying Change Point
Identifying Change Point
Identifying Change Point
Identifying Change Point, sparse data

![Graph showing time series data and change point identification](image-url)
Identifying Change Point, different $\rho$’s
## Identifying Models

<table>
<thead>
<tr>
<th>Model 0</th>
<th>$\mu_1 = \mu_2$</th>
<th>$\sigma_1 = \sigma_2$</th>
<th>$\rho_1 = \rho_2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 1</td>
<td>$\mu_1 \neq \mu_2$</td>
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<tr>
<td>Model 2</td>
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<tr>
<td>Model 3</td>
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<td>$\sigma_1 = \sigma_2$</td>
<td>$\rho_1 \neq \rho_2$</td>
</tr>
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<tr>
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<td>$\sigma_1 = \sigma_2$</td>
<td>$\rho_1 \neq \rho_2$</td>
</tr>
<tr>
<td>Model 6</td>
<td>$\mu_1 = \mu_2$</td>
<td>$\sigma_1 \neq \sigma_2$</td>
<td>$\rho_1 \neq \rho_2$</td>
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<tr>
<td>Model 7</td>
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How to choose?

\[
\text{AIC} : I_A(X, T) = -2n \log \left( L(\hat{\theta}|X, T) \right) + 2d
\]

\[
\text{BIC} : I_B(X, T) = -2n \log \left( L(\hat{\theta}|X, T) \right) + d \log(n)
\]
Identifying Models

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<tr>
<td>S0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>S1</td>
<td>-1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>S2</td>
<td>0</td>
<td>0</td>
<td>0.5</td>
<td>2</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>S3</td>
<td>0</td>
<td>0</td>
<td>0.5</td>
<td>1</td>
<td>0.2</td>
<td>0.9</td>
</tr>
<tr>
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<td>-1</td>
<td>1</td>
<td>0.5</td>
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<td>0.9</td>
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Algorithm for Identifying Multiple Changepoints

- Select Window
- Find MLBP
- Identify Model
- Record estimates based on model selected.
- Move window forward and repeat
Algorithm for Identifying Multiple Changepoints

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BCPA analysis output
BCPA Track Analysis

V_{\cos(\theta)}

V_{\sin(\theta)}

Trip 1
Behavior can be very complex! But patterns can be robustly picked out of messy data. Method suggests the possibility of asking more sophisticated questions.

Summary points

- Behavior can be very complex!
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So how’d we do on the CIF’s and ESF’s?

1. Multi-dimensionality: Component decomposition (and continuous time)

2. Correlation: Explicit Estimation of $\rho$

3. Gappiness: Continuous-time model

4. Errors: Ignored (scale of measurement > scale of error), Other systems: test robustness

5. Heterogeneity: Change Point Analysis
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Washington sea otters (*Enhydra lutris kenyoni*)

- Extirpated by fur-trade hunting in the early 20th century
- Re-established by translocations of 59 sea otters from Alaska in 1969-70
- Population index counts annually conducted since late 80’s

Photo: G. Jameson

- 75 individuals captured using Wilson traps and instrumented (43 AF, 14 AM, 9 SF, and 9 SM)
Individuals tracked on average for 684 days (SD 515, range 7 days to 5.9 years).

Average of 34 radio locations per individual (SD 29).

Mean number of resightings per sea otter per month ranged from 1.6 (December) to 5.8 (August) - mean of 2.9.
Linearizing Otter movements
Linearizing Otter movements

Discretize coastline (~600 m)
Linearizing Otter movements

Discretize coastline (~600 m)

Perpendicularly project sea otter location to "coast".
Discretize coastline (~600 m)

Perpendicularly project sea otter location to “coast”.

Estimate “coastal kilometer value”.

Linearizing Otter movements
Analysis challenge: Quantify space use

- Home ranges
- Seasonality

SO11: Female

SO22: Male
One-dimensional kernelized distributions

- Minimum of 20 observations (46 out of 75 individuals: 34 F, 12 M)
- Weighted according to number of days to neighboring observations, max 1 month

- 4 obs/month = weight 7 day
- 1 obs/year = weight 30 day
Home Range: 95% of time spent

Sometimes, discontinuous!
95% kernel home range by age class and sex.

Both significant (p<0.01)
How to quantify “seasonality”? 

Summer (May-October) and Winter (November – April): 

Seasonal Distribution Overlap Index 

Sea Otter 43 (M) 

(A) Adult Male 

SDOI = 0.15 

Summer (May-October) and Winter (November – April): Seasonal Distribution Overlap Index
How to quantify “seasonality”? 

