iSSA, Part 2

Movement and Habitat Interactions

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27 March 2025

Analysis of Animal Movement Data in R
J. Signer & B. Smith

Review of iSSA

Review of iSSA

Availability in (i)SSA is defined at the step level.

- Analyzed with *conditional* logistic regression, comparing used and available for each observed step paired with many available steps.
- Allows time-varying covariates.

Review of iSSA

Unlike *unconditional* HSFs, (i)SSFs are appropriate for movement data with high fix rates.

Review of iSSA

Ordinary step-selection analysis estimates habitat selection parameters with **bias** (Forester et al. 2009).

- Due to the unmodeled dependency between realized movement and realized habitat selection.
- Sampling available steps from the observed movement distributions propagates this correlation to the conditional logistic regression.

Review of iSSA

Integrated step-selection analysis parameterizes two independent processes:

1. Movement-free habitat selection
2. Selection-free movement

These two processes combine to give rise to the observed movement trajectory.

Review of iSSA

iSSA requires available steps to be sampled from a parametric distribution.

- Distributions must be from the exponential family to be fit via GLM.
- Step lengths and turn angles are modeled separately. Note that we can have correlations between them by either using interactions (this lecture) or circular-linear copulae (Hodel and Fieberg 2022).
- Movement parameters estimated by GLM *adjust* tentative distribution to estimate the parameters of the true selection-free movement distribution.

Methods in Ecology and Evolution

REVIEW | Open Access

Understanding step selection analysis through numerical integration

Théo Michelot, Natasha J. Klappstein, Jonathan R. Potts, John Fieberg

First published: 08 December 2023 | https://doi.org/10.1111/2041-210X.14248 | Citations: 1

Handling Editor: David Soto

Review of iSSA

Habitat selection parameters can still be interpreted using (log-)RSS.

- RSS is how much more likely a step is to land in habitat x_1 vs. habitat x_2, conditional on the starting location of the step and the movement parameters.
  - Don't forget the conditional nature of steps.

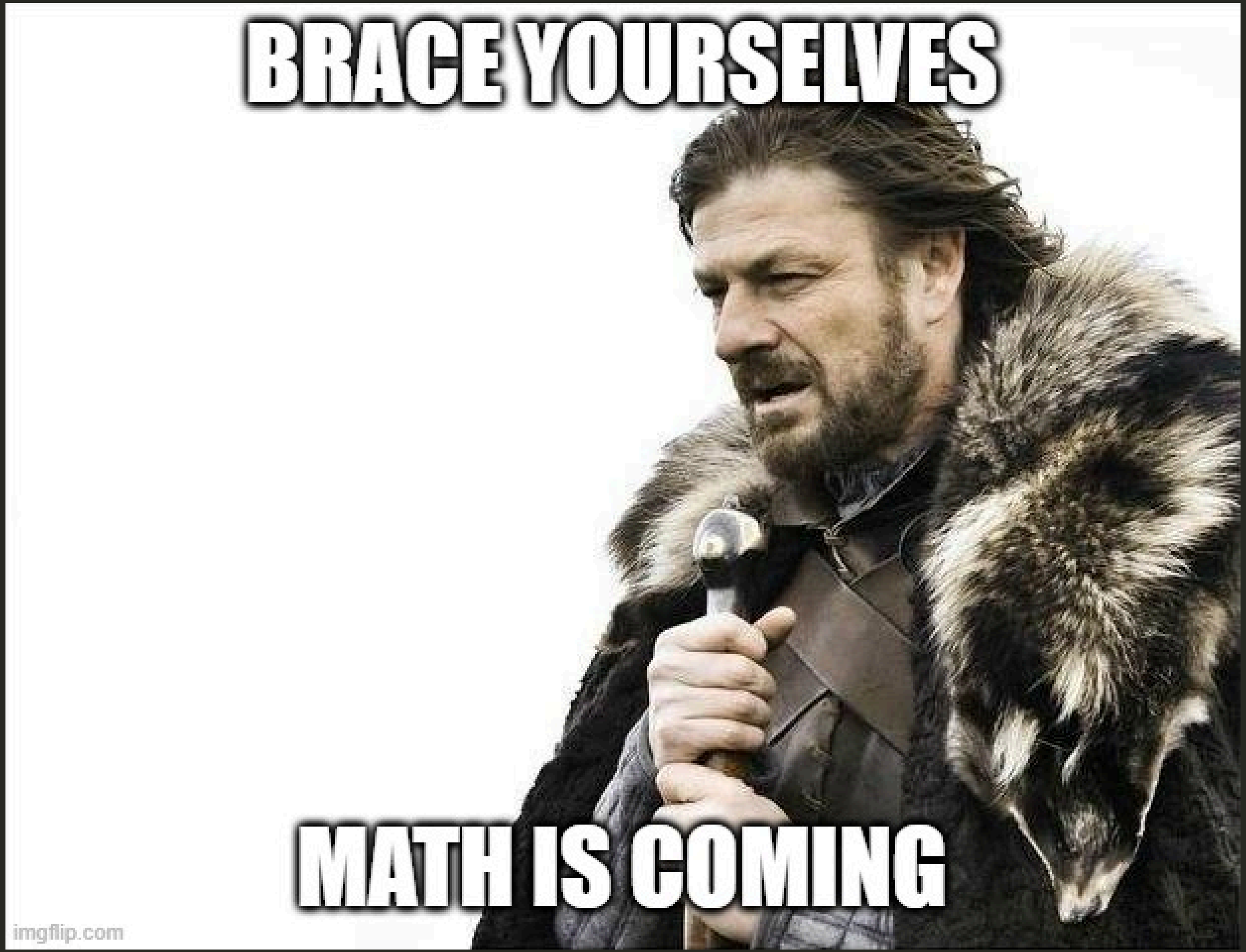
Take-home messages

- (i)SSFs define availability at the step level and so are appropriate for high-fix-rate movement data.
- Use iSSA to avoid the bias introduced by ordinary SSA.
    - Sample available steps from a theoretical, rather than empirical, distribution.
    - Include movement parameters in the GLM.
- Intepretation of βs is still log-RSS.

Recall that the βs from a fitted exponential habitat selection model can be interpreted as the log-RSS for a one-unit change in that covariate.

What if the log-RSS depends on another variable?

Interactions in GLMs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Interactions in GLMs

Let's consider a simple Gaussian GLM.

$$\mu_i = \beta_0 + \sum_{j=1}^{k} \beta_j x_{j,i}$$

$$y_i \sim N(\mu_i, \sigma^2)$$

Interactions in GLMs

Let's assume our model has 2 covariates, x_1 and x_2, and we would like to include an interaction between x_1 and x_2 in the model. This implies that we need to estimate 3 slope parameters $(\beta_1, \beta_2, \beta_3)$.

$$\mu_i = \beta_0 + \beta_1 x_{1,i} + \beta_2 x_{2,i} + \beta_3 x_{1,i} x_{2,i}$$

$$y_i \sim N(\mu_i, \sigma^2)$$

Interactions in GLMs

For brevity, I'm going to drop the observation subscript (i).

$$\mu = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2$$

Interactions in GLMs

$$\mu = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2$$

To create the interaction variable, we literally multiply x_1 by x_2.

This works for any covariate, including categorical covariates (which are represented by binary dummy variables).

Parameters as functions

We can think of the parameters in an interaction as linear functions of covariates.

Parameters as functions

$$\mu = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2$$

$$\mu = \beta_0 + [\beta_1 x_1 + \beta_3 x_1 x_2] + \beta_2 x_2$$

$$\mu = \beta_0 + [\beta_1 + \beta_3 x_2] x_1 + \beta_2 x_2$$

Parameters as functions

$$\mu = \beta_0 + [\beta_1 + \beta_3 x_2] x_1 + \beta_2 x_2$$

$$Let\ \beta_1^* = \beta_1 + \beta_3 x_2$$

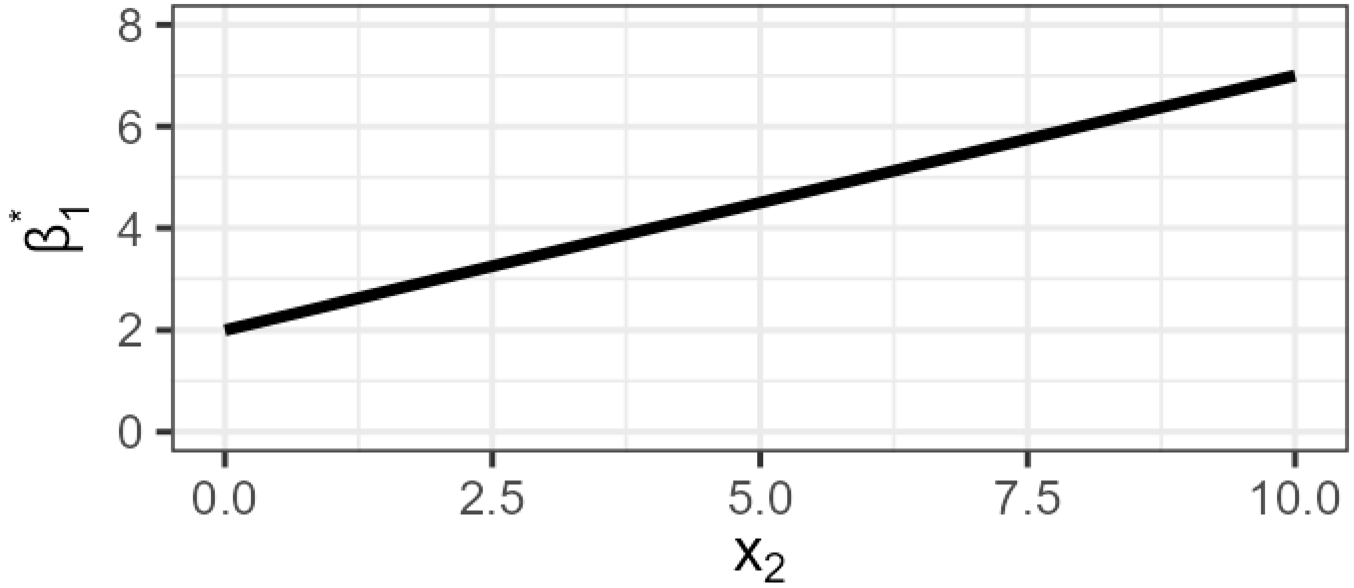
$$\Rightarrow$$

$$\mu = \beta_0 + \beta_1^* x_1 + \beta_2 x_2$$

$$\beta_1^* = f(x_2) = \beta_1 + \beta_3 x_2$$

Parameters as functions

$$\beta_1^* = f(x_2) = \beta_1 + \beta_3 x_2$$



The main effect (β_1) is the intercept, and the interaction slope (β_3) is the slope.

