

Model complexity and model choice for animal movement models

Ben Bolker, McMaster University

Departments of Mathematics & Statistics and Biology

Guelph Biomathematics & Biostatistics Symposium

9 June 2016

Outline

- 1 Animal movement
- 2 Florida panthers
- 3 Hidden Markov models
- 4 Basic analysis (van de Kerk et al., 2015)
- 5 Incorporating diurnal variation (Li, 2015)
- 6 Broader issues/outlook

Acknowledgements

People Michael Li, Madelon van de Kerk,
Dave Onorato, Madan Oli

Agencies US Fish and Wildlife Service, US Geological Survey,
US National Park Service

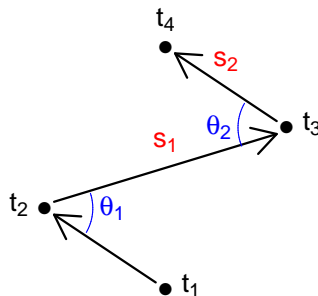
Funding NSERC Discovery grant, NSF IGERT program

Outline

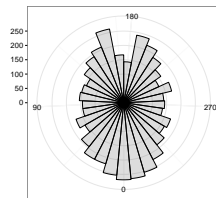
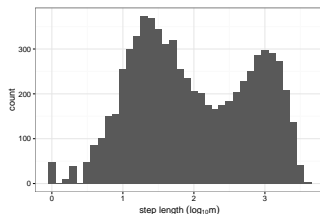
- 1 Animal movement
- 2 Florida panthers
- 3 Hidden Markov models
- 4 Basic analysis (van de Kerk et al., 2015)
- 5 Incorporating diurnal variation (Li, 2015)
- 6 Broader issues/outlook

Animal movement: data

- observations:
e.g. mass mark-recapture,
longitudinal density, direct
observation, telemetry
(VHF, GPS)
- most methods provide a
sequence of times and
locations for each individual



- summaries:
 - home range
(convex hull, kernel density estimate, etc.)
 - root-mean-squared displacement
 - step length and turning angle
- covariates:
 - e.g. habitat map,
 - individual characteristics
(sex, age, weight ...)



Animal movement: questions

- simple description
- how do animals' movements change as a function of their (internal or external) environment?
what does that tell us about their biology?
- how might animals' distributions, etc. change when conditions (density, habitat, ...) change?

Outline

- 1 Animal movement
- 2 Florida panthers**
- 3 Hidden Markov models
- 4 Basic analysis (van de Kerk et al., 2015)
- 5 Incorporating diurnal variation (Li, 2015)
- 6 Broader issues/outlook

Biological/conservation issues

- Florida panther: *Puma concolor coryi*
- endangered subspecies
- severely reduced habitat
- small, isolated population
- currently recovering



www.peer.org



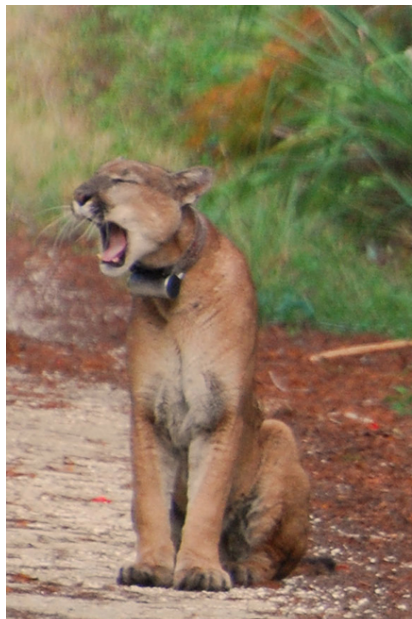
Panther movement questions

- movement variation by sex and life history stage (juvenile, adult, mom with kittens . . .)
- effects of movement on threats (intraspecific aggression, roadkill) ?
- predicting the effects of future changes in population density / population structure / habitat

