

How resource abundance and stochasticity affect animals' space-use
requirements

Appendix 2: Simulations

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1 Overview

This appendix illustrates all the steps necessary to produce the simulation figures in the main manuscript. For ease of reference, we also include the figures here (figs. 1 and 2). To achieve full transparency while minimizing computational times, the code illustrated in this pdf is not executed during the knitting of the document. Instead, the R Markdown document (`writing/appendix-2-simulations.Rmd`) contains code chunks that import the RDS files saved by the scripts used during the analysis via R code that is not printed in the pdf file. Although one can replicate the analyses by running the code in this pdf, we suggest only using this document for illustrative purposes and as a general guide. We suggest using the R scripts to replicate the simulations, instead.

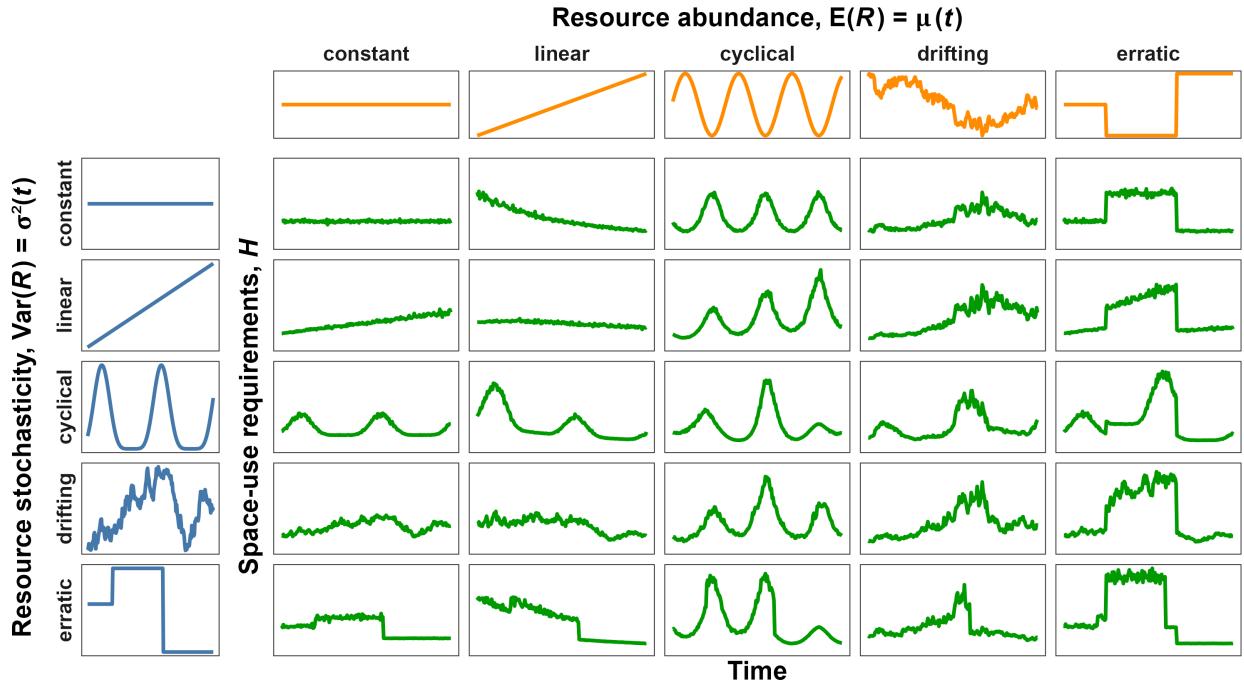


Figure 1: Simulated home range sizes, H , of an organism living in habitats where the mean and variance in resources are constant, linearly increasing, cyclical, drifting, or erratic over time (and homogenous over space). Note how H decreases nonlinearly as $\mu(t)$ increases and increases nonlinearly as $\sigma^2(t)$ increases. Additionally, the variance in H is higher when $\mu(t)$ is lower or $\sigma^2(t)$ is higher, and changes in $\sigma^2(t)$ have greater impacts when $\mu(t)$ is low.