Parameters as functions

$$\beta_1^* = f(x_2) = \beta_1 + \beta_3 x_2$$

Since the βs in our analyses can be interpreted as log-RSS, interactions allow us to define the log-RSS for a one-unit change in one variable as a *function* of another variable.

Parameters as functions

Note that this the case for either interacting variable.

$$\mu = \beta_0 + \beta_1^* x_1 + \beta_2 x_2$$

$$\beta_1^* = f(x_2) = \beta_1 + \beta_3 x_2$$

OR

$$\mu = \beta_0 + \beta_1 x_1 + \beta_2^* x_2$$

$$\beta_2^* = g(x_1) = \beta_2 + \beta_3 x_1$$

Parameters as functions

BUT NOT the case for both interacting variables.

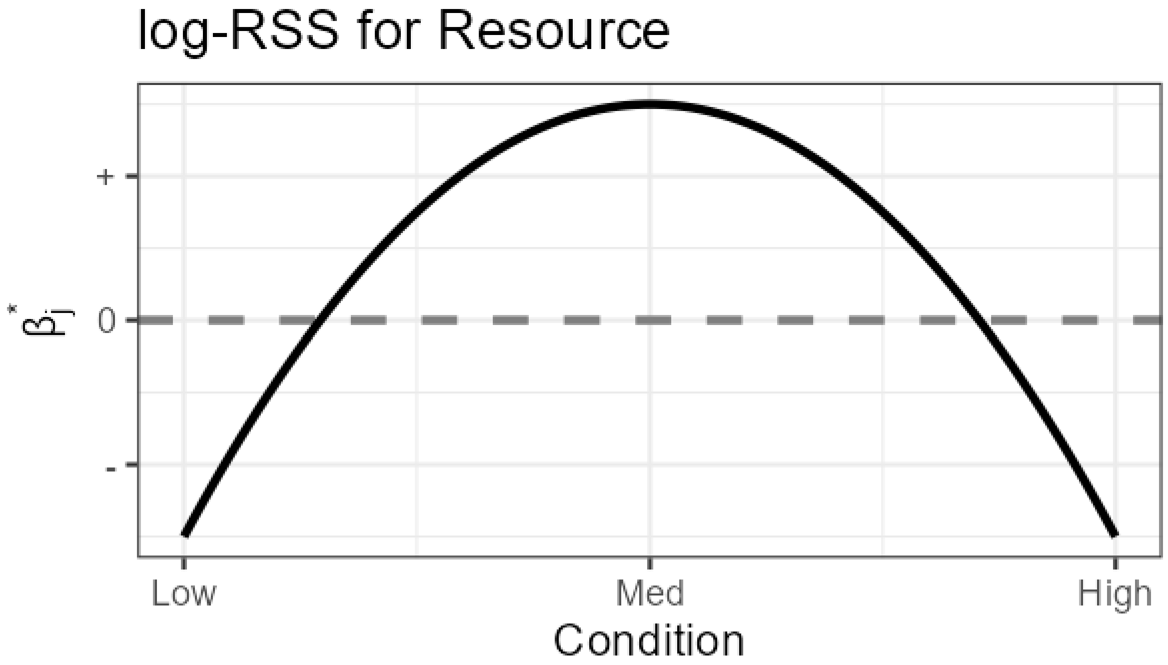
$$\mu \neq \beta_0 + \beta_1^* x_1 + \beta_2^* x_2$$

$$\beta_1^* = f(x_2) = \beta_1 + \beta_3 x_2$$

$$\beta_2^* = g(x_1) = \beta_2 + \beta_3 x_1$$

Interactions with a quadratic term

Sometimes we want to model the relationship between μ and x with a parabola, *e.g.*, if we are modeling habitat selection as a function of a **condition**.



Interactions with a quadratic term

It is important to remember that the location of the vertex of a parabola depends upon both the first-order and the second-order term (*we already saw this when we simulated data in the HSF module*).

For a parabola of the form:

$$\mu = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2$$

The vertex is located at:

$$(x, y) = \left(\frac{-\beta_1}{2\beta_2}, \frac{-\beta_1^2}{4\beta_2} + \beta_0 \right)$$

Interactions with a quadratic term

If you want to estimate a parabola that changes with another variable, you need an interaction with both x_1 and x_1^2.

$$\mu = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2 + \beta_4 x_1 x_2 + \beta_5 x_1^2 x_2$$

Interactions with a quadratic term

We can rearrange as before and see that

$$
\begin{aligned}
\mu &= \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2 + \beta_4 x_1 x_2 + \beta_5 x_1^2 x_2 \\
&= \beta_0 + \beta_1^* x_1 + \beta_2^* x_1^2 + \beta_3 x_2
\end{aligned}
$$

$$
\begin{aligned}
\beta_1^* &= f(x_2) = \beta_1 + \beta_4 x_2 \\
\beta_2^* &= g(x_2) = \beta_2 + \beta_5 x_2
\end{aligned}
$$

I.e., both the linear and the quadratic parameters are linear functions of x_2.

Interactions with a quadratic term

This also implies that the location of the vertex (*e.g.*, the most preferred condition) is a function of x_2.

E.g., the x-coordinate is:

$$x = \frac{-\beta_1^*}{2\beta_2^*} = -\frac{\beta_1 + \beta_4 x_2}{2(\beta_2 + \beta_5 x_2)}$$

Interactions with a quadratic term

Equivalently, we can rearrange as:

$$\mu = \beta_0 + \beta_1 x_1 + \beta_2 x_1^2 + \beta_3^* x_2$$

$$\beta_3^* = h(x_1) = \beta_3 + \beta_4 x_1 + \beta_5 x_1^2$$

I.e., β_3^* is a quadratic function of x_1.

Take-home messages

- An interaction variable is created by multiplying together the two (or more) interacting variables.
    - This applies to any variable, continuous or categorical.
- Interactions can be thought of as expressing the slope of one of the interacting variables as a function of the other variable.
- Since our slope parameters are directly interpretable as log-RSS, interactions allow us to write the log-RSS for a variable as a function of another variable.
- Interactions with a parabola should include both the linear and quadratic terms.

Interactions between Habitat Variables

Interactions between habitat variables

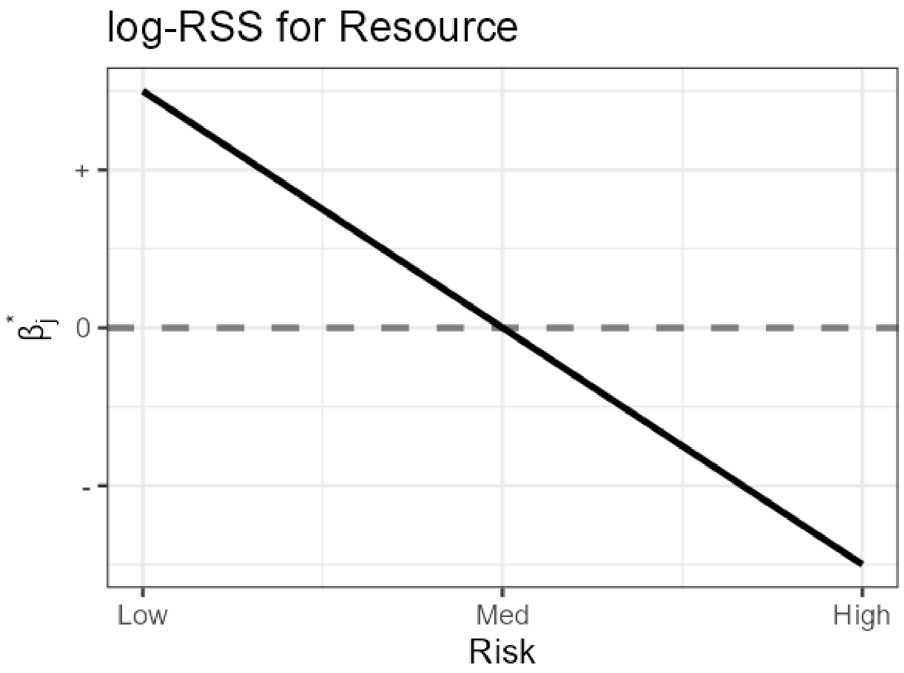
Let's begin by considering an interaction between two habitat variables.

Interactions between habitat variables

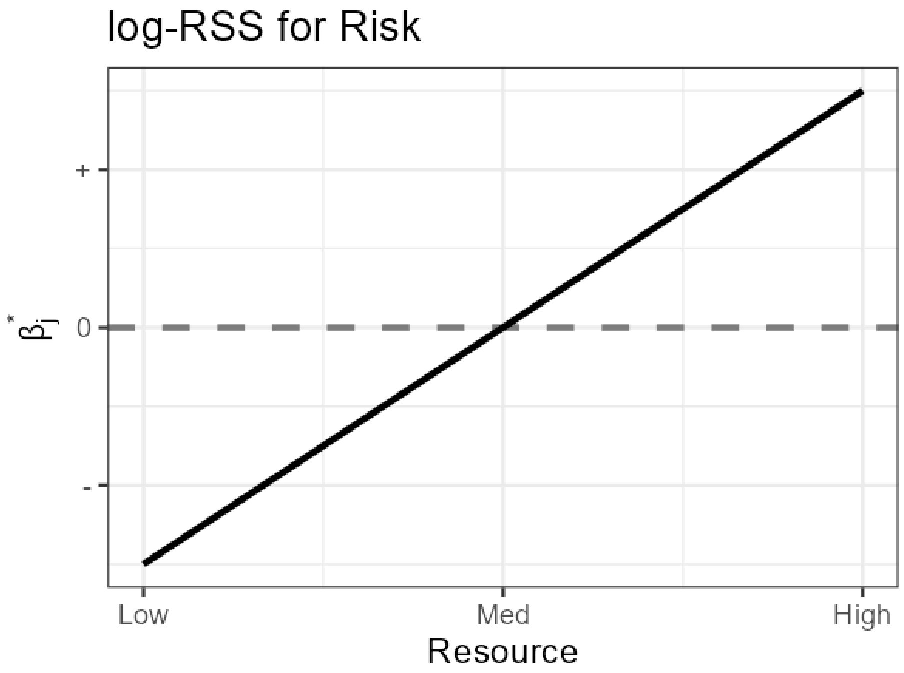
As we've already discussed, we can classify habitat axes as resources, risks, or conditions.

Resource-risk interaction

E.g., an animal might avoid patches with high resource density if predation risk is also high $(\beta_{res} > 0; \beta_{intxn} < 0)$.

