

How resource abundance and stochasticity affect organisms' range sizes

Appendix C: Empirical modeling

Contents

1	Modeling R	2
2	Estimating R using NDVI	3
3	Reproducing the analyses	4
4	Modeling the tapir's movement over time	6
5	Modeling $E(R)$ and $\text{Var}(R)$ over time	8
6	Modeling the effects of $E(R)$ and $\text{Var}(R)$ on space use	14
	References	20

We start by providing examples and considerations on how one may model R and the effects of $E(R)$ and $\text{Var}(R)$ on organisms’ home-range sizes. Next, we apply the methods to the tapir’s GPS tracking data and use NDVI as a proxy for R . Finally, we offer suggestions on how this approach can be used to inform conservation-related decisions, including assessing habitat quality and estimating organisms’ range sizes under different scenarios.

1 Modeling R

Location-scale models (theory: Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007; examples: Bjørndahl et al. 2022; Mariën et al. 2022; Gushulak et al. 2024) are a class of statistical models that allow us to estimate changes in a random variable’s mean (i.e. its location) and variance (which depends on its scale) while allowing the mean-variance relationship to vary. `mgcv` (Simon N. Wood 2017) is a commonly used package for **R** (R Core Team 2023) that allows one to fit Generalized Linear Models (GLMs, see Zuur 2009) and Generalized Additive Models (GAMs, see Simon N. Wood 2017), including hierarchical and location-scale GLMs and GAMs. Currently, the `mgcv` package allows one to fit location-scale models with various families of distributions, including Gaussian (i.e., normal), gamma, and Tweedie location-scale families.

The Gaussian location-scale family of distributions is very flexible, since the mean and variance parameters are assumed to be independent, and the response can be either positive or negative. However, the distribution’s flexibility can also result in unreliable estimates for non-Gaussian responses, such as strictly positive data (e.g. available biomass), count data (e.g., number of prey), proportions (e.g., percentage of forested habitat), and bounded ratios (e.g., NDVI, see N. Pettorelli et al. 2011).

The Gamma location-scale family is best for strictly positive responses, such as areas (including home ranges), elemental compositions (e.g., carbon to nitrogen ratio, see Rizzuto et al. 2021), total biomass, or energetic intake. The Tweedie location-scale family is sim-

ilar to the Gamma family, but it allows for zero data, so it is appropriate for data with a non-trivial amount of zeros, such as daily precipitation or prey density (but see zero-inflated distributions: Zuur et al. 2009). In this paper, we estimate R by modeling NDVI using `mgcv` and a beta location-scale family (not available in `mgcv` at the time of publication). If one is interested in families of distributions which are not available in `mgcv`, we suggest using the `brms` package (Bürkner 2017), which allows full control over all of a family’s parameters via a fully Bayesian approach (as opposed to `mgcv`’s Empirical Bayes method – see Bürkner 2018).

Modeling the mean and variance terms of R should be done carefully. Since trends in both $E(R)$ and $\text{Var}(R)$ can be spatiotemporally nonlinear and non-monotonic, we suggest using a GAM rather than a GLM. However, the complexity of the spatiotemporal terms should be chosen carefully, particularly for the mean’s terms. An excessively wiggly $\hat{\mu}(t)$ will cause $\sigma^2(t)$ to be under-estimated, while an excessively smooth $\hat{\mu}(t)$ will cause $\sigma^2(t)$ to be over-estimated. Although there is no error-proof system, choosing the complexity of the terms based on the organism’s ability to detect change and adapt is a reasonable starting point. Additionally, setting the basis dimension (\mathbf{k}) of the scale terms to be half or less than that of the mean terms and using restricted marginal likelihood (S. N. Wood 2011) should provide reasonably accurate results. We suggest starting with low values of \mathbf{k} and adjusting \mathbf{k} based on the trends in the residuals. Note that since R is likely spatiotemporally autocorrelated, it may be easy to overfit the model. Simpson (2018) provides a useful introduction to GAMs for biological time series.

2 Estimating R using NDVI

Although there is no commonly-used distribution with a support over the full range of NDVI (i.e., $[-1, 1]$), we use beta distribution (support $(0, 1)$) since the all NDVI values were sufficiently greater than 0 (range: 0.3534 to 0.9475). Thus, here we can define R as

following a beta distribution with mean and variance that depend on time using the notation $B(\mu(t), \sigma^2(t))$. We use this parameterization here for ease of explanation, but note that beta distributions are generally parameterized using the shape parameters α and β such that the mean is

$$E(R) = \frac{\alpha}{\alpha + \beta} \quad (1)$$

while the variance is

$$\text{Var}(R) = \frac{\alpha\beta}{(\alpha + \beta)^2(\alpha + \beta + 1)}. \quad (2)$$

Particular attention should be given when deciding what distribution to use and how to estimate means and variances in R . Improper models and simulations of resource abundance can fail to produce robust, sensible, and accurate estimates of R . The following section addresses these concerns.

3 Reproducing the analyses

This section of the appendix illustrates the steps necessary to reproduce the tapir movement analysis and the related figure in the manuscript (fig. 5). The tapir data used here is from the work of Medici et al. (2022) and can be found at the GitHub repository located at <https://github.com/StefanoMezzini/tapirs>. Estimating the effects of resource abundance and unpredictability on the tapir’s home-range size requires us to first estimate the changes in the tapir’s home-range sizes (section 4) and the changes in resource abundance and variance experienced by the tapir (section 5) before we can estimate the relationship between resource dynamics and space use (section 6).