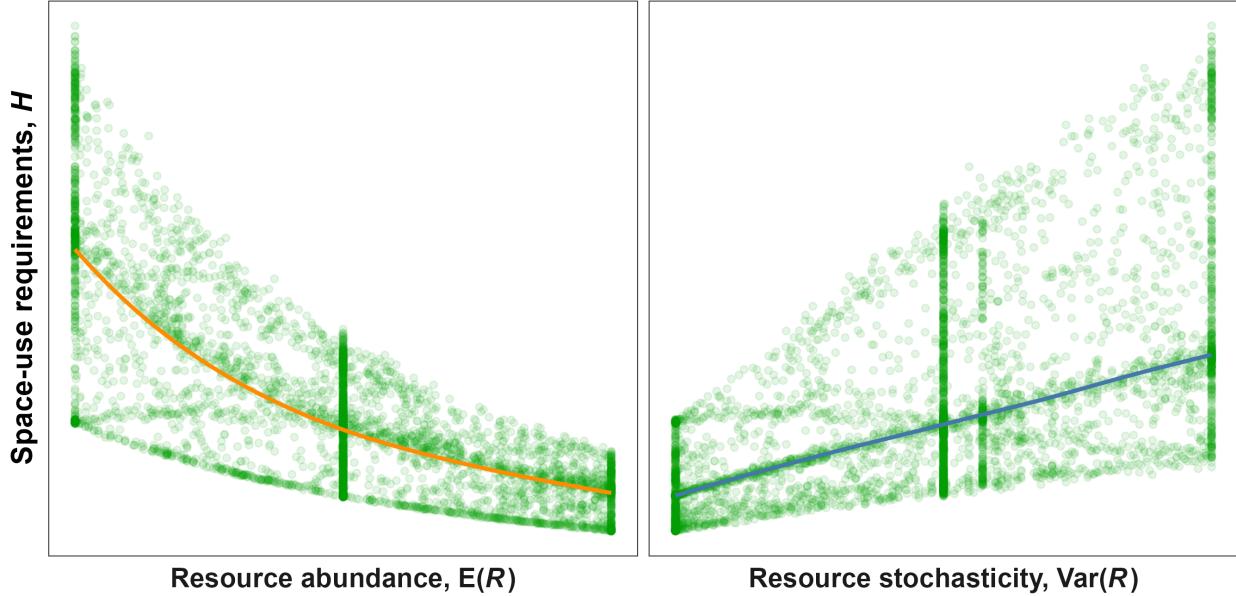


Figure 2: Effects of $E(R)$ and $\text{Var}(R)$ on simulated space-use requirements. The relationships were estimated using a Generalized Additive Model for Location and Scale (GAMLS; Rigby and Stasinopoulos 2005; Stasinopoulos and Rigby 2007) with a Gamma location-scale family of distributions (`mgcv::gamals`). The model accounted for the effects of $E(R)$ and $\text{Var}(R)$ and the interaction effects between the two on both the location (i.e., mean) of H and its scale parameter. Note the nonlinear decrease in H as $E(R)$ increases and the increase in H as $\text{Var}(R)$ increases. Additionally, note how the variance in space-use requirements strongly increases with mean space-use requirements.

2 Simulating the movement tracks

To reduce sampling variance between simulations at each time point in each panel of figure 1), we used the same set of 200 simulated tracks, which we generate in the `analysis/simulations/tracks.R` script. Most intermediate and diagnostic checks are not included in this document for the sake of brevity and simplicity, but their outputs and conclusions are listed in this section. In this script, we use the `ctmm` package (version 1.1.0, Fleming and Calabrese 2021) for movement modeling; the `terra` package (version 1.7-39, Hijmans 2023) to work with the simulated resource rasters; the `dplyr` (version 1.0.10, Wickham et al. 2022), `purrr` (version 0.3.5, Henry and Wickham 2022), and `tidyverse` (version 1.2.1, Wickham and Girlich 2022) packages for data wrangling; and the `ggplot2` (version 3.4.0, Wickham 2016) and `cowplot` (version 1.1.1, Wilke 2020) packages for plotting.