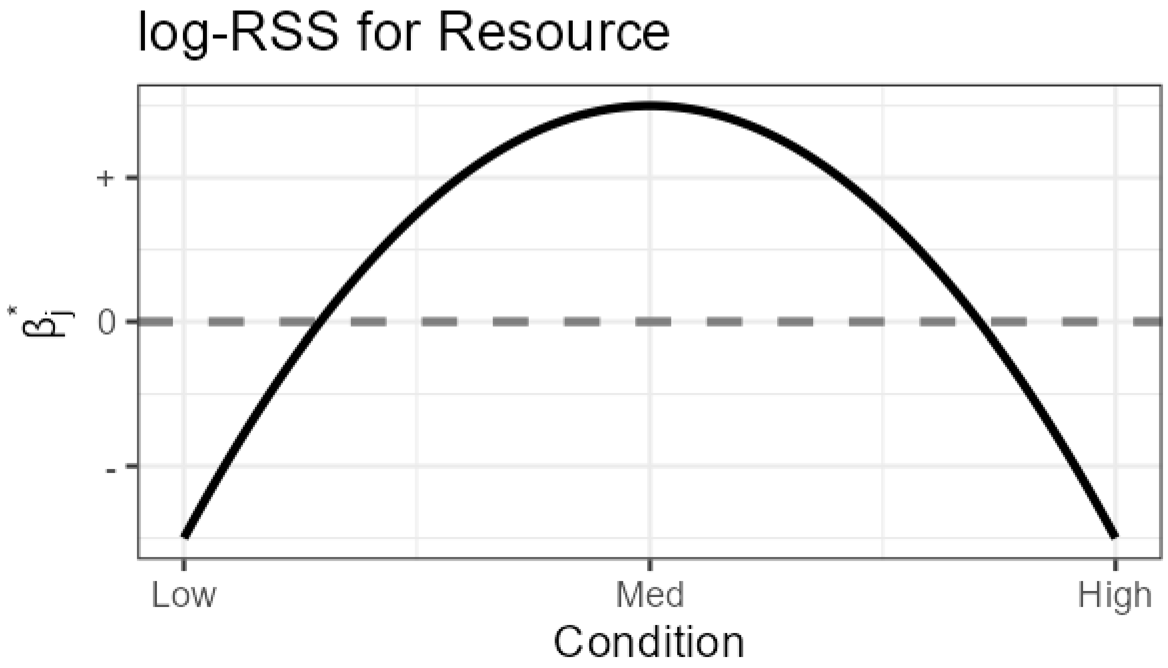


E.g., an animal might accept patches with high risk if resource density is also high $(\beta_{risk} < 0; \beta_{intxn} > 0)$.



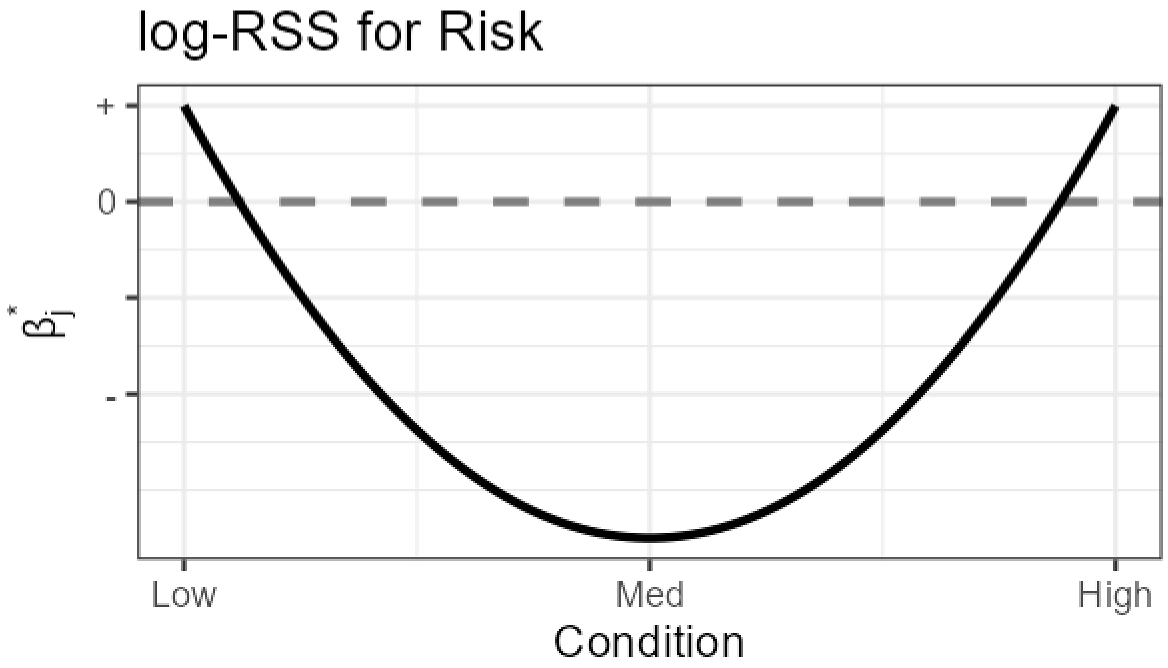
Resource-condition interaction

E.g., an animal might avoid foraging in places where it is too cold or too hot.



Risk-condition interaction

E.g., an arboreal animal might be most vulnerable to predation at intermediate canopy cover.



Resource-resource interaction

If resources are *perfectly substitutable*, then they combine additively in a model $(\beta_{intxn} = 0)$.

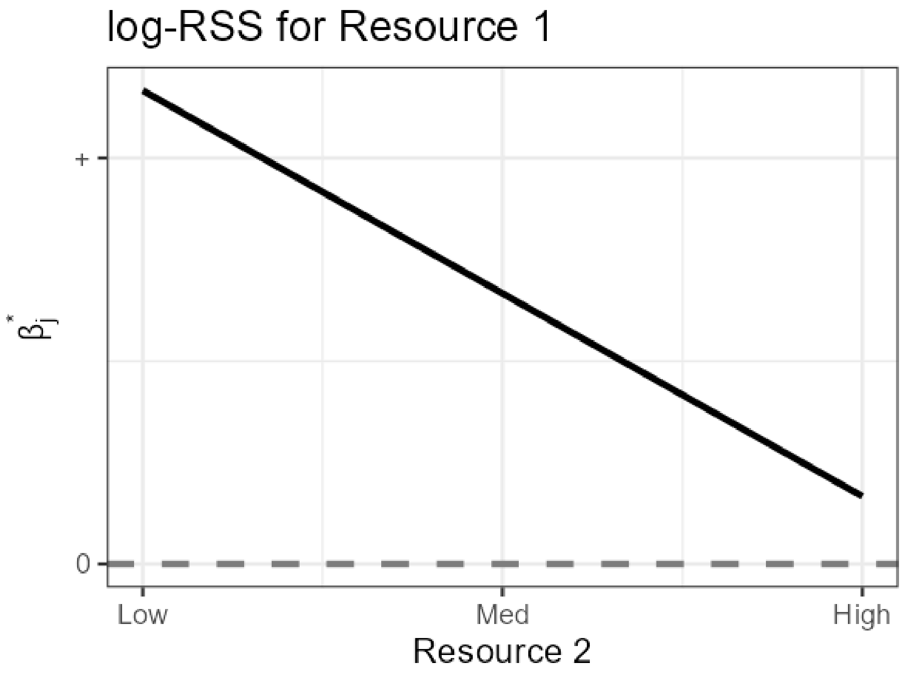
Two resources can be *antagonistic* if they only partially substitute each other, such that the consumer requires more total resources $(\beta_{intxn} < 0)$.

Two resources can be *complementary* if they augment each other, such that the consumer requires fewer total resources $(\beta_{intxn} > 0)$.

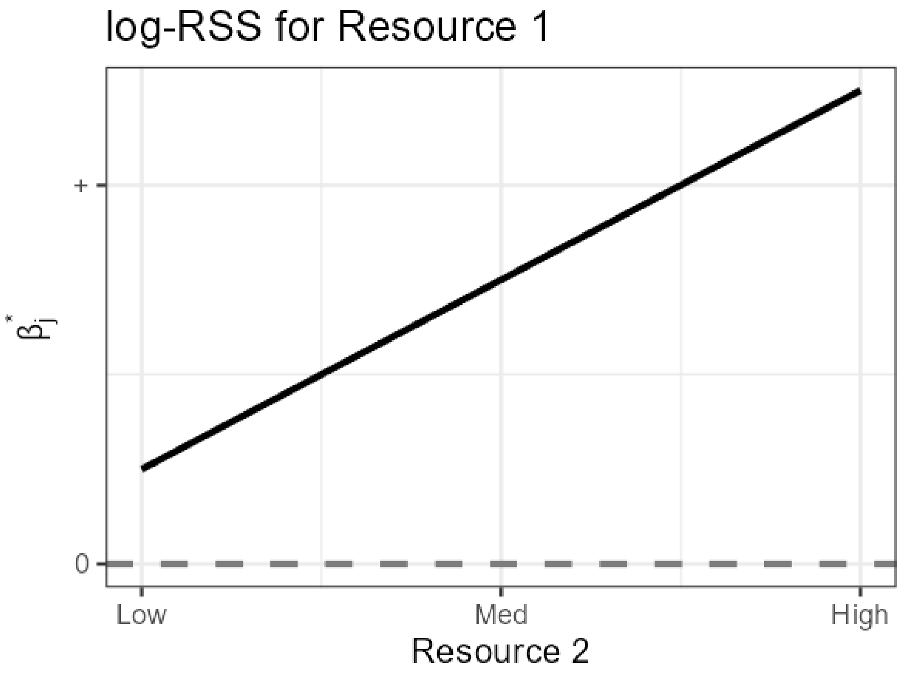
See Matthiopoulos et al. (2023) for more discussion of this. Resource substitutability terms from Tilman (1980).

Resource-resource interaction

Resource antagonism ($\beta_{intxn} < 0$).