To minimize the computational costs of creating this appendix, we load the necessary objects through hidden R chunks rather than re-running all the code. Still, those interested in replicating the analyses can do so by using the code in the pdf document or the related R

Markdown (`Rmd`) document (as well as the `R` scripts). All the packages and source scripts required to run the analyses in this document are listed in the code chunk below. For spatial data, we use the `MODISTsp` package (version 2.0.9, Busetto and Ranghetti 2016) to download the NDVI rasters, the `terra` package (version 1.7-39, Hijmans 2023) to work with the NDVI rasters, and the `sf` package (version 1.0-8, Pebesma 2018). We use the `dplyr` (version 1.0.10, Wickham et al. 2022), `purrr` (version 0.3.5, Henry and Wickham 2022), and `tidyr` (version 1.2.1, Wickham and Girlich 2022) packages for data wrangling and the `lubridate` package (version 1.8.0, Grolemund and Wickham 2011) for converting calendar dates to decimal dates. Finally, we used the `ctmm` package (version 1.1.0, Fleming and Calabrese 2021) and the `mgcv` package (version 1.8-41, Simon N. Wood 2017) for modeling and the `ggplot2` (version 3.4.0, Wickham 2016) and `cowplot` (version 1.1.1, Wilke 2020) packages for plotting.

We start by attaching all necessary packages and custom functions we need:

4 Modeling the tapir's movement over time

The script `analysis/tapir/tapirs-moving-window.R` estimates the seven-day spatial use of various tapirs from the Brazilian Cerrado. Here, we simplified the code so that it only estimates the spatial use of the tapir in the manuscript, Anna:

```
# import tapir data from https://github.com/StefanoMezzini/tapirs
anna <- readRDS('../tapirs/models/tapirs-final.rds') %>%
  filter(name.short == 'ANNA')
anna_tel <- anna$data[[1]] # telemetry data

# re-project using the appropriate UTM projection for the Brazilian Cerrado
ctmm::projection(anna_tel) <- '+proj=utm +zone=22 +datum=NAD83 +units=m'

# calculate the 7-day home range estimate
window_hr(
  tel = anna_tel,
  window = 7 %>% 'day', # 1 week of data for sufficient sample size
  dt = 1 %>% 'day', # move window over by a single day each time
  fig_path = 'figures',
  rds_path = 'models')
anna_mw <- readRDS('../models/tapirs/CE_31_ANNA-window-7-days-dt-1-days.rds')
anna_mw
```

A tibble: 457 x 15

	t_start	t_end	dataset	guess	model	akde	hr_est_50	hr_lwr_50
	<dbl>	<dbl>	<list>	<list>	<list>	<lis>	<dbl>	<dbl>
1	1498285500	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.555	0.362
2	1498371900.	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.418	0.280
3	1498458300.	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.482	0.337
4	1498544700.	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.597	0.403
5	1498631100.	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.566	0.382
6	1498717500.	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.708	0.459
7	1498803900.	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.642	0.427
8	1498890300.	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.758	0.492
9	1498976700.	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.814	0.534
10	1499063100.	1.50e9	<telemetry[,18]>	<ctmm>	<ctmm>	<UD>	0.895	0.574

i 447 more rows

i 7 more variables: hr_upr_50 <dbl>, hr_est_95 <dbl>, hr_lwr_95 <dbl>,

hr_upr_95 <dbl>, t_center <dbl>, posixct <dtm>, date <date>

The `window_hr()` function estimates the tapir's home range using a sliding window approach with a window size of 7 days (using `ctmm`'s `%#%` operator for unit conversions) that starts with the set of days from 2017-06-24 to 2017-07-01 (extremes included), then shifts by one day (`dt = 1 %#% 'day'`), repeats the analysis for the next seven-day set (2017-06-25 to 2017-07-02), and continues doing so until it reaches the last set of days, 2018-09-23 to 2018-09-30. For each set of days, it fits a positional variogram, a continuous-time movement model (Fleming and Calabrese 2021), and a utilization distribution via autocorrelated kernel density estimation (Silva et al. 2022; Noonan et al. 2019). Finally, it saves an exploratory figure (fig. C1) to the `figures` folder and the tibble of times, telemetries, movement models, utilization distributions, and home range estimates (with 95% confidence intervals) to the `models` folder.