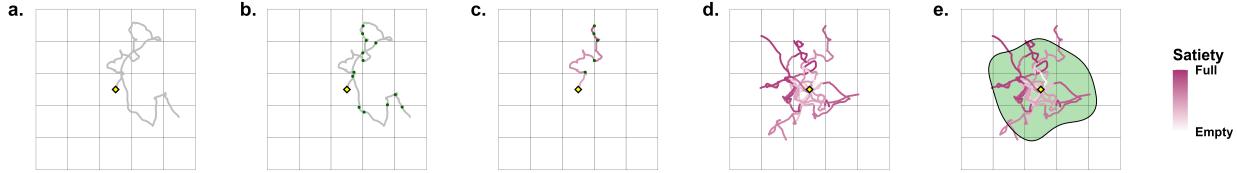


Figure 3: Overview of how animals' space-use requirements were simulated. (a.) Tracks were simulated using an Integrated Ornstein-Uhlenbeck model (IOU model, an infinitely diffusive and continuous-velocity movement model), starting from the point $\langle 0, 0 \rangle$ (black and yellow square). (b.) Each time the track crossed into a new cell (green dots), the animal collected a random amount of resources that followed a Gamma distribution with common mean $\mu(t)$ and variance $\sigma^2(t)$. (c.) Each time the animal collected more resources, its satiety (purple) increased. Once the animal collected sufficient resources, the animal stopped moving (i.e., the track was truncated). (d.) The process was repeated 200 times (13 tracks pictured in this panel). (e.) The final set of (truncated) tracks was then modeled using Ornstein-Uhlenbeck Foraging models to estimate the 95% home range estimates using Autocorrelated Kernel Density Estimates.

```

# NOTE: change working directory to "hr-resource-stoch" or modify paths

# attach all necessary packages
library('ctmm')      # for generating movement models and movement modeling
library('terra')       # for working with raster data
library('dplyr')       # for data wrangling
library('purrr')       # for functional programming
library('tidyverse')   # for data wrangling (e.g., nested tibbles)
library('mgcv')        # for empirical Bayes GAMs
library('ggplot2')     # for fancy plots
library('cowplot')     # for fancy multi-panel plots
theme_set(theme_bw())  # change default theme

# source custom functions
source('functions/rgamma2.R') # rgamma() parameterized by mean and variance
source('analysis/mean-variance-trends-panel-data.R') # mu and sigma2
source('analysis/simulations/movement-model.R') # for consistency
source('functions/get_hr.R') # for extracting gaussian home range
source('functions/label_visits.R') # decides when animal encounters food
source('analysis/figures/default-figure-styling.R') # for color palette

DELTA_T <- 60 # sampling interval in seconds
SAMPLES <- seq(0, 60 * 60 * 12, by = DELTA_T) # 12 hours by DELTA_T seconds

# projected raster of resources
PROJECTION <- '+proj=aeqd +lon_0=0 +lat_0=0 +datum=WGS84'
HABITAT <- matrix(data = 1, nrow = 500, ncol = 500) %>%
  raster(xmx = 1e3, xm = -1e3, ymx = 1e3, ym = -1e3, crs = PROJECTION)

# infinitely diffusive movement model
model <- ctmm(tau = c(Inf, 1e3), sigma = 0.1, mu = c(0, 0))

```

```

N_DAYS <- 2^10 # number of "days" (i.e., tracks with different seeds)

# extracts tracks from a ctmm movement model for given sample times
get_tracks <- function(day, times = SAMPLES) {
  simulate(model, # ctmm movement model
            t = times, # sampling times in seconds
            seed = day, # for a consistent track each day
            complete = TRUE, # add lat, long, and timestamp to telemetry
            crs = PROJECTION) # CRS projection string
}

# generate simulated tracks (will be truncated at satiety later)
tels <- tibble(day = 1:N_DAYS, # a simulation for each day
               tel = map(.x = day, # set a seed for consistent results
                         .f = get_tracks)) # function to generate tracks
tels

```

```

# A tibble: 1,024 x 2
  day   tel
  <int> <list>
1     1 <telemtry[,8]>
2     2 <telemtry[,8]>
3     3 <telemtry[,8]>
4     4 <telemtry[,8]>
5     5 <telemtry[,8]>
6     6 <telemtry[,8]>
7     7 <telemtry[,8]>
8     8 <telemtry[,8]>
9     9 <telemtry[,8]>
10    10 <telemtry[,8]>
# i 1,014 more rows

```

```

# find patch visits and calories consumed from the tracks
tracks <- transmute(tels, # drop tel column
                     day, # keep day column
                     track = map(.x = tel, # add a column of full tracks
                                 .f = \ (x) {
                                   label_visits(.tel = x, .habitat = HABITAT)
                                 }))
tracks <- tidyr::unnest(tracks, track) # make a single, large tibble
tracks