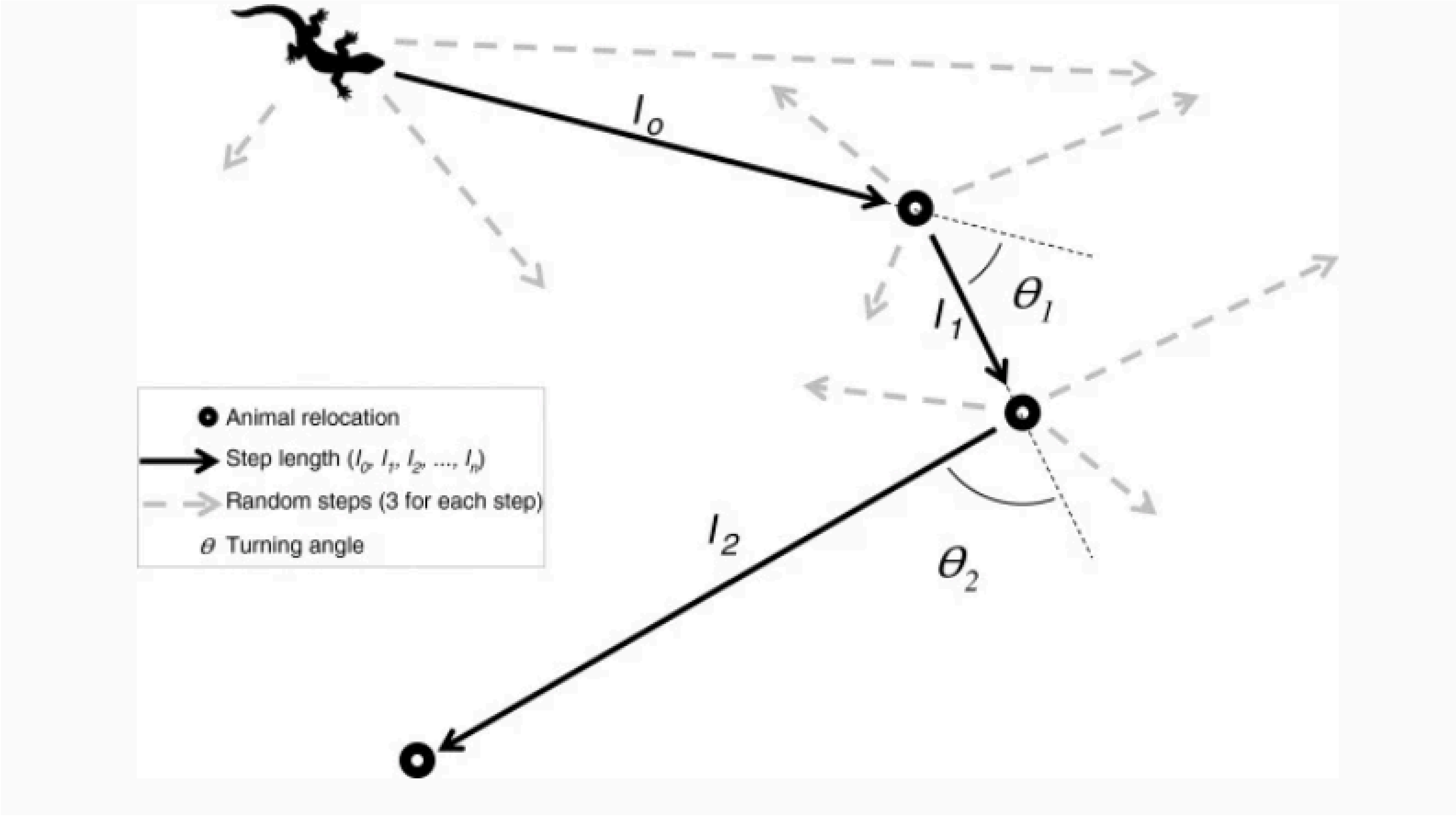
Resource complementarity ($\beta_{intxn} > 0$).



Note in both cases that the log-RSS remains positive.

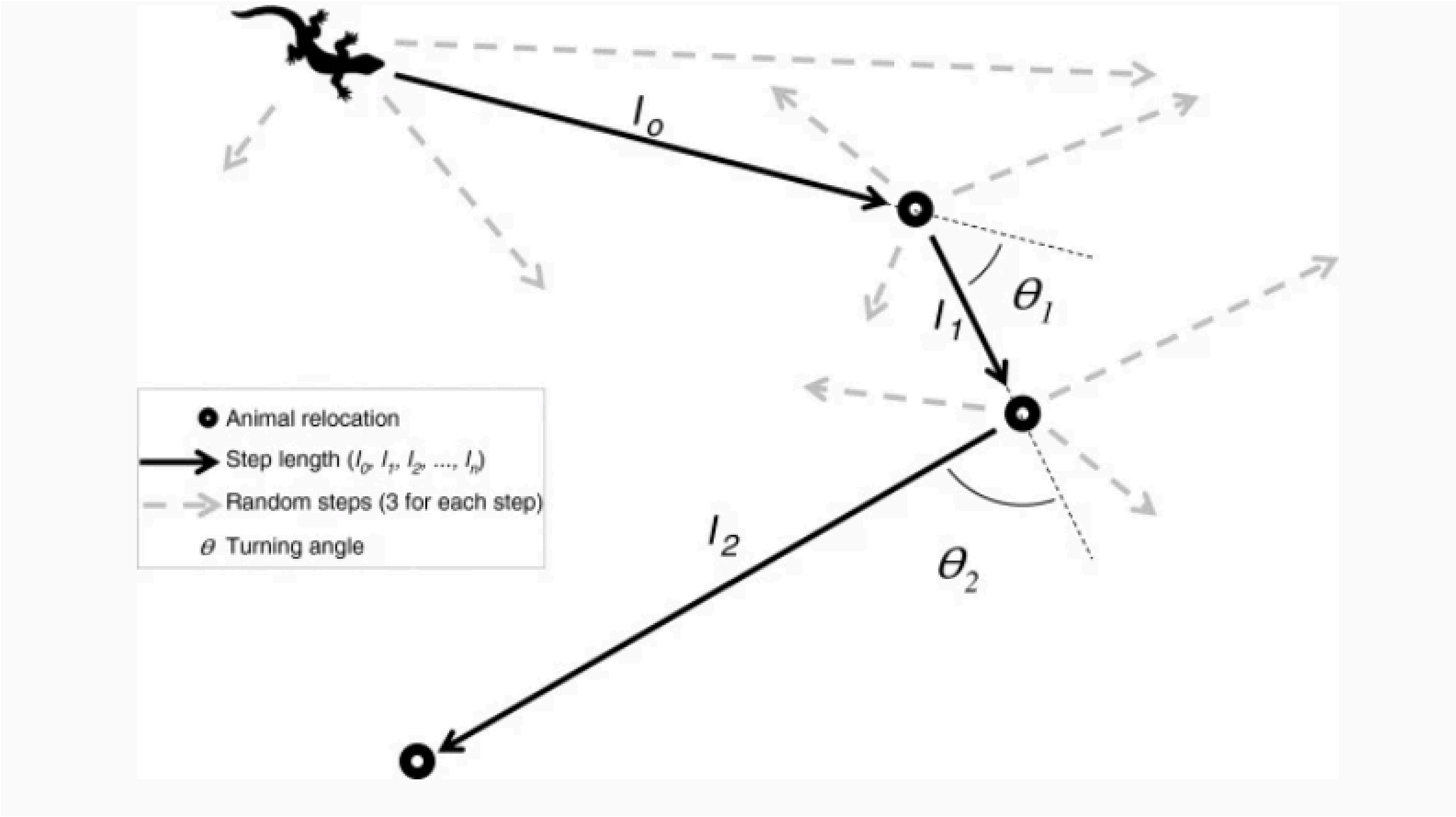
Habitat at start or end of step

Recall that all the steps in a stratum have the same starting location.



Habitat at start or end of step

(i)SSFs compare use vs. availability within a stratum.



Habitat at start or end of step

If there is no variation in a habitat variable within a stratum, then we cannot estimate a slope for that habitat variable.

So we cannot include habitat at the start of a step by itself.

Habitat at start or end of step

However, we can include an **interaction** between a habitat at the start of a step and some other feature of that step which varies within a stratum.

E.g., an interaction between land cover at the start of a step and land cover at the end of the step would help us estimate transition probabilities between land cover types.

E.g., is it more likely for a step to end in forest, given that it started in forest?

Interactions between Movement and Habitat Variables

Interactions between movement and habitat variables

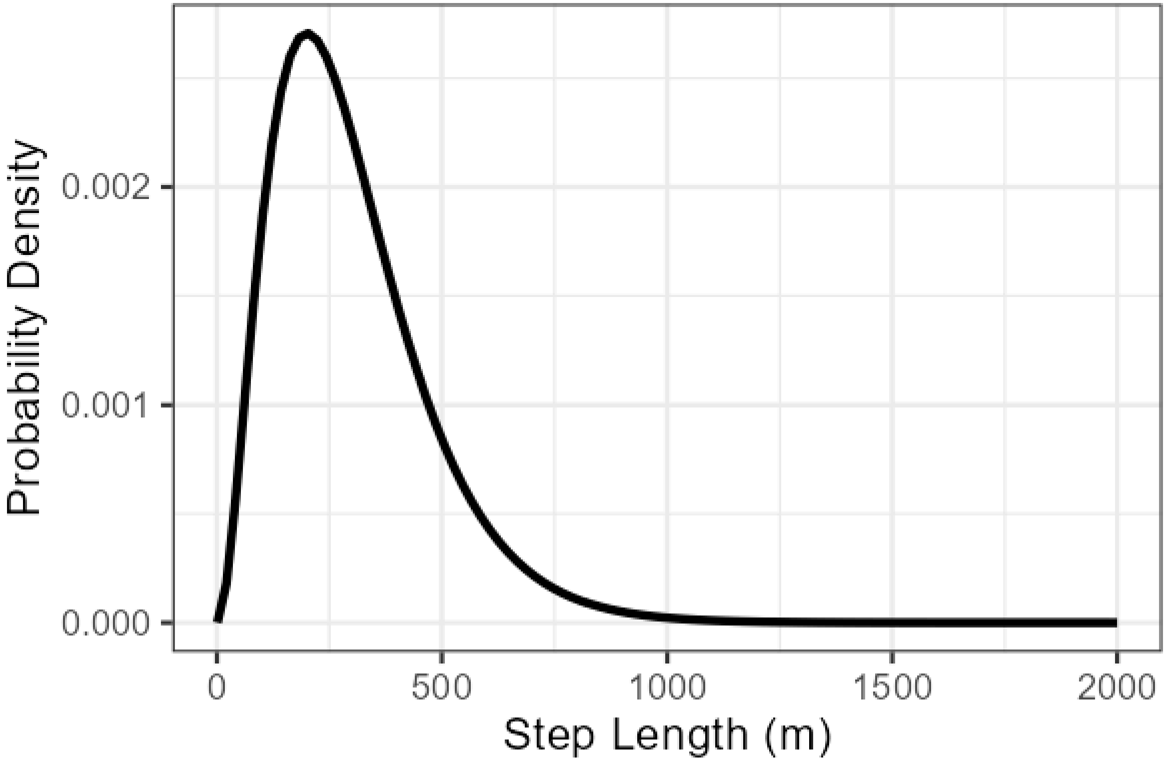
Recall that the βs for the movement parameters adjust the tentative movement distributions.