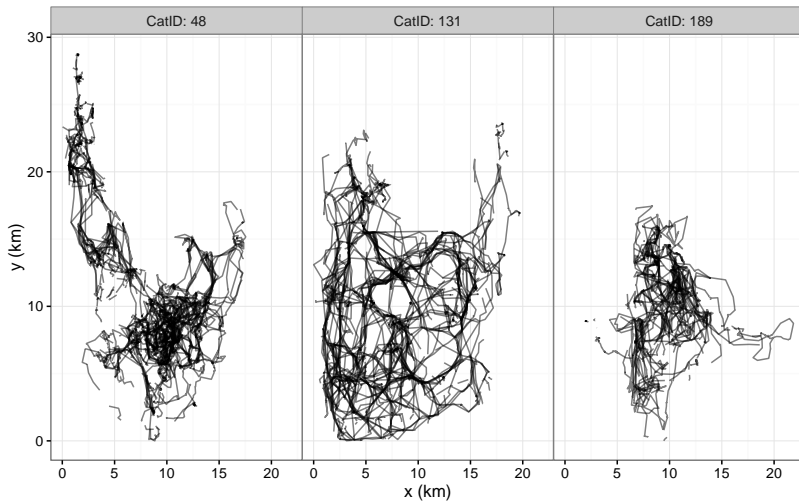


Panther movement data

- panthers tracked, captured
- GPS collars
- 18 males (13 male, 5 female, 1-15 years old)
- 3200 panther days, hourly/bihourly; 49000 locations
- ?? per panther



example movement tracks

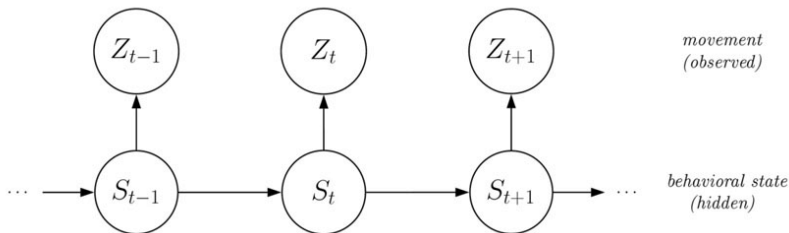


Outline

- 1 Animal movement
- 2 Florida panthers
- 3 Hidden Markov models**
- 4 Basic analysis (van de Kerk et al., 2015)
- 5 Incorporating diurnal variation (Li, 2015)
- 6 Broader issues/outlook

Hidden Markov models

- finite mixture model with temporal dependence
- discrete time steps
- discrete latent state; *transition matrix*
- observations from *emission distributions*
(continuous or discrete, univariate or multivariate)
- **multiphasic movement** (Fryxell et al., 2008; Langrock et al., 2012)



Hidden Markov models (cont.)

state:

$$S_t \sim \text{Multinomial}(S_{t-1}, \mu_{S,t})$$
$$\mu_{S,t} = \text{multi-logistic}(\mathbf{X}_{S,t} \boldsymbol{\beta}_S)$$

emission:

$$\mathbf{Z}_t \sim \{\text{Dist}_1(\mu_{Z_1,S_t}), \dots, \text{Dist}_n(\mu_{Z_n,S_t})\}$$
$$\mu_{Z_i,S_t} = g^{-1}(\mathbf{X}_{Z_i,t} \boldsymbol{\beta}_{Z_i,S_t})$$

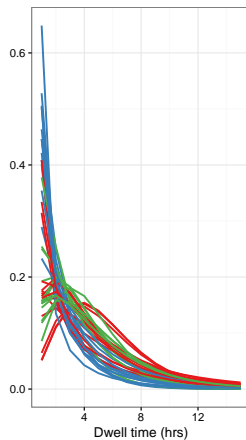
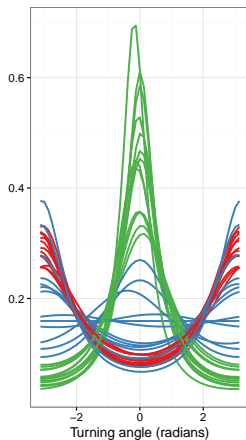
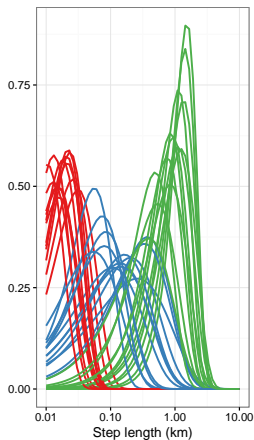
Hidden Markov models (part 3)