```

```

# A tibble: 738,304 x 11
  day      t      x      y      vx      vy longitude latitude
  <int> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl>
1     1     0     0     0     0     0     0     0
2     1    60   0.0363 0.0593 -0.000529 0.00271 0.000000326 0.000000536
3     1   120   0.0722 0.395  0.000595 0.00755 0.000000648 0.00000358
4     1   180   0.0276 0.967 -0.00517  0.0102  0.000000248 0.00000875
5     1   240  -0.273  1.66  -0.00323  0.0130  -0.00000245  0.0000150
6     1   300  -0.351  2.42  0.000977 0.00894 -0.00000315  0.0000219
7     1   360  -0.221  2.92  0.00258  0.00534 -0.00000199  0.0000264
8     1   420  -0.126  3.39  0.00182  0.00871 -0.00000113  0.0000307
9     1   480   0.0258 3.74  0.00272  0.00354 0.000000231 0.0000338
10    1   540   0.138  4.07  0.00133  0.00783 0.00000124  0.0000368
# i 738,294 more rows
# i 3 more variables: timestamp <dttm>, cell_id <dbl>, new_cell <lgl>

```

After generating the tracks, we performed the following tests to ensure the number and length of the tracks were large enough for results to be stable. For the sake of conciseness, the code for each of the checks is not presented in this appendix, but it is available in the R scripts referenced in each section.

2.1 Checking whether adding return trips is necessary

Script: `analysis/figures/return-sensitivity.R`

Adding return trips to $\langle 0, 0 \rangle$ after an animal reached satiety doubled computational times without appreciable improvements on the home range estimates (including the 95% confidence intervals of the estimates).

2.2 Checking whether the sampling interval is sufficiently small

Script: `analysis/figures/delta-t-sensitivity.R`

Using three tracks generated with three arbitrary seeds (1, 2, and 3), we explored the effects of sampling interval (Δt) on the number of encounters with food (i.e., movements to new

cells) detected. From each of the four checks, we created an exploratory plot that we present in figure 4.

Exploratory plot 4a. The amount of time between encounters ranged from 1 second (the minimum sampling interval) to 24 minutes and 10 seconds. Approximately 93% of the encounters (500/536, excluding the first 3 events of each track) occurred with 30 or more seconds between events.

Exploratory plot 4b. Halving the sampling interval had little to no effect on the total number of encounters for $\Delta t \lesssim 60\text{ s}$.

Exploratory plot 4c. A sampling interval of $\Delta t = 30$ seconds was small enough to capture fine-scale movement in the tracks but large enough to avoid excessive amounts of data and an inflated amount of encounters when an animal was near cell boundaries.

Exploratory plot 4d. The three tracks used for these exploratory plots are sufficiently different that we considered them to be a representative sample of movement tracks simulated by the OUF model. All three tracks have a reasonable amount of both tortuous and directed movement.