If we formulate the movement parameters as functions of habitats, that will give us a different movement distribution depending on the value of the habitat.

Interactions between step length and habitat

Assume we model step lengths as samples from this gamma distribution.

$$l_{tentative} \sim gamma(k_0 = 3, q_0 = 100)$$



Interactions between step length and habitat

Recall that the selection-free step-length distribution would be:

$$l_{updated} \sim gamma(\hat{k}, \hat{q}\,)$$

$$\hat{k} = k_0 + \beta_{ln(l)}$$

$$\hat{q} = 1/\left(\frac{1}{q_0} - \beta_l\right)$$

See Appendix C of Fieberg et al. (2021).

Interactions between step length and habitat

Now say that our iSSF includes an interaction between the βs and a habitat variable, x.

$$logit(p) = \beta_0 + \beta_1 x + \beta_2 l + \beta_3 ln(l) + \beta_4 xl + \beta_5 xln(l)$$

R formula:

```
case_ ~ sl_ * x + log_sl_ * x
```

Interactions between step length and habitat

As before, we can rearrange to write the βs for l and $ln(l)$ as functions of x.

$$logit(p) = \beta_0 + \beta_1 x + \beta_2 l + \beta_3 ln(l) + \beta_4 xl + \beta_5 xln(l)$$

$$logit(p) = \beta_0 + \beta_1 x + \beta_l^* l + \beta_{ln(l)}^* ln(l)$$

$$\beta_l^* = \beta_2 + \beta_4(x)$$

$$\beta_{ln(l)}^* = \beta_3 + \beta_5(x)$$

Interactions between step length and habitat

That implies that our gamma distribution is now a function of x.

$$l_{updated} \sim gamma(\hat{k}, \hat{q}\,)$$

$$\hat{k} = k_0 + \beta^*_{ln(l)}$$

$$\hat{q}\, = 1/\left(\frac{1}{q_0} - \beta^*_l\right)$$

$$\beta^*_l = \beta_2 + \beta_4(x)$$

$$\beta^*_{ln(l)} = \beta_3 + \beta_5(x)$$

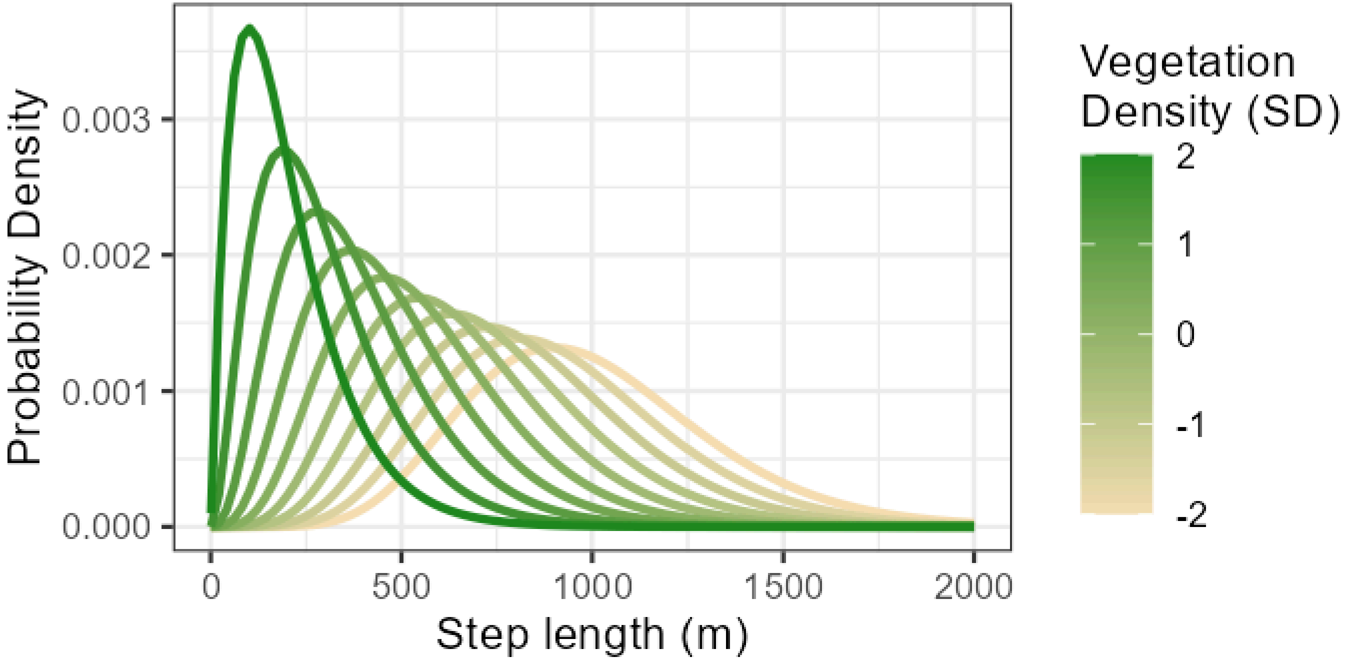
Interactions between step length and habitat

What does this look like with some numbers?

Interactions between step length and habitat

Continuous habitat

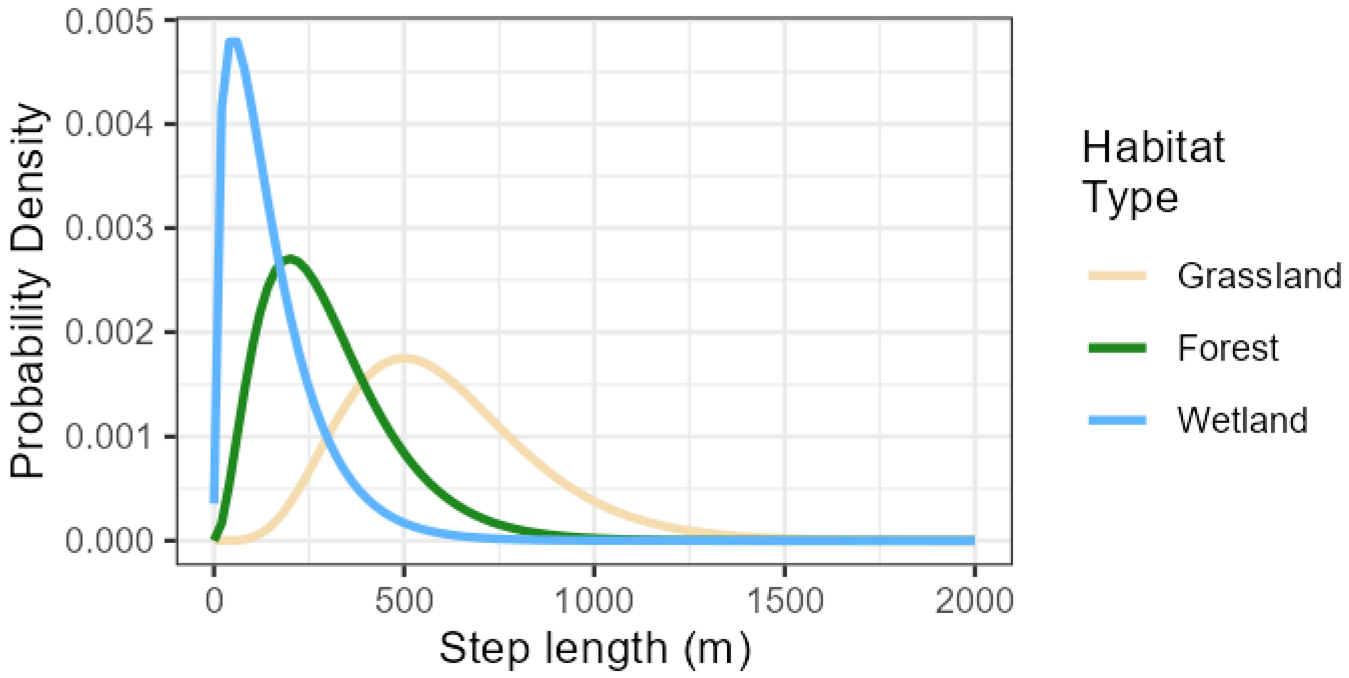
Say our x represents vegetation density, and denser vegetation makes it harder for our animal to move quickly.



Interactions between step length and habitat

Categorical habitat

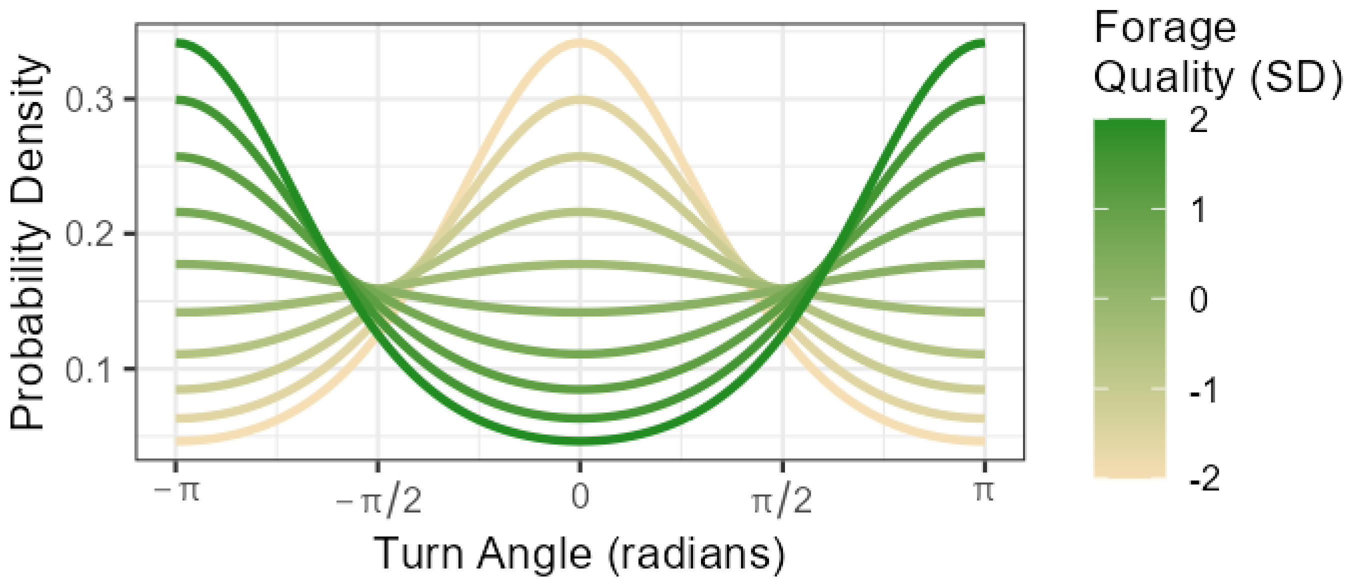
Say our x represents habitat types, and our animal moves fastest in grassland, slowest in wetland, and intermediate in forest.