- *forward-backward algorithm* for estimating parameters
- *Viterbi algorithm* for estimating most probable state sequences
- depmixS4 package (Visser and Speekenbrink, 2010) (also moveHMM (Michelot et al., 2016))
- hidden *semi-Markov* models: allow for non-geometric *dwell distributions* (Langrock, 2011; Augustine, 2016): move.HMM

Outline

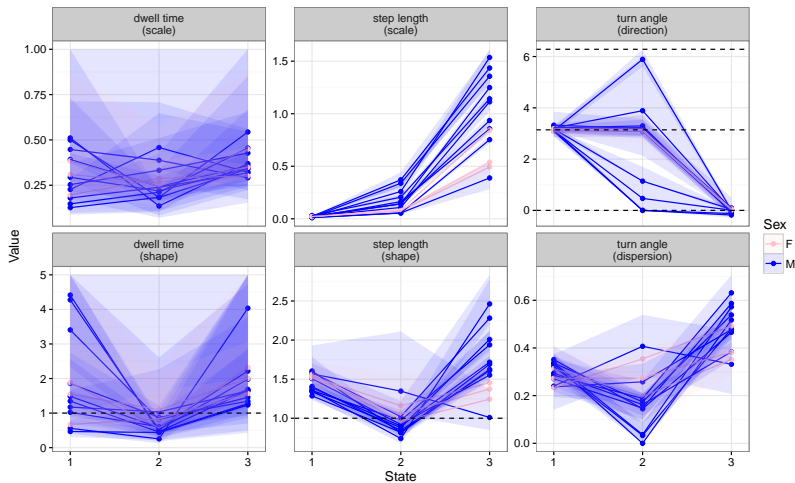
- 1 Animal movement
- 2 Florida panthers
- 3 Hidden Markov models
- 4 Basic analysis (van de Kerk et al., 2015)**
- 5 Incorporating diurnal variation (Li, 2015)
- 6 Broader issues/outlook