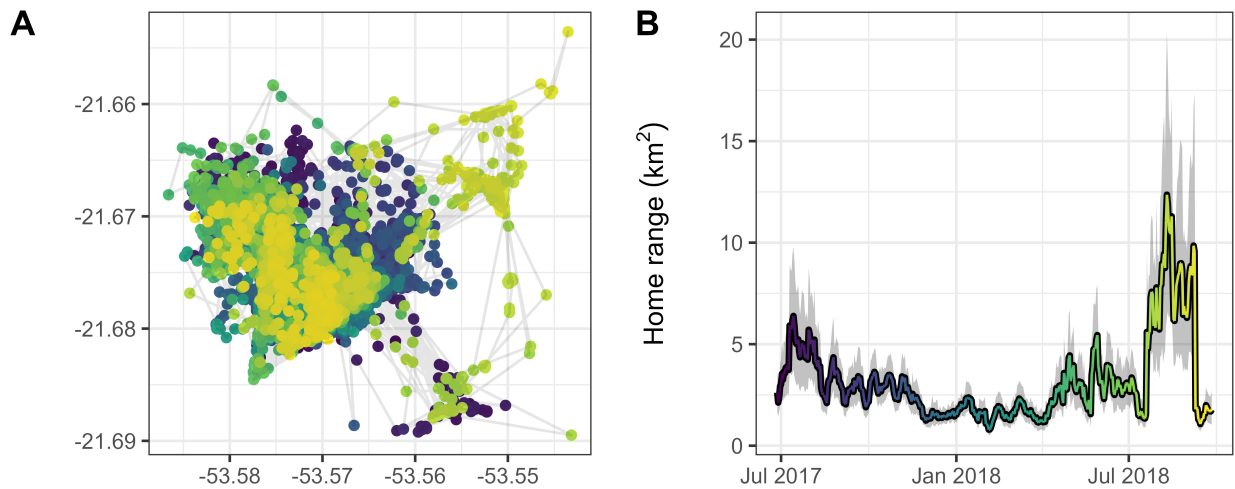


Figure C1: Exploratory figure created by the `window_hr()` function. Panel **A** shows the tapir's GPS locations, while panel **B** shows the seven-day home range estimates (95% utilization quantile) with 95% confidence intervals.

5 Modeling $E(R)$ and $\text{Var}(R)$ over time

To estimate the resources in the tapir's habitat, we used satellite-measured Normalized Difference Vegetation Index (NDVI, see Nathalie Pettorelli et al. 2005; N. Pettorelli et al. 2011). We downloaded the data using the MODISTsp R package with the following code:

```
anna_ud <- anna$akde[[1]] # extract the tapir's utilization distribution

bbox <-
  SpatialPolygonsDataFrame.UD(anna_ud, # convert to a spatial object
                              level.UD = 0.9995, # utilization quantile
                              level = 0) %>% # no CIs

  st_as_sf() %>%
  st_transform(crs = '+proj=longlat') %>%
  st_bbox()

# download NDVI rasters (if needed, create all necessary folders first)
MODISTsp(gui = FALSE, # do not use the browser GUI, only run in R
         out_folder = 'data/ndvi-rasters/tapir-anna',
         selprod = 'Vegetation Indexes_16Days_250m (M*D13Q1)',
         prod_version = '061', # 2022 raster version
         bandsel = 'NDVI', # NDVI layer only
         sensor = 'Terra', # only terrestrial values, ignore water
         user = USERNAME, # Earthdata username for urs.earthdata.nasa.gov
         password = PASSWORD, # your Earthdata password
         start_date = format(min(anna_tel$timestamp) - 16, '%Y.%m.%d'),
         end_date = format(max(anna_tel$timestamp) + 16, '%Y.%m.%d'),
         spatmeth = 'bbox', # use a bounding box for the extent
         bbox = bbox, # spatial file for raster extent
         out_projsel = 'User Defined', # use specified projection
         output_proj = '+proj=longlat', # download unprojected raster
         resampling = 'bilinear', # raster resampling method for new proj
         delete_hdf = TRUE, # delete HDF files after download is complete
         scale_val = TRUE, # convert from integers to floats within [-1, 1]
         out_format = 'GTiff', # output format
         verbose = TRUE) # print processing messages
```



```

# save NDVI data as an rds file of a tibble
list.files(path = 'data/ndvi-rasters/tapir-anna/VI_16Days_250m_v61/NDVI/',
           pattern = '.tif', full.names = TRUE) %>%
  rast() %>% # import all rasters as a single stack
  as.data.frame(xy = TRUE) %>% # convert to a data frame
  pivot_longer(-c(x, y)) %>% # change to long format (x, y, name, value)
  transmute(long = x, # rename x column
            lat = y, # rename y column
            date = substr(name, # change name to a date
                          start = nchar('MOD13Q1_NDVI_x'),
                          stop = nchar(name)) %>%
            as.Date(format = '%Y_%j'), # format is year_julian date
            ndvi = value, # rename value column
            dec_date = decimal_date(date)) %>%
  saveRDS('data/ndvi-rasters/tapir-anna/tapir-anna-data.rds')

# import NDVI data
anna_ndvi <-
  readRDS('data/ndvi-rasters/tapir-anna/tapir-anna-data.rds') %>%
  mutate(dec_date = decimal_date(date))
anna_ndvi