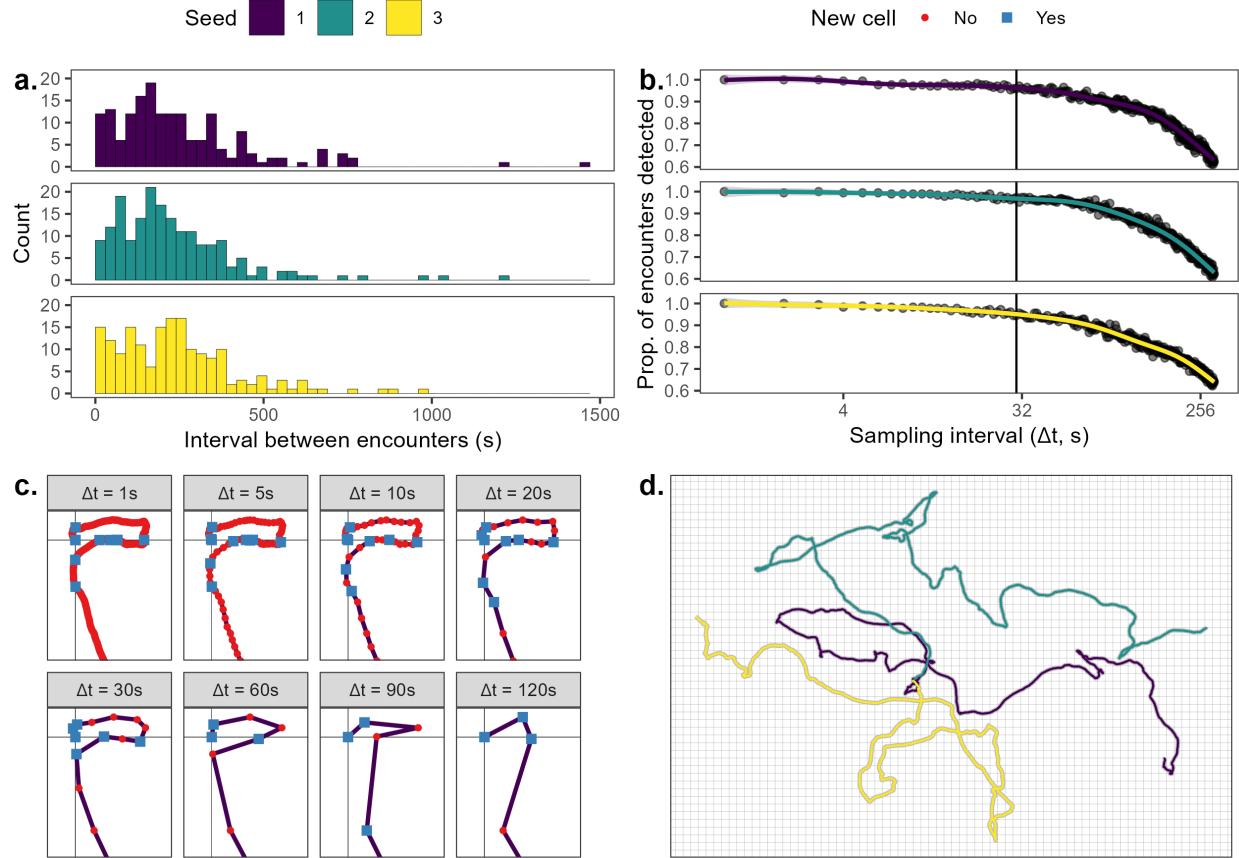


Figure 4: Exploratory plots used to decide an appropriate sampling interval. (a.) Histograms of the number of encounters as a function of the interval between encounters, with a binwidth of 30 seconds. Although some encounters occur with less than 30 seconds between them, approximately 93% of them occur at least 30 seconds apart. (b.) Number of detected encounters as a function of sampling interval. The colored lines indicate the estimated relationship based on a Generalized Additive Model fit using the `geom_smooth` function from the `ggplot2` package. Although the number of encounters detected decreases as sampling interval doubles, the loss at $\Delta = 30$ s is negligible. (c.) Beginning of the track generated with seed "1" (purple line) for different sampling intervals. Red dots indicate locations where the animal remained in the same cell, while the blue squares indicate when an animal was in a new cell and thus encountered food. While the number of encounters detected decreases as the sampling interval increases, most of the encounters lost at $\Delta t = 30$ s occurred because the animal remained almost adjacent to the borders between cells. Additionally, the track at $\Delta t = 30$ s is still sufficiently tortuous to represent realistic animal movement. (d.) The three tracks used in these tests over the raster used for determining when the animals encountered food.

2.3 Checking how many tracks were necessary

Script: analysis/simulations/2-hr-mean-variance-simulations-days.R

The end of this script generates figures that show the mean time spent searching for resources before reaching satiety. This appendix includes the two figures that show the absolute and relative differences in time required to reach satiety as a function of the number of tracks. The estimated times for each number of replicates can be found in the figures/5-by-5-sensitivity-analysis/ folder.

```
all <-  
  tibble(d = map_dfr(  
    list.files('simulations', pattern = '*-replicates.rds',  
              full.names = TRUE),  
    function(fn) {  
      readRDS(fn) %>%  
        mutate(mean = paste(mean, 'mean'),  
               variance = paste(variance, 'var'),  
               replicates = max(day)) %>%  
        group_by(mean, variance, animal, replicates) %>%  
        summarize(est = mean(t_expl),  
                  .groups = 'drop')  
    })) %>%  
  unnest(d) %>%  
  mutate(est = est / (1 %#% 'hours')) %>%  
  pivot_wider(names_from = replicates, values_from = est) %>%  
  pivot_longer(cols = as.character(2^(4:9)), values_to = 'est',  
               names_to = 'replicates') %>%  
  mutate(diff_est = est - `1024`,  
         rel_est = est / `1024`,  
         replicates = factor(replicates, levels = 2^(4:9)))  
  
ggplot(all) +  
  facet_wrap(~ replicates) +  
  geom_line(aes(animal, diff_est, group = paste(mean, variance)),  
            alpha = 0.1) +  
  geom_hline(yintercept = 0, color = 'red') +  
  labs(x = 'Time',  
       y = 'Difference in average daily exploration time (hours)')
```