State distributions

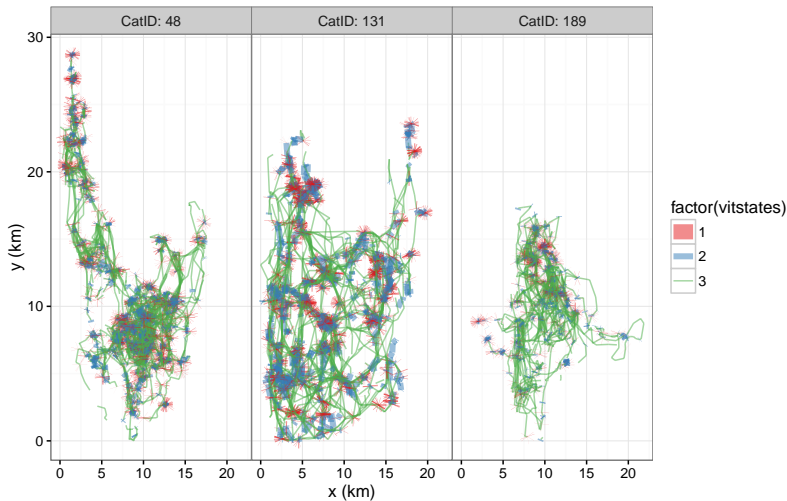


State — 1 — 2 — 3

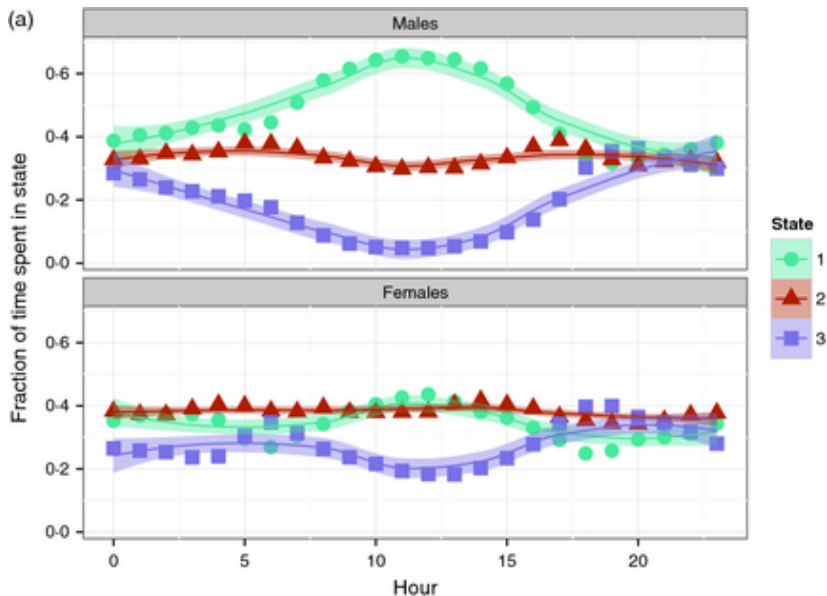
Parameter estimates



Tracks with Viterbi estimates



Diurnal variation



what can we conclude so far?

good news

- basic biology: males move faster, farther
- three states are identifiable, sensible
- dwell distributions approximately geometric (HSMM \rightarrow HMM)

bad news

- diurnal variation in Viterbi results - but it's not in the model!
- estimates of model complexity are too high

what can we conclude so far?

good news

- basic biology: males move faster, farther
- three states are identifiable, sensible
- dwell distributions approximately geometric (HSMM \rightarrow HMM)

bad news

- diurnal variation in Viterbi results - but it's not in the model!
- estimates of model complexity are too high

Animal movement
○○○

Panthers
○○○○

HMM
○○○

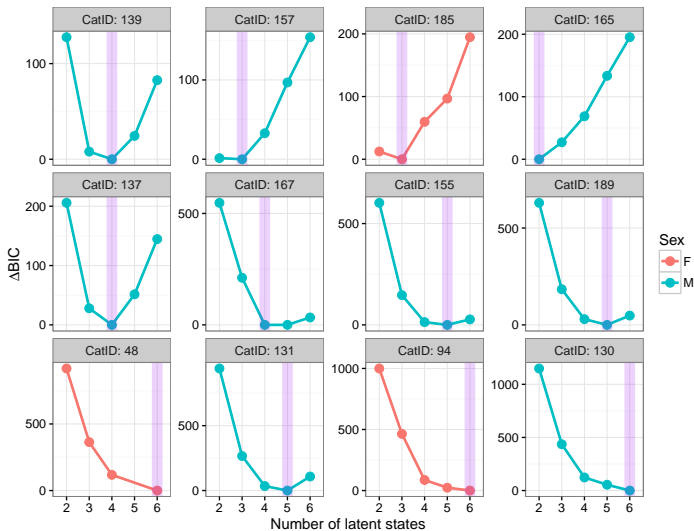
Basic analysis
○○○○○●○

Diurnal model
○○○○○○○

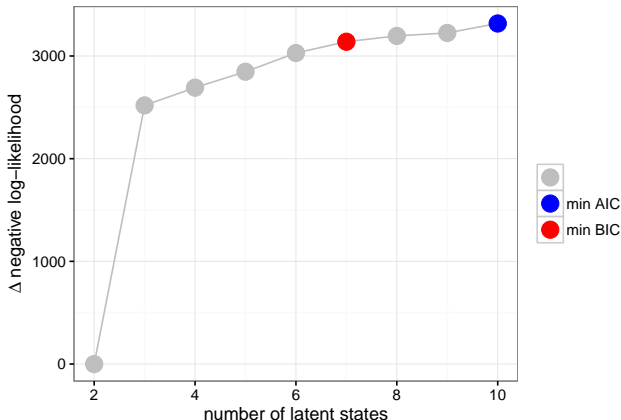
Broader issues/outlook
○○○○

References

Model complexity (bad news)