Interactions between turn angle and habitat

We can do the same thing with the concentration parameter of the von Mises distribution.

E.g., foraging animals (at the right timescale) typically have turn angles concentrated around $\pm\pi$, whereas traveling animals typically have turn angles concentrated around 0.



Habitat at the start or end of the step?

If we think that a habitat affects movement, we often include an interaction between the habitat at the **start** of the step interacting with the movement parameters.

E.g. an animal starting in dense vegetation won't be able to make it very far.

Contrast that with an animal choosing an end point *because* of the habitat.

Interactions between Movement Variables

Interactions between movement variables

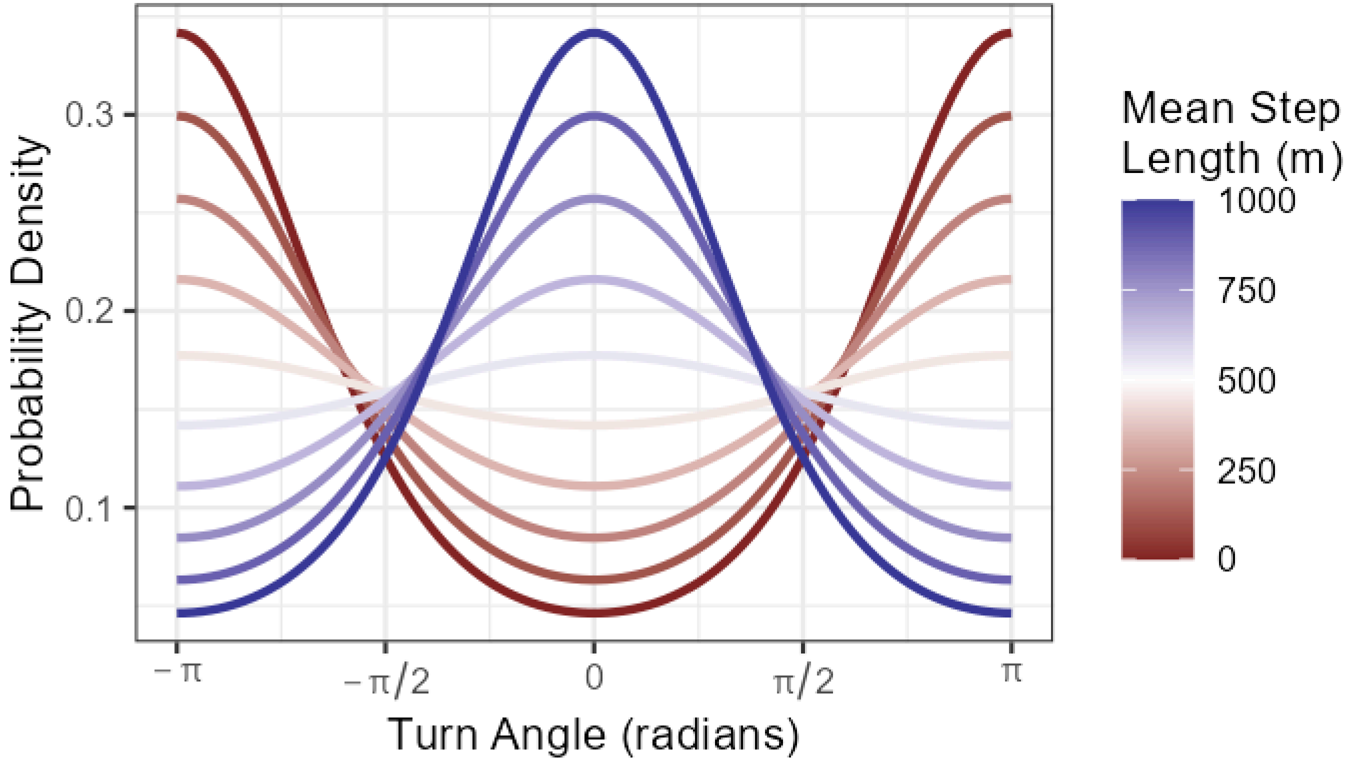
It is plausible to think that step length and turn angle might be correlated.

A travelling animal might be moving fast (long step lengths) and turning very little (turn angle concentrated around 0).

A foraging animal might be moving slowly (short step lengths) and turning quite a lot (turn angle concentrated around $\pm\pi$).

Interactions between movement variables

An interaction between step length and turn angle can capture this correlation.



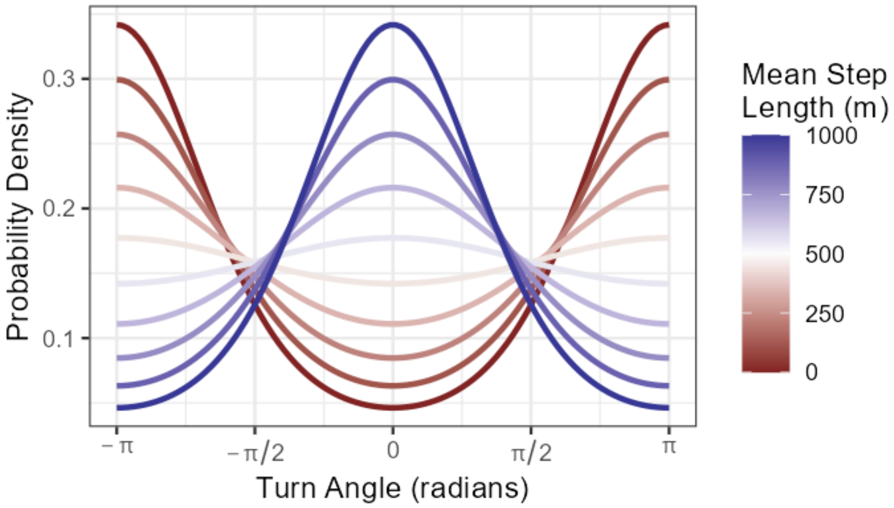
Interactions between movement variables

In this case, an iSSA will likely estimate a **negative** κ for the von Mises distribution (which is not allowed).

That is because μ is fixed at 0 when it should be at $\pm\pi$.

You can fix this by manually changing μ to $\pm\pi$ and taking the absolute value of κ.

(It is not possible to estimate μ with the iSSA.)



Interactions with Other Variables

Interactions with other variables

You may have other hypotheses about how some factor affects habitat selection and/or movement.

Interactions with temporal variables

Perhaps your animal is primarily nocturnal. Maybe they have long movements during the night and short movements during the day.

Include an interaction between step length (and maybe log step length) and time-of-day.

Interactions with temporal variables

Perhaps your animal is primarily nocturnal. Maybe they like to sleep in forests during the day, but they forage in grasslands at night.

Include an interaction between habitat type and time-of-day.

Interactions with temporal variables

Temporal interactions can be at a coarser scale, too.

For example, maybe you are studying a game species and comparing movement patterns during hunting and non-hunting seasons.

Interactions with behavioral state

Maybe you've already segmented your trajectory using an HMM. By definition, your step-length and turn-angle distributions should vary with state.

Include an interaction between behavioral state and the movement parameters.

Interactions with behavioral state

Maybe you've already segmented your trajectory using an HMM. Your animal might use habitat differently depending on whether they are resting, foraging, or travelling.

Include an interaction between behavioral state and the habitat parameters.

Take-home messages

- Interactions can capture complex biological realism in a habitat selection model.
- Give careful thought to the form of interactions to understand what they mean biologically.
- Remember that the βs for habitats represent selection strength and the βs for movement represent adjustments to the tentative movement distribution.
  - If you hypothesize that selection or movement is a function of some covariate, you can include it as an interaction.