SDOI = 0.15
Sea Otter 44 (F)

(D)

Subadult Female
SDOI = 0.98

SDOI = 0.98
Sea Otter 02 (F)

SDOI = 0.53

Adult Female
SDOI = 0.53

SDOI = 0.53
<table>
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<tr>
<th>Age-Sex</th>
<th>Number of individuals</th>
<th>Mean seasonal distribution overlap (SD)</th>
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</thead>
<tbody>
<tr>
<td>AF</td>
<td>29</td>
<td>0.63 (0.2)</td>
</tr>
<tr>
<td>AM</td>
<td>7</td>
<td>0.50 (0.24)</td>
</tr>
<tr>
<td>SF</td>
<td>5</td>
<td>0.70 (0.26)</td>
</tr>
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<td>5</td>
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Sex significant but not age.
Some Sea Otter Conclusions

Movements between 1992-1999 best described as semi-seasonal shifts within the range. The range expanded both North and South over the study period—driven primarily by males. High seasonal periodicity in range use in summer and winter, distributions were generally bimodal for adult males with adult females more variable more likely to have high year-round site fidelity.

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So how’d we do on the CIF’s and ESF’s?

Multi-dimensionality:
1D-projection

Correlation:
Choose time scale (1 month) and distance kernel (15km) that makes data independent

Errors:
Ignored (scale of measurement > scale of error)

Heterogeneity:
Analysis according Sex/Age, Seasonality
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Wolf (*Canis lupus*) in Finland

- Extirpated by hunting by early 20\(^{th}\) century.
- Since 1980’s influx from Western Russia.
- Currently, roughly 200 individuals. **Hunter vs. Conservation tensions.**
Movement Data

Eastern Finland, two wolves: 
  Viki: female 2006
  Niki: male 2008

GPS and radio collared, 1/2 hour transmission interval

2-months of intensive ground tracking of every location away from den.
Movement Data

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Habitat Data

Habitat Map of the Territory of a GPS-collared Wolf

Legend
- GPS locations of the Study Wolf Niki

Habitat type
- agricultural area
- conifer forest
- mixed forest
- half-open habitat
- swamp
- lake

Maps: Johanne Susarinem
Data Source: Finnish Game and Fisheries Research Institute (RKKL), Finnish Environmental Institute (SYKE)
Mixed/Open Forest Edge
Linear Elements

Primary Roads
Forest Roads
Rivers
Power Lines
Railways
Reindeer Fence
Prey

Moose
Reindeer
(wild/semi-domesticated)
Miscellaneous

(before)

Photo: Johanna
Prey

![Graph showing the distribution of prey with various symbols representing different types of prey like Cacheward, Homeward, Kill, AtPrey, ReturnToPrey, Unknown, and AtDen. The x-axis represents the X distance (km), ranging from -20 to 20, and the y-axis represents the Y distance (km), ranging from -15 to 20.]

- **Cacheward**
- **Homeward**
- **Kill**
- **AtPrey**
- **ReturnToPrey**
- **Unknown**
- **AtDen**

- **Moose Adult**
- **Moose Calf**
- **Reindeer Adult**
- **Reindeer Calf**
- **Unknown Calf**
Behavior

(show some images from file)
Behavior: time series
Goal

To model:

*BEHAVIOR*,

(movement and predation)

with respect to

*HABITAT*

(landscape and linear elements).
Behavior Vectors

$Z_i$ – position

$B_i$ – behavior

$P_i$ – purpose

$K_i$ – kill

Habitat Vectors

$H_i$ – habitat land class

$N_i$ – nearest neighbor habitat

$L_i$ – linear element
Testing Hypotheses: Null Sets

RI: All Possible Points in Home Range
RII/RIII: Points Localized Around Each Location
Localized Null Set

RII: Points Localized Around Each Location
RIII: Points reflecting “actual movements”
Localized Null Set