Model complexity (Manx shearwaters, Dean et al. (2013))



Outline

- 1 Animal movement
- 2 Florida panthers
- 3 Hidden Markov models
- 4 Basic analysis (van de Kerk et al., 2015)
- 5 Incorporating diurnal variation (Li, 2015)**
- 6 Broader issues/outlook

Expanding the model

Attempting to fix these problems:

- extend the model to allow covariates
- specifically, allow for diurnal variation
 - simplify model (log-Normal step length only)
 - *fixed* state-specific emissions parameters (step length mean and std dev)
 - time-varying transition parameters
 - also try *finite mixture models* (independent occupancy)
- how much does this help?

Expanding the model

Attempting to fix these problems:

- extend the model to allow covariates
- specifically, allow for diurnal variation
 - simplify model (log-Normal step length only)
 - *fixed* state-specific emissions parameters (step length mean and std dev)
 - time-varying transition parameters
 - also try *finite mixture models* (independent occupancy)
- how much does this help?

Animal movement
ooo

Panthers
oooo

HMM
ooo

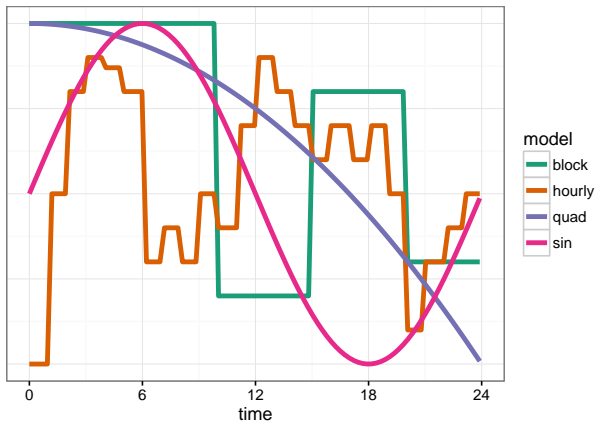
Basic analysis
ooooooo

Diurnal model