Case Studies

Dickie et al. 2020

Received: 10 May 2019 | Accepted: 23 September 2019

DOI: 10.1111/1365-2656.13130

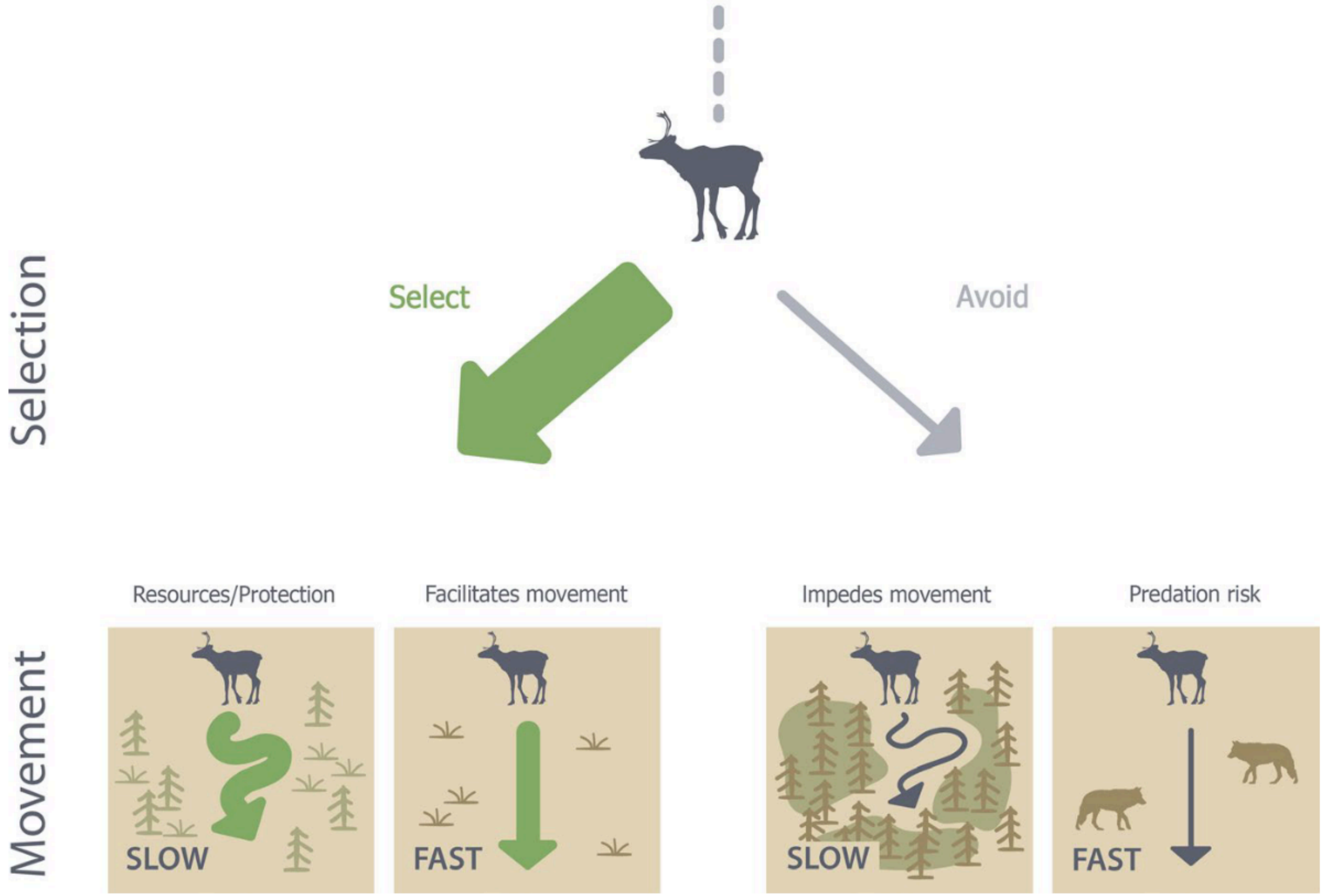
RESEARCH ARTICLE

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

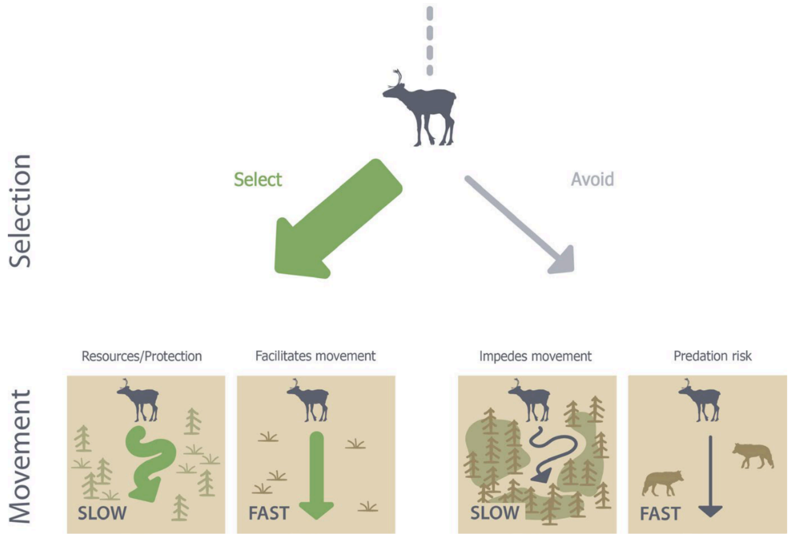
Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species

Melanie Dickie[1] | Scott R. McNay[2] | Glenn D. Sutherland[2] | Michael Cody[3] | Tal Avgar[4]

Dickie et al. 2020



Dickie et al. 2020



Interaction between habitat type and movement parameters.

Roberts et al. 2021

Received: 22 September 2020 | Accepted: 22 October 2020

DOI: 10.1002/2688-8319.12035

Ecological Solutions and Evidence

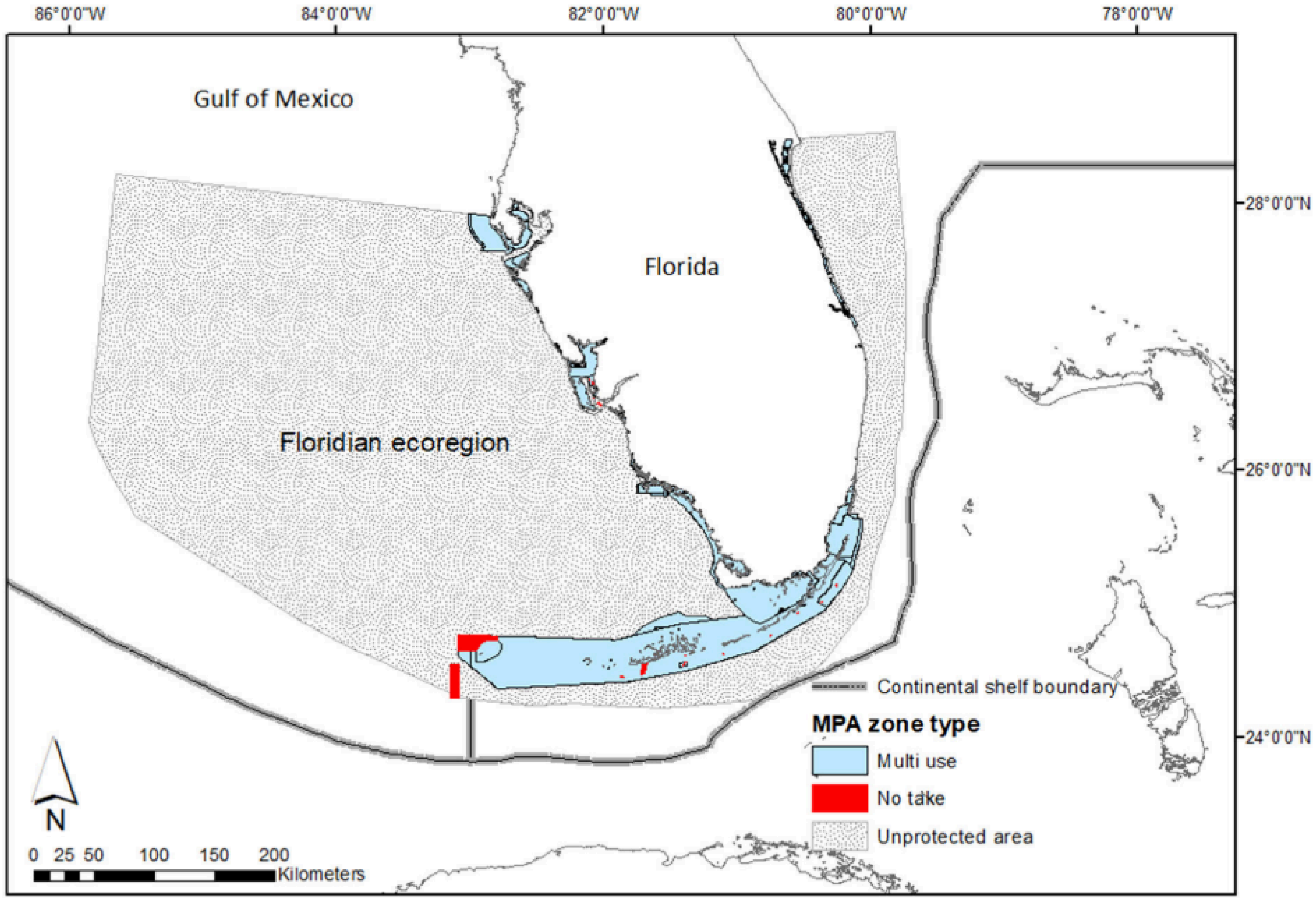
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

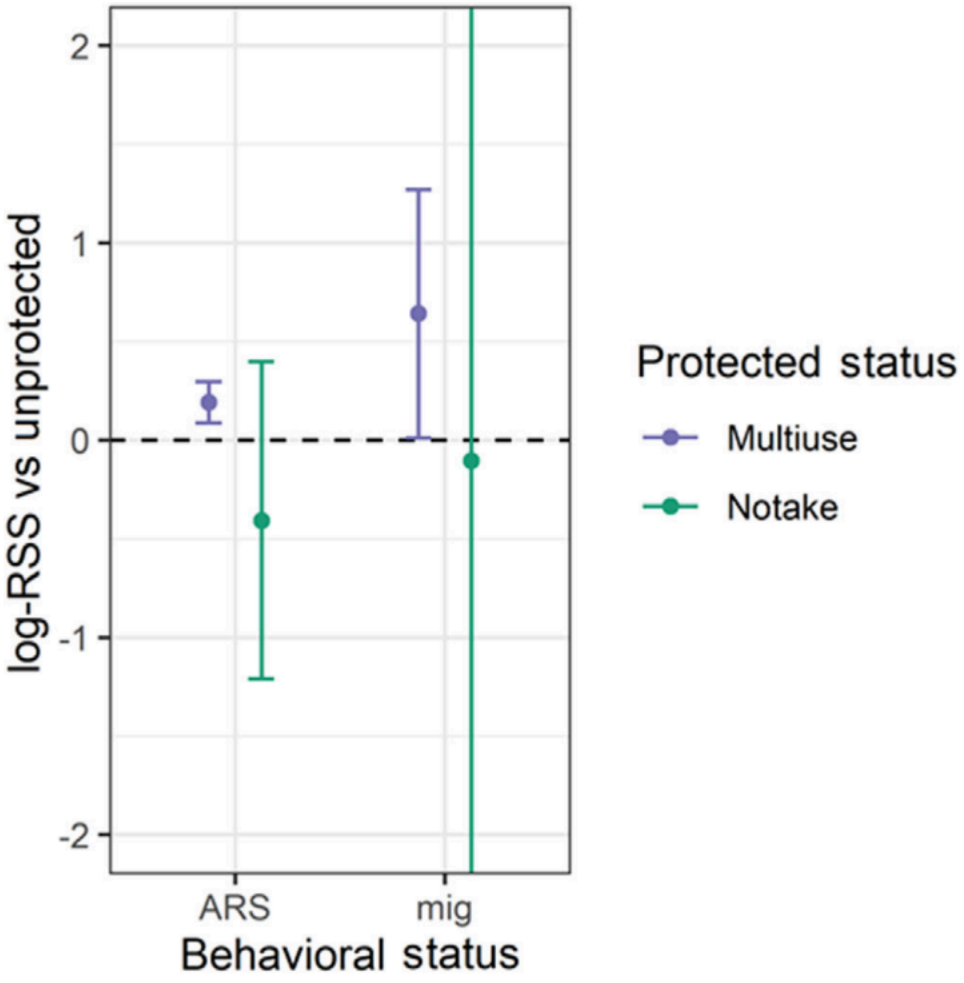
Evaluating the use of marine protected areas by endangered species: A habitat selection approach

Kelsey E. Roberts[1,2] | Brian J. Smith[3] | Derek Burkholder[4] | Kristen M. Hart[5]

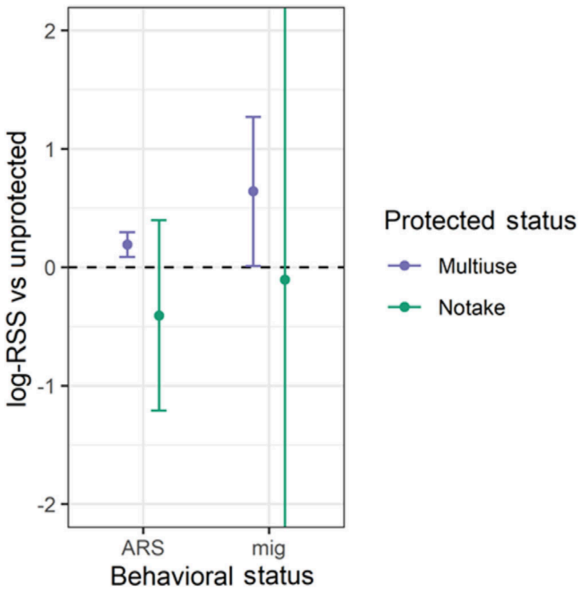
Roberts et al. 2021



Roberts et al. 2021



Roberts et al. 2021



Interaction between habitat (protected status) and behavioral state.