RIII: Points Localized Around Each Location
## Results: Habitat Use

<table>
<thead>
<tr>
<th>Habitat types</th>
<th>Viki</th>
<th>Niki</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>movement</td>
<td>RI</td>
<td>RII</td>
<td>homing</td>
<td>hunting</td>
<td>kill</td>
</tr>
<tr>
<td>Fields</td>
<td>0.007</td>
<td>0.009</td>
<td>0.01</td>
<td>0.004</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Coniferous forest</td>
<td>0.283</td>
<td>0.269</td>
<td>0.291</td>
<td>0.256</td>
<td>0.284</td>
<td>0.225</td>
</tr>
<tr>
<td>Mixed forest</td>
<td>0.233</td>
<td><strong>0.315</strong></td>
<td>0.247</td>
<td>0.264</td>
<td><strong>0.177</strong></td>
<td>0.225</td>
</tr>
<tr>
<td>Open woodland</td>
<td>0.347</td>
<td><strong>0.314</strong></td>
<td>0.336</td>
<td>0.392</td>
<td>0.372</td>
<td>0.475</td>
</tr>
<tr>
<td>Peatbogs</td>
<td>0.130</td>
<td><strong>0.093</strong></td>
<td>0.122</td>
<td><strong>0.084</strong></td>
<td>0.167</td>
<td>0.075</td>
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<tr>
<td>Fields</td>
<td>0.008</td>
<td>0.012</td>
<td>0.006</td>
<td>0.006</td>
<td>0.007</td>
<td>0.000</td>
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<tr>
<td>Coniferous forest</td>
<td>0.167</td>
<td><strong>0.194</strong></td>
<td>0.180</td>
<td>0.129</td>
<td>0.182</td>
<td>0.180</td>
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<tr>
<td>Mixed forest</td>
<td>0.284</td>
<td>0.302</td>
<td>0.310</td>
<td>0.246</td>
<td><strong>0.195</strong></td>
<td>0.200</td>
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<tr>
<td>Open woodland</td>
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<td><strong>0.333</strong></td>
<td><strong>0.351</strong></td>
<td><strong>0.544</strong></td>
<td><strong>0.492</strong></td>
<td>0.460</td>
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<tr>
<td>Peatbogs</td>
<td>0.106</td>
<td><strong>0.159</strong></td>
<td><strong>0.154</strong></td>
<td>0.075</td>
<td>0.124</td>
<td>0.160</td>
</tr>
</tbody>
</table>

$\chi^2$ test against: movement, movement, movement, movement, movement, hunting
# Results: Linear Element Use

<table>
<thead>
<tr>
<th>Viki</th>
<th>movement</th>
<th>RI</th>
<th>RII</th>
<th>homing</th>
<th>hunting</th>
<th>kill</th>
</tr>
</thead>
<tbody>
<tr>
<td>$n$</td>
<td>717</td>
<td>$10^5$</td>
<td>5512</td>
<td>227</td>
<td>317</td>
<td>40</td>
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<tr>
<td>Forest roads</td>
<td>0.117</td>
<td><strong>0.068</strong></td>
<td><strong>0.077</strong></td>
<td>0.075</td>
<td>0.097</td>
<td>0.050</td>
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<tr>
<td>Rivers</td>
<td>0.041</td>
<td>0.034</td>
<td>0.036</td>
<td><strong>0.097</strong></td>
<td><strong>0.075</strong></td>
<td>0.075</td>
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<tr>
<td>Roads</td>
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<td>0.011</td>
<td>0.004</td>
<td>0.004</td>
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</tr>
<tr>
<td>Railways</td>
<td>0.012</td>
<td><strong>0.003</strong></td>
<td><strong>0.003</strong></td>
<td>0.000</td>
<td>0.016</td>
<td>0.000</td>
</tr>
<tr>
<td>Forest edge</td>
<td>0.297</td>
<td><strong>0.266</strong></td>
<td>0.280</td>
<td>0.335</td>
<td>0.328</td>
<td>0.450</td>
</tr>
<tr>
<td>Bog edge</td>
<td>0.106</td>
<td><strong>0.063</strong></td>
<td>0.093</td>
<td>0.075</td>
<td><strong>0.147</strong></td>
<td>0.125</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Niki</th>
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<th>RII</th>
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<th>kill</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest roads</td>
<td>0.129</td>
<td><strong>0.054</strong></td>
<td><strong>0.052</strong></td>
<td><strong>0.176</strong></td>
<td>0.091</td>
<td>0.060</td>
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<tr>
<td>Rivers</td>
<td>0.071</td>
<td><strong>0.046</strong></td>
<td><strong>0.046</strong></td>
<td>0.075</td>
<td><strong>0.267</strong></td>
<td>0.140</td>
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<tr>
<td>Roads</td>
<td>0.021</td>
<td>0.020</td>
<td>0.016</td>
<td>0.029</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Railways</td>
<td>0.017</td>
<td><strong>0.004</strong></td>
<td><strong>0.004</strong></td>
<td>0.003</td>
<td>0.000</td>
<td>0.000</td>
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<tr>
<td>Forest edge</td>
<td>0.298</td>
<td>0.279</td>
<td>0.286</td>
<td>0.257</td>
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<td>Bog edge</td>
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<td><strong>0.092</strong></td>
<td>0.098</td>
<td>0.114</td>
<td>0.123</td>
<td>0.100</td>
</tr>
</tbody>
</table>