o●ooooo

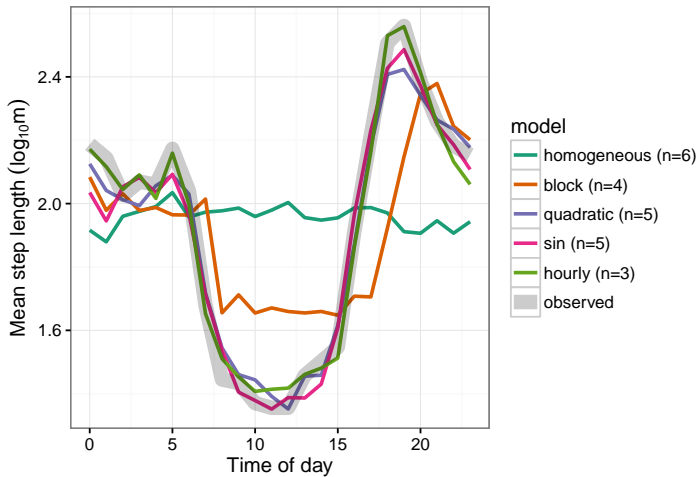
Broader issues/outlook
oooo

References

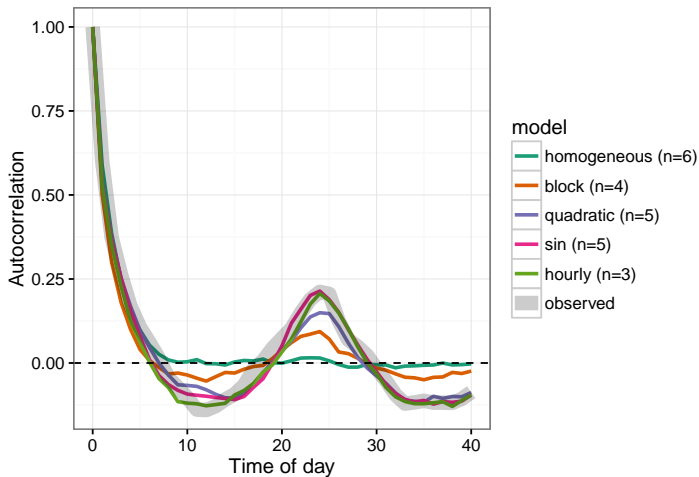
Temporal models



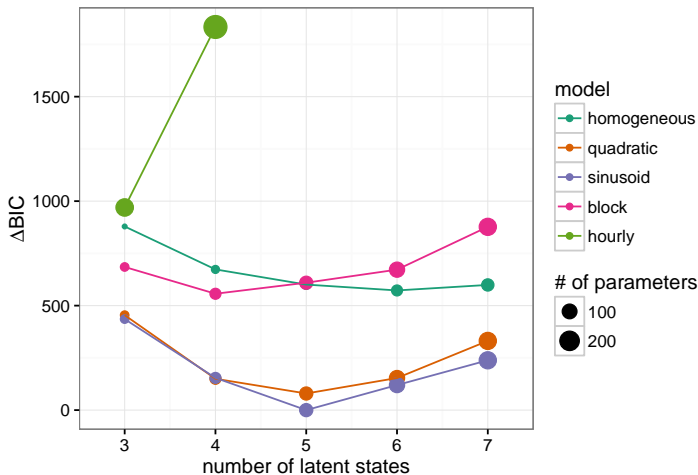
Temporal patterns (step length)



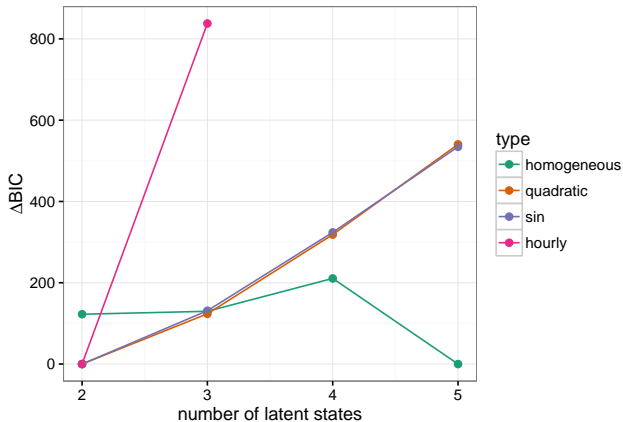
Temporal patterns (autocorrelation)



Goodness of fit/model complexity



Model complexity: simulation



Diurnal model: conclusions

- diurnal structure greatly improves fit ($\Delta\text{BIC} \approx 500$)
- slightly improves latent-state issue ($n = 6 \rightarrow 5$)
- lots left to do!
 - seasonal variation
 - incorporate habitat, home range behaviour
 - etc. etc. etc.

Outline

- 1 Animal movement
- 2 Florida panthers
- 3 Hidden Markov models
- 4 Basic analysis (van de Kerk et al., 2015)
- 5 Incorporating diurnal variation (Li, 2015)
- 6 Broader issues/outlook**

Big data and small models

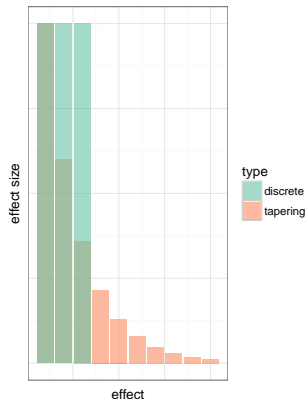
- simple model families + model misspecification → overparameterization

- Gelman: “Sample sizes are never large”: ([blog post](#))

N is never enough because if it were “enough” you’d already be on to the next problem for which you need more data.