```

```

# A tibble: 13,376 x 5
   long lat date      ndvi dec_date
   <dbl> <dbl> <date>      <dbl>    <dbl>
1 -53.6 -21.7 2017-06-10 0.626    2017.
2 -53.6 -21.7 2017-06-26 0.595    2017.
3 -53.6 -21.7 2017-07-12 0.469    2018.
4 -53.6 -21.7 2017-07-28 0.421    2018.
5 -53.6 -21.7 2017-08-13 0.426    2018.
6 -53.6 -21.7 2017-08-29 0.479    2018.
7 -53.6 -21.7 2017-09-14 0.440    2018.
8 -53.6 -21.7 2017-09-30 0.488    2018.
9 -53.6 -21.7 2017-10-16 0.468    2018.
10 -53.6 -21.7 2017-11-01 0.524    2018.
# i 13,366 more rows

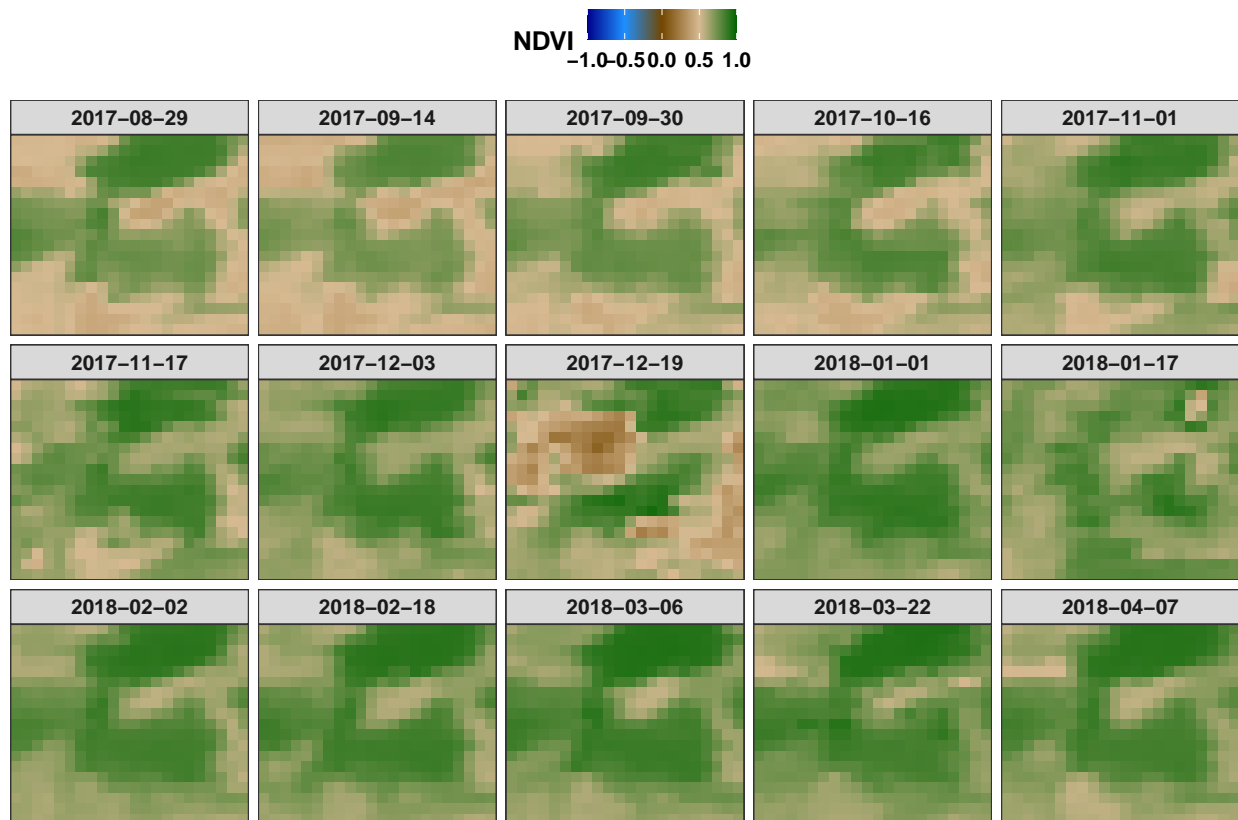
```

We removed the raster for 2017-12-19 because the values were unusually low for the region. We hypothesize the change in NDVI was drastic, temporary, and widespread because of a sudden flood. While sudden floods are common for the Cerrado, we believe NDVI was not representative of the available forage availability.

```

anna_ndvi %>%
  filter(date >= as.Date('2017-08-29'), date <= as.Date('2018-04-07')) %>%
  ggplot() +
  facet_wrap(~ date, nrow = 3) + # a raster for each date
  coord_equal() + # keep the scaling of x and y equal
  geom_tile(aes(long, lat, fill = ndvi)) +
  scale_x_continuous(NULL, breaks = NULL, expand = c(0, 0)) +
  scale_y_continuous(NULL, breaks = NULL, expand = c(0, 0)) +
  scale_fill_gradientn('NDVI', colours = ndvi_pal, limits = c(-1, 1)) +
  theme(legend.position = 'top')

```



```

anna_ndvi <- filter(anna_ndvi, date != '2017-12-19') # remove bad values

```

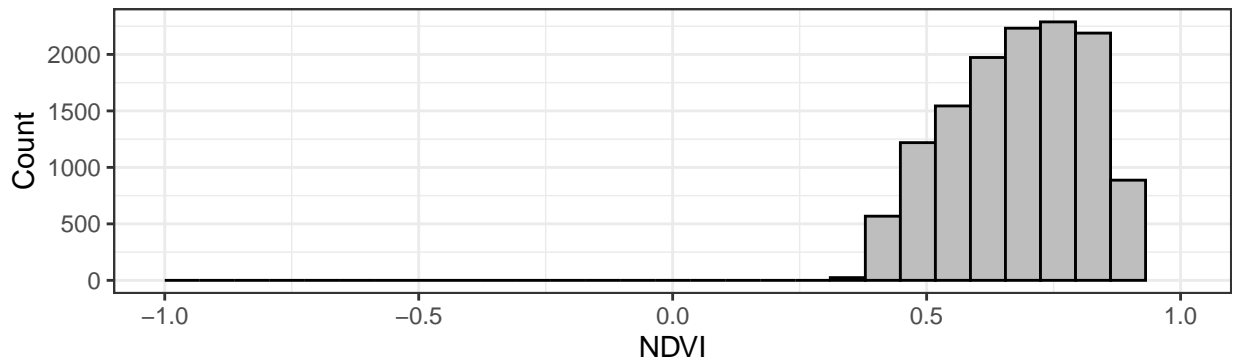
Next, we estimate the mean and variance in NDVI using a Generalized Additive Model for location and scale (GAMLS: Stasinopoulos and Rigby 2007). Ideally, we would model NDVI

using a family of distributions that accounts for the fact that NDVI cannot be less than -1 or greater than 1, but no such family is available in the `mgcv` package. However, since the NDVI data is far from 0 (see the histogram below), we decided to keep NDVI unscaled. This prevents the model from predicting values that correspond to water or snow (which are not expected to occur in the study area). Mathematically, this approach would be comparable to predicting in a Bayesian framework with a prior with zero probability for any NDVI values below zero. In environments where values below zero are probable, one could use the beta family after applying the linear transformation

$$y^* = \frac{y + 1}{2},$$

where y is the original NDVI value (between -1 and 1) and y^* is the NDVI value scaled between 0 and 1.