$\chi^2$ test against: movement movement movement movement hunting
Results: Large Road Avoidance
Road Network

Niki

Viki
Movement Parameters

<table>
<thead>
<tr>
<th></th>
<th>$\cos(\theta)$</th>
<th>$\vec{V}$ (km/hour)</th>
<th>IQR (25%-75%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>F06</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All movements</td>
<td>0.52</td>
<td>3.21</td>
<td>2.88 - 9.96</td>
</tr>
<tr>
<td>Hunting</td>
<td>0.42</td>
<td>2.42</td>
<td>1.1 - 8.2</td>
</tr>
<tr>
<td>Homing</td>
<td>0.74</td>
<td>5.45</td>
<td>6.14 - 12.66</td>
</tr>
<tr>
<td><strong>M08</strong></td>
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<td></td>
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</tr>
<tr>
<td>All movements</td>
<td>0.61</td>
<td>3.59</td>
<td>3.68 - 9.42</td>
</tr>
<tr>
<td>Hunting</td>
<td>0.58</td>
<td>3.56</td>
<td>4.44 - 8.96</td>
</tr>
<tr>
<td>Homing</td>
<td>0.59</td>
<td>3.39</td>
<td>0.4 - 9.56</td>
</tr>
</tbody>
</table>
Some Tentative Wolf Conclusions

- Wolves like using natural and manmade corridors for movement,
- but they avoid large roads!
- Higher road density disrupts freedom of movement, efficiency of habitat use, with possible consequences for pup-rearing success, etc.

E. Gurarie, I. Kohola, J. Suutarinen, O. Ovaskainen. Wolf (Canis lupus) movement and kill behavior with respect to human-influenced habitat features in Finland. *in prep*
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A Big Problem With Conclusions

Only 2 data points!
(Different years, different sexes, etc.)
But we have More Wolves ...
(More coarsely sampled and without behaviors, but still...)
Possible Hypothesis ...

Road Intensity

Some index of homogeneity of habitat use

Viki

Niki

everyone else
So how’d we do on the CIF’s and ESF’s?

Multi-dimensionality:
Analyzed habitat variables and step-length properties
So how’d we do on the CIF’s and ESF’s?

**Multi-dimensionality:** Analyzed habitat variables and step-length properties.

**Correlation:** Used randomization set (RIII) derived from actual movements to create null-hypotheses.
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- **Multi-dimensionality:** Analyzed habitat variables and step-length properties
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- **Errors:** Ignored
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**Heterogeneity:**
Sequential $\chi^2$ comparisons of data and randomization in terms of habitat covariates.
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General Principles of Movement Analysis:

If you keep track of your:

Correlations! Dimensions! Gaps! Errors!
General Principles of Movement Analysis:

If you keep track of your:

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Match your questions to your data,
General Principles of Movement Analysis:

If you keep track of your:
- Correlations!
- Dimensions!
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Match your questions to your data,
Explore all the heterogeneities ...
General Principles of Movement Analysis:

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Match your questions to your data,
Explore all the heterogeneities ...

(and maybe make up some acronyms on the way)
If you keep track of your:
   Correlations! Dimensions! Gaps! Errors!

Match your questions to your data,
Explore all the heterogeneities ...

(and maybe make up some acronyms on the way)

Then you’re bound to learn **SOMETHING**
# Acknowledgments

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- **Co-authors:** R. Andrews and K. Laidre.
- V. Burkanov and all colleagues/friends in the field in Russia
- **Discussions:** T. Gneiting, M. Kot, V. Minin, H. Nesse

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- **Co-authors:** K. Laidre, R. Jameson, S. Jeffries
- **Trackers:** M. Stafford, B. Krause
- Capture, tagging and tracking of sea otters was funded by USGS, Fish and Wildlife and WDFW and Olympic Coast National Marine Sanctuary (OCNMS).

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- **Co-authors:** Ilpo Kojala, Johanna Suutarinen, Otso Ovaskainen
- **Support:** Metapopulation Research Group, University of Helsinki
Thank you!