Green et al. 2025

Landsc Ecol (2025) 40:40
https://doi.org/10.1007/s10980-025-02056-6

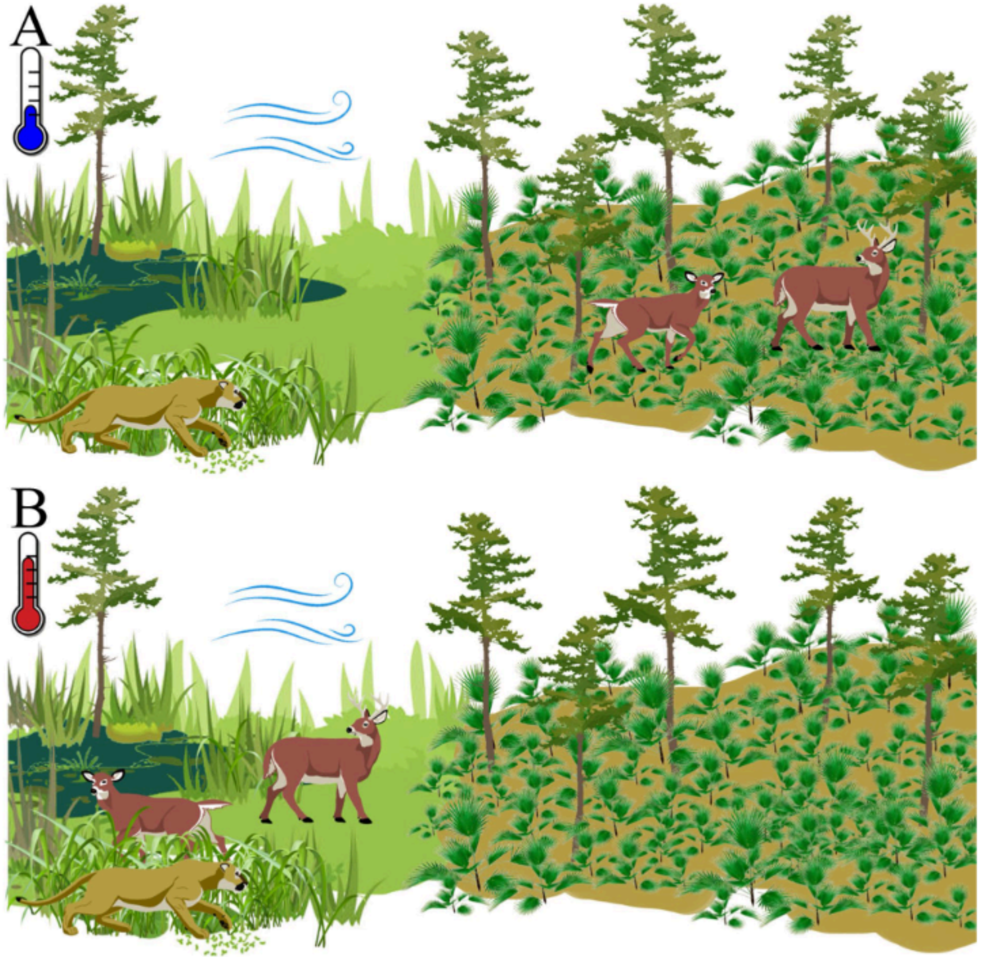
RESEARCH ARTICLE

Check for updates

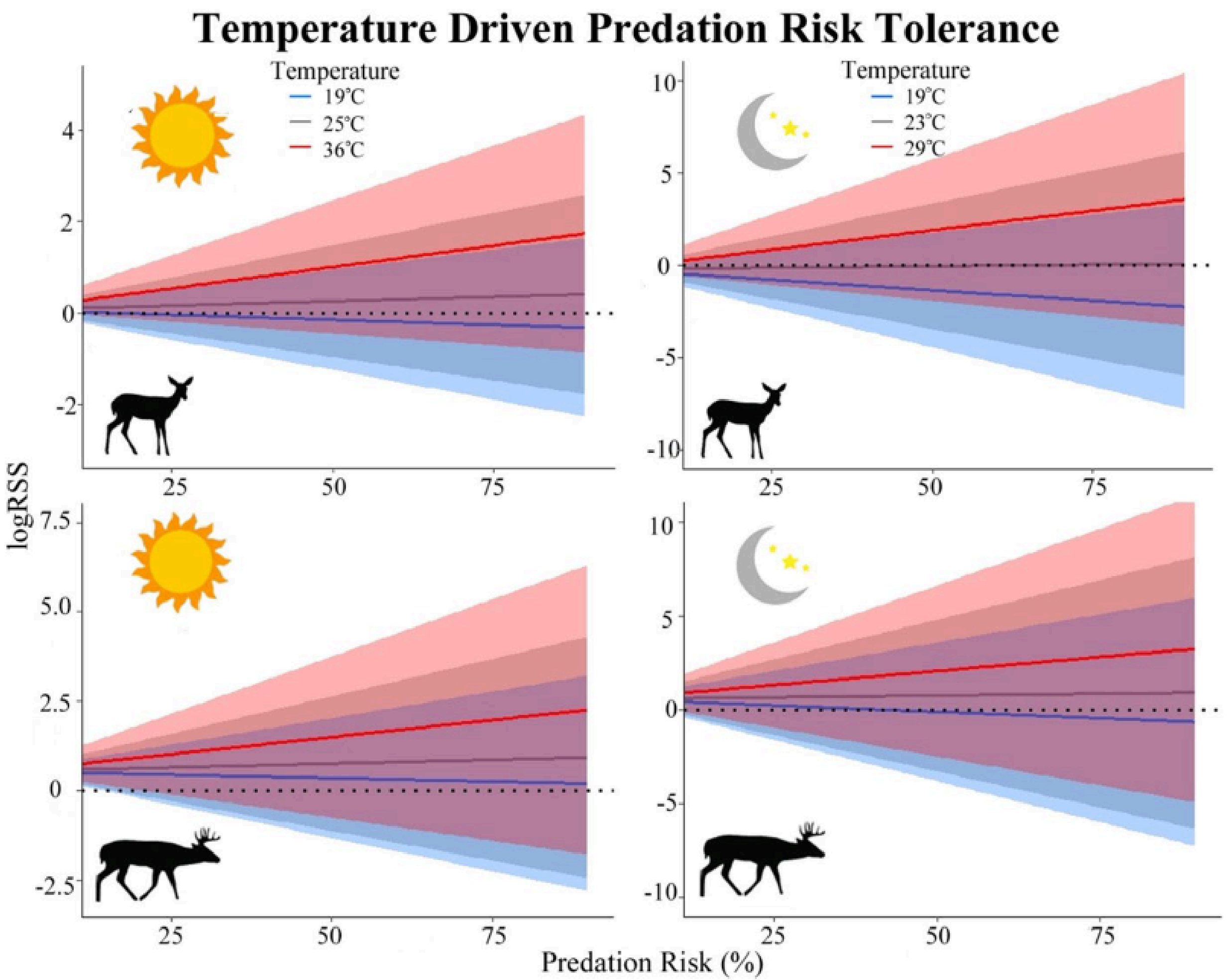
Temperature influences resource selection and predation risk tolerance in a climate generalist

Breanna R. Green · Evan P. Tanner · Richard B. Chandler · Heather N. Abernathy · L. Mike Conner · Elina P. Garrison · David B. Shindle · Karl V. Miller · Michael J. Cherry

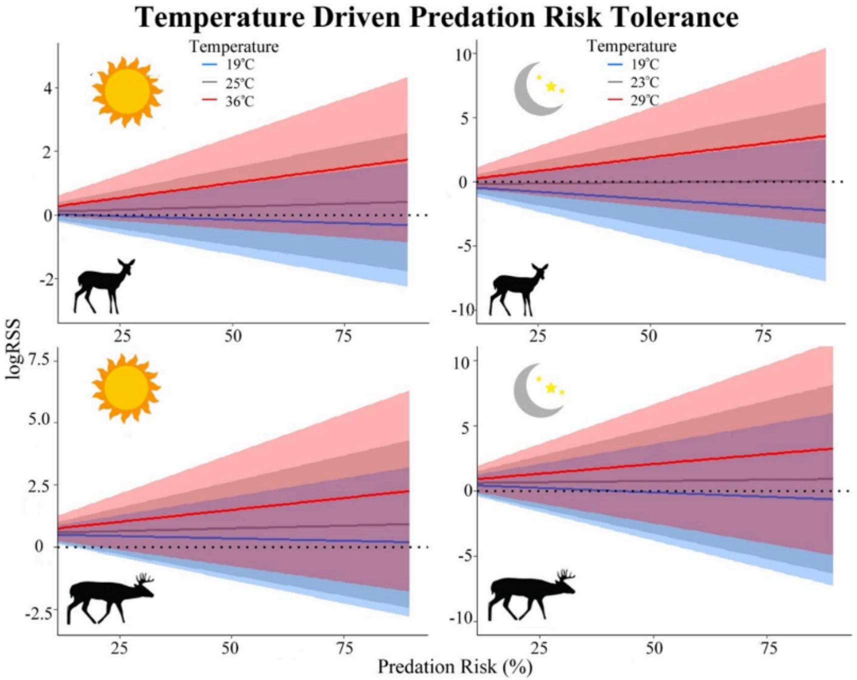
Green et al. 2025



Green et al. 2025



Green et al. 2025



Interaction between predation risk and temperature.

Take-home messages

- Recently published studies are beginning to leverage the power of interactions in iSSA to answer complex ecological questions.

Questions?

References

Dickie, M., S. R. McNay, G. D. Sutherland, et al. (2020). "Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species". In: *Journal of Animal Ecology* 89.2. Ed. by A. Loison, pp. 623-634. DOI: 10.1111/1365-2656.13130.

Fieberg, J., J. Signer, B. Smith, et al. (2021). "A 'How to' guide for interpreting parameters in habitat-selection analyses". In: *Journal of Animal Ecology* 90.5, pp. 1027-1043. DOI: 10.1111/1365-2656.13441.

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See also Fieberg et al. 2021 Appendix B for coded iSSF examples and Appendix C for formulas for updating tentative movement distributions.