We fit the beta GAMLS via the `mgcv` package (note `family = betals()` in the code chunk below). The `betals` family accepts a list of two predictors: one for the mean parameter, μ , and one for the scale parameter, ϕ , and it uses logit link functions for both parameters (see fig. C2). The variance of the distribution is a function of both parameters: $\sigma^2 = \mu(1 - \mu)\phi$.



```

m_ndvi <-
  gam(list(
    # mean predictor
    ndvi ~ # not scaling because range is in (0, 1)
      s(long, lat, bs = 'ds', k = 50) + # mean over space
      s(dec_date, bs = 'tp', k = 10), # mean over time
    # scale predictor (sigma2 = mu * (1 - mu) * scale)
    ~
      s(long, lat, bs = 'ds', k = 30) + # scale over space
      s(dec_date, bs = 'tp', k = 10)), # scale over time
    family = betals(),
    data = anna_ndvi,
    method = 'REML') # REstricted Maximum Likelihood

```

Note that when fitting location-scale GAMs, one should pay particular attention to the number of knots used for each smooth term. While using a penalized maximum likelihood method such as REML (`method = 'REML'`) helps avoid over-fitting the model, it does not prevent over-fitting, so finding the right balance between each of the `k` values is crucial. Excessively smooth terms for the mean can inflate the scale term, while excessively wiggly terms for the mean can cause the scale to be under-estimated. Ultimately, each of the `k` values should be decided in such a way as to mimic the animal's responsiveness, adaptability, motility, and memory (or ability to predict cycles or events). If one is unsure where to start from, keeping the `k` for the scale terms below half the `k` for the mean terms is a good starting point.