An aside on AIC vs BIC

- “should I use AIC or BIC? I heard that AIC is inconsistent ...”
- complexity penalty = 2 (AIC) vs $\log(n)$ (BIC)
- best prediction vs. model identification (Yang, 2005)
- *effect size spectrum*: tapering or discrete?



Animal movement: open challenges

- Cognition/memory (Bracis et al., 2015)
- Intraspecific interaction/collective movement (Delgado et al., 2014)
- Continuous-time movement models (Calabrese et al., 2016)
- Edges, barriers, and corridors (Beyer et al., 2016)
- Efficient (big-data) approaches (Brillinger et al., 2008)
- Putting it all together ...



Tools needed

- cross-validation (Wenger and Olden, 2012)
- protocols and tools for model checking (Potts et al., 2014);
score tests?
- flexible computational frameworks
(ecologists can't afford consultants/
there are too many species out there)

References

- Augustine, B., 2016. Flexible, user-friendly hidden (semi) Markov models for animal movement data.
- Beyer, H.L., Gurarie, E., et al., 2016. *Journal of Animal Ecology*, 85(1):43–53. ISSN 00218790. doi:10.1111/1365-2656.12275.
- Bracis, C., Gurarie, E., et al., 2015. *PLOS ONE*, 10(8):e0136057. ISSN 1932-6203. doi:10.1371/journal.pone.0136057.
- Brillinger, D.R., Stewart, B.S., et al., 2008. In *Probability and statistics: Essays in honor of David A. Freedman*, pages 246–264. Institute of Mathematical Statistics.
- Calabrese, J.M., Fleming, C.H., and Gurarie, E., 2016. *Methods in Ecology and Evolution*, pages n/a–n/a. ISSN 2041-210X. doi:10.1111/2041-210X.12559.
- Dean, B., Freeman, R., et al., 2013. *Journal of The Royal Society Interface*, 10(78):20120570. ISSN 1742-5689, 1742-5662. doi:10.1098/rsif.2012.0570.
- Delgado, M.d.M., Penteriani, V., et al., 2014. *Methods in Ecology and Evolution*, 5(2):183–189.
- Fryxell, J.M., Hazell, M., et al., 2008. *Proceedings of the National Academy of Sciences*, 105(49):19114–19119. ISSN 0027-8424, 1091-6490. doi:10.1073/pnas.0801737105.
- Langrock, R., 2011. *Computational Statistics and Data Analysis*, 55(1):715–724. ISSN 01679473.
- Langrock, R., King, R., et al., 2012. *Ecology*, 93(11):2336–2342. ISSN 0012-9658. doi:10.1890/11-2241.1.
- Li, M., 2015. *Incorporating Temporal Heterogeneity in Hidden Markov Models For Animal Movement*. Master's thesis.
- Michelot, T., Langrock, R., and Patterson, T.A., 2016. *Methods in Ecology and Evolution*, in press. doi:10.1111/2041-210X.12578.
- Potts, J.R., Auger-MÃ©thÃ©, M., et al., 2014. *Methods in Ecology and Evolution*, 5(10):1012–1022.
- van de Kerk, M., Onorato, D.P., et al., 2015. *Journal of Animal Ecology*, 84(2):576–585.
- Visser, I. and Speekenbrink, M., 2010. *Journal of Statistical Software*, 36(7):1–21.
- Wenger, S.J. and Olden, J.D., 2012. *Methods in Ecology and Evolution*, 3(2):260–267. ISSN 2041210X. doi:10.1111/j.2041-210X.2011.00170.x.
- Yang, Y., 2005. *Biometrika*, 92(4):937–950. doi:10.1093/biomet/92.4.937.