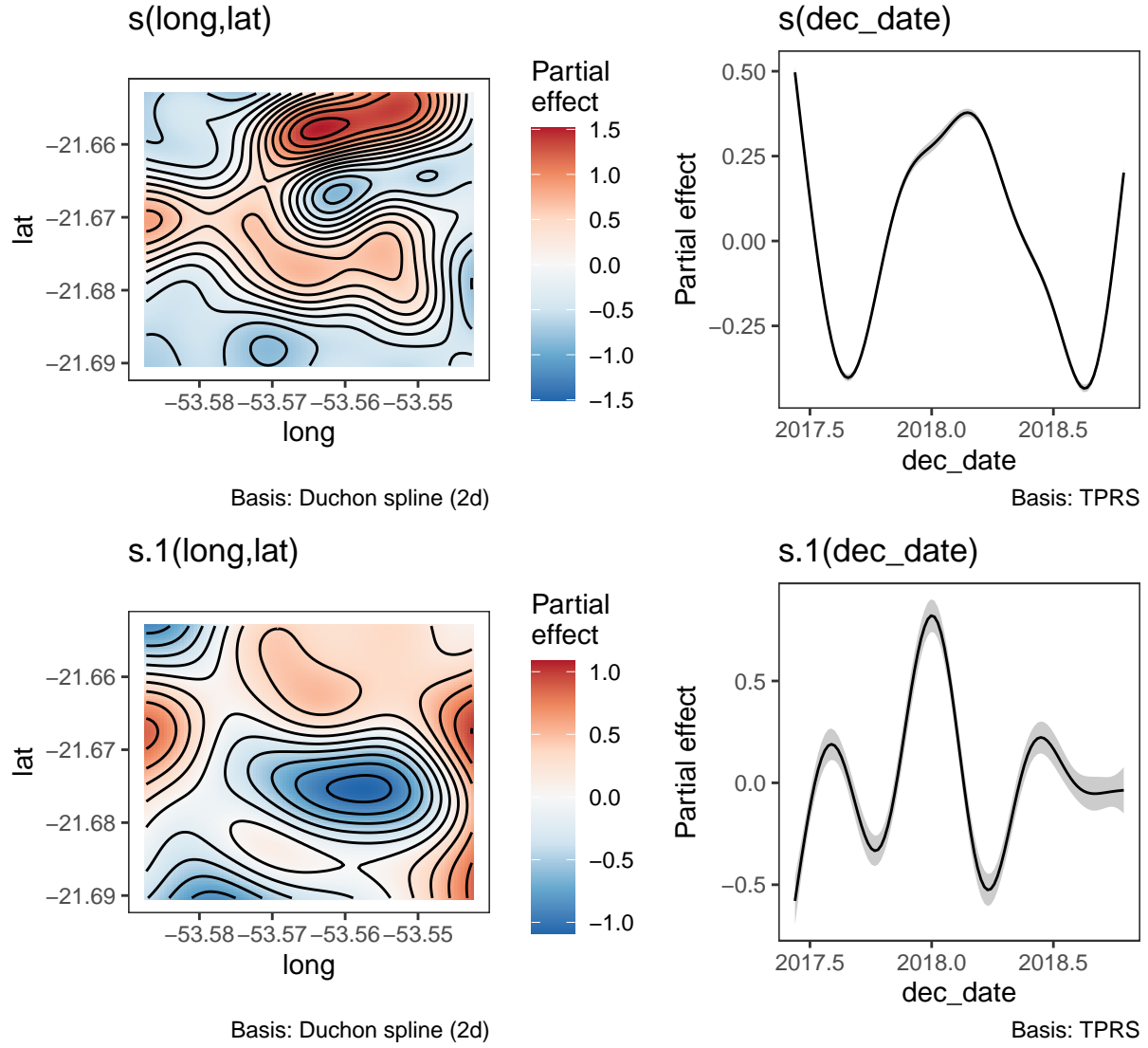


Figure C2: Estimated spatiotemporal trends in mean and scale parameters using the model detailed in the code chunk above. Estimates are provided on the logit link scale. The estimated degrees of freedom for each term can be seen in parentheses in the title of the spatial terms and the y-axis labels of the temporal terms. Shaded ribbons indicate the 95% credible intervals for the temporal terms.

6 Modeling the effects of $E(R)$ and $\text{Var}(R)$ on space use

We start by predicting the mean and variance in NDVI experienced by the tapir in the known positions using the beta GAMLS.

```
anna_tel <-  
  data.frame(anna_tel) %>% # convert telemetry to data frame  
  rename(long = longitude, lat = latitude) %>%  
  mutate(dec_date = decimal_date(timestamp)) %>% # needed for predictions  
  bind_cols(., # bind telemetry to predictions  
    predict(m_ndvi, newdata = ., type = 'response',  
      se.fit = FALSE) %>%  
    data.frame() %>% # convert list of predictions to data frame  
    # didn't scale NDVI to [0, 1], so no need to back-transform  
    transmute(mu = X1, sigma2 = X1 * (1 - X1) * X2)) %>%  
  as_tibble()
```

Next, we can estimate the mean and variance in NDVI for each 7-day period by taking the average for the GPS locations within each period.

```
tapir <-  
  readRDS('models/tapirs/CE_31_ANNA-window-7-days-dt-1-days.rds') %>%  
  mutate(sub_tel = map(dataset,  
    \(.d) filter(tel, timestamp %in% .d$timestamp)),  
    mu = map_dbl(sub_tel, \(.d) mean(.d$mu)),  
    sigma2 = map_dbl(sub_tel, \(.d) mean(.d$sigma2))) %>%  
  select(date, mu, sigma2, hr_est_95)
```

We now have all we need to create the left side of figure 5 from the main manuscript.

```

# need to set the theme again for some reason
theme_set(theme_bw() + theme(panel.grid = element_blank()))

# axis labels (unicode characters removed because they knitting errors)
e_r <- bquote(paste(bold('Resource abundance'))))
v_r <- bquote(paste(bold('Resource stochasticity'))))
hr_lab <- bquote(bold(paste('7-day home-range size (', km^2, ')'))))

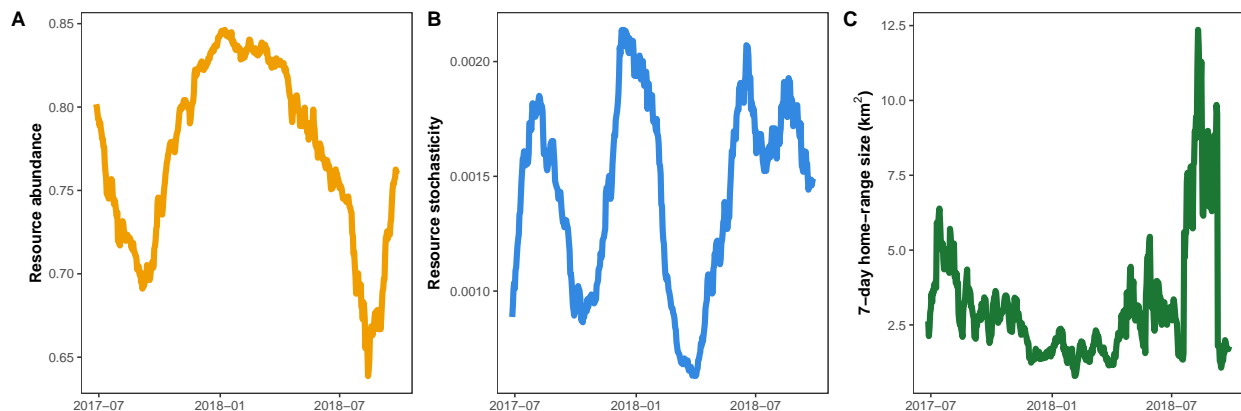
l_grobs <- lapply(
  list(ggplot(tapir, aes(date, mu)) + # mean
    geom_line(color = pal[1], linewidth = 2) +
    labs(x = NULL, y = e_r),
    ggplot(tapir, aes(date, sigma2)) + # variance
    geom_line(color = pal[2], linewidth = 2) +
    labs(x = NULL, y = v_r),
    ggplot(tapir, aes(date, hr_est_95)) + # 95% home range
    geom_line(color = pal[3], linewidth = 2) +
    labs(x = NULL, y = hr_lab)),
  as_grob) # convert to grid graphical objects (grobs)

# align left margins of all plots
aligned_widths <- align_margin(map(l_grobs, \(x) {x$widths}), 'first')

# Setting the dimensions of plots to the aligned dimensions
for(i in seq_along(l_grobs)) l_grobs[[i]]$widths <- aligned_widths[[i]]

# Draw aligned plots
plot_grid(plotlist = l_grobs, nrow = 1, labels = 'AUTO')

```



To create the right side of the figure, we will need to estimate the effects of $E(R)$ and $\text{Var}(R)$ on the tapir's space use. To do this, we fit a GAM to the the tapir's 7-day home range estimates using the mean and variance in NDVI as predictors.

We can now fit a GAM similar to the one used for the simulated data. However, since this dataset is much smaller and autocorrelated, we should be more parsimonious with the number of terms and their complexity. A model with a Gamma family of distributions and relatively smooth (i.e., not wiggly) marginal terms of $\mu(t)$ and $\sigma^2(t)$ is a reasonable start. This dataset is too small (and autocorrelated) to estimate changes in scale parameters with reasonable accuracy and precision. As in Appendix B, we provide the causal Directed Acyclical Graph (DAG) in figure C3. See the section on strengths and limitations of the empirical approach in the main text for a discussion of the DAG.

```
dag <- dagitty('dag{
  Z -> R -> "NDVI" <- S <- R
  R -> H <- Z
}')
coordinates(dag) <- list(x = c(R = 0, 'NDVI' = 0, Z = 1, S = 1, H = 0),
  y = c(R = 0, 'NDVI' = 1, Z = 0, S = 1, H = -1))
ggdag(dag) + theme_dag()
```

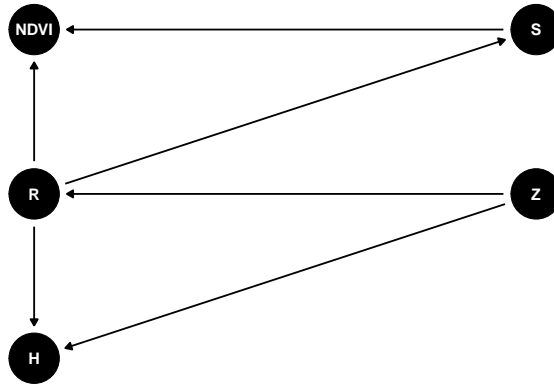


Figure C3: Directed Acyclical Graph assumed for inferring the causal effects of $E(R)$ and $\text{Var}(R)$ on H , where NDVI was used as a proxy for R . Z and S indicate unaccounted confounding factors that result from habitat-level variables (e.g., competition, predation, etc.) and satellite-level variables (e.g., noise, cloud cover).


```
m <- gam(hr_est_95 ~ s(mu, k = 4) + s(sigma2, k = 4),
         family = Gamma('log'), data = tapir, method = 'REML')
draw(m) & theme_bw() + theme(panel.grid = element_blank())
```

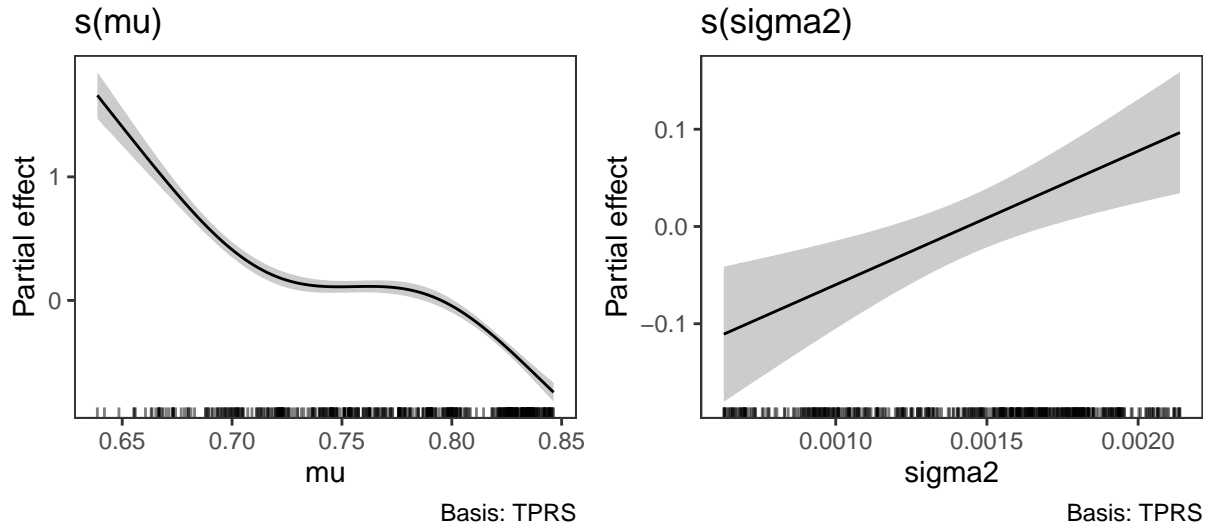


Figure C4: Marginal effects of $\mu(t)$ and $\sigma^2(t)$ on the tapir's space use (on the log link scale). The estimated degrees of freedom for each term can be seen in parentheses in the y-axis labels. Shaded areas indicate the 95% credible intervals.

We can now create the predictions from the GAM.

```
# predict marginal effects for each term
preds <- tibble(mu = gratia::seq_min_max(tapir$mu, n = 250),
               sigma2 = seq(5e-4, 25e-4, length.out = 250)) %>%
  bind_cols(
    # predictions for the marginal effect of mu
    predict(m, newdata = ., exclude = 's(sigma2)',
           type = 'link', se.fit = TRUE, unconditional = TRUE) %>%
    as.data.frame() %>%
    transmute(hr_mu_est = exp(fit),
              hr_mu_lwr = exp(fit - 1.96 * se.fit),
              hr_mu_upr = exp(fit + 1.96 * se.fit)),
    # predictions for the marginal effect of sigma2
    predict(m, newdata = ., exclude = 's(mu)',
           type = 'link', se.fit = TRUE, unconditional = TRUE) %>%
    as.data.frame() %>%
    transmute(hr_sigma2_est = exp(fit),
              hr_sigma2_lwr = exp(fit - 1.96 * se.fit),
              hr_sigma2_upr = exp(fit + 1.96 * se.fit)))
```

```

theme_set(theme_bw() + theme(panel.grid = element_blank()))

p_d <- ggplot() +
  coord_cartesian(ylim = c(0, 12.5)) +
  geom_point(aes(mu, hr_est_95), tapir, alpha = 0.3, color = pal[3]) +
  geom_ribbon(aes(mu, ymin = hr_mu_lwr, ymax = hr_mu_upr), preds,
    fill = pal[1], alpha = 0.3) +
  geom_line(aes(mu, hr_mu_est), preds, color = pal[1], linewidth = 2) +
  labs(x = e_r, y = hr_lab)

p_e <- ggplot() +
  geom_point(aes(sigma2, hr_est_95), tapir, alpha = 0.3, color = pal[3]) +
  geom_ribbon(aes(sigma2, ymin = hr_sigma2_lwr, ymax = hr_sigma2_upr),
    preds, fill = pal[2], alpha = 0.3) +
  geom_line(aes(sigma2, hr_sigma2_est), preds, color = pal[2],
    linewidth = 2) +
  labs(x = v_r, y = hr_lab)

p_f <-
  expand_grid(mu = seq(from = floor(min(tapir$mu) * 100) / 100,
    to = ceiling(max(tapir$mu) * 100) / 100,
    length.out = 250),
    sigma2 = seq(from = 0, to = 0.0035, length.out = 250)) %>%
  mutate(hr_full_est = predict(m, newdata = ., type = 'response')) %>%
  ggplot() +
  geom_raster(aes(mu, sigma2, fill = hr_full_est)) +
  geom_contour(aes(mu, sigma2, z = hr_full_est), color = 'black') +
  geom_point(aes(mu, sigma2), tapir, alpha = 0.3, show.legend = FALSE) +
  scale_x_continuous(e_r, expand = c(0, 0)) +
  scale_y_continuous(v_r, expand = c(0, 0)) +
  scale_fill_gradient(bquote(atop(bold('7-day home-range'),
    paste(bold('size (km)'), '\\U00B2',
      bold(')'))))),
    low = 'grey90', high = pal[3], limits = c(0, NA)) +
  theme(legend.position = c(1, 1),
    legend.justification = c('right', 'top'),
    legend.box.background = element_rect(),
    legend.background = element_rect(),
    legend.key.width = unit(0.35, 'in')) +
  guides(fill = guide_colorbar(
    title.position = 'top',
    theme = theme(legend.title = element_text(hjust = 1)),
    direction = 'horizontal'))

```

Warning: A numeric 'legend.position' argument in 'theme()' was deprecated in ggplot2 3.5.0.

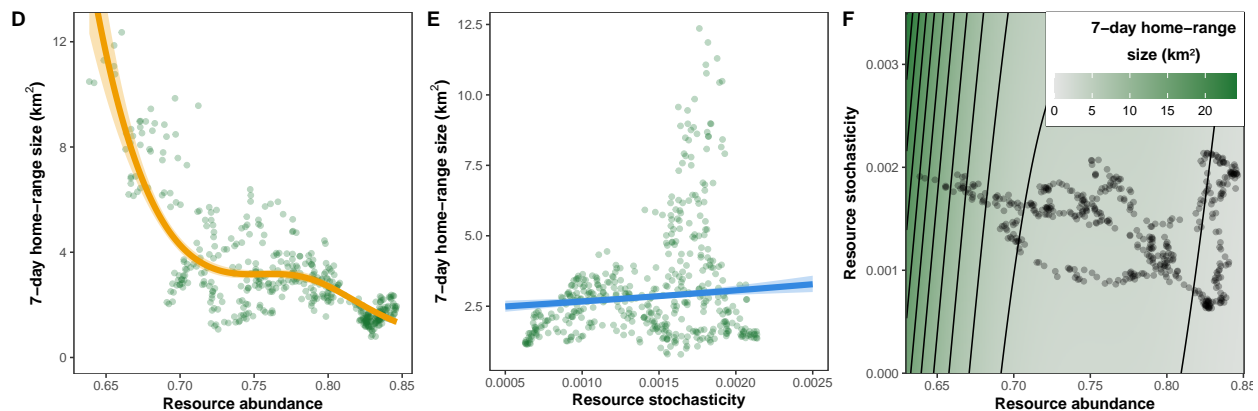
i Please use the 'legend.position.inside' argument of 'theme()' instead.

This warning is displayed once every 8 hours.

Call 'lifecycle::last_lifecycle_warnings()' to see where this warning was generated.

```
# align right margins of all plots
r_grobs <- map(list(p_d, p_e, p_f), as_grob)
aligned_widths <- align_margin(map(r_grobs, \(x) {x$widths}), 'first')
for(i in seq_along(r_grobs)) r_grobs[[i]]$widths <- aligned_widths[[i]]

plot_grid(plotlist = r_grobs, ncol = 3, labels = c('D', 'E', 'F'))
```



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