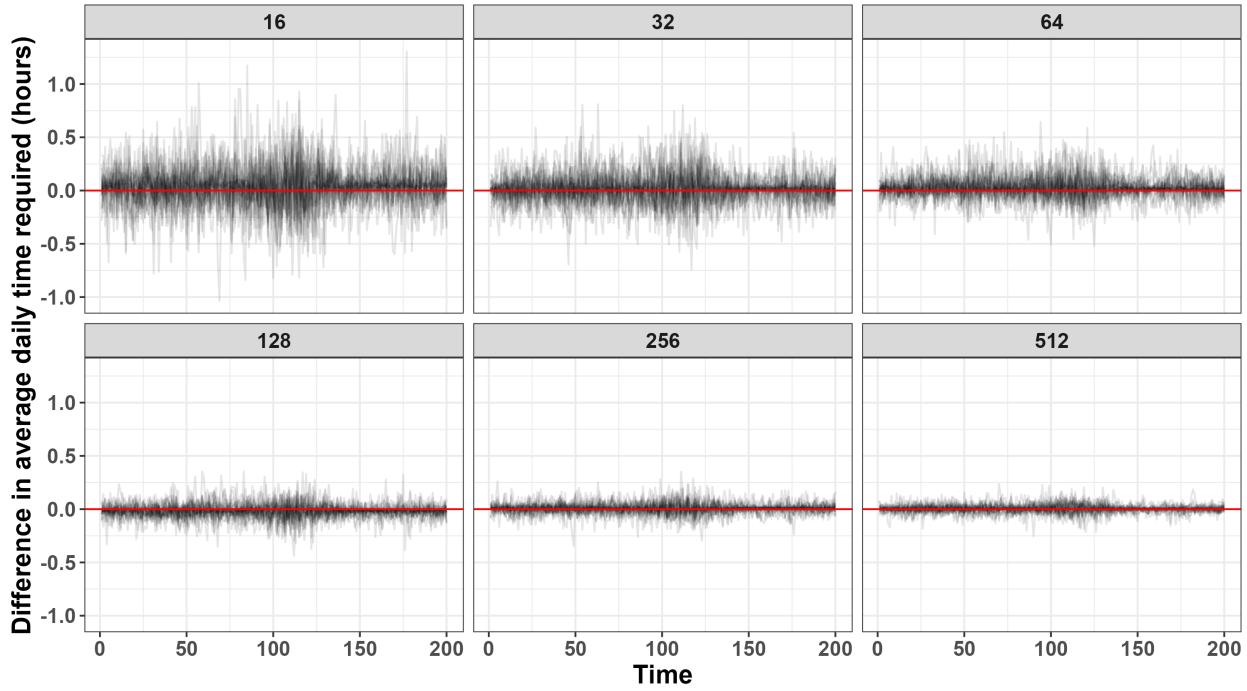


Figure 5: Difference in average time required to reach satiety for each scenario in figure 1 (indicated by each line) and different amounts of tracks (indicated at the top of each facet). The differences are relative to simulations with $2^{10} = 1024$ tracks for each time point on the x axis (and each scenario in figure 1). The amount of time stabilizes for $\gtrsim 100$ tracks, which suggests that the home range estimates should also be stable with more than 100 tracks.

```
ggplot(all) +
  facet_wrap(~ replicates) +
  geom_line(aes(animal, rel_est, group = paste(mean, variance)),
            alpha = 0.1) +
  geom_hline(yintercept = 1, color = 'darkorange') +
  scale_y_continuous(
    trans = 'log2', breaks = 2^seq(-1, 1, by = 0.5),
    labels = parse(text = paste0('2^', seq(-1, 1, by = 0.5)))) +
  labs(x = 'Time',
       y = expression(paste('Relative difference from estimates with',
                            '1024 replicates'^~(log[2]^~-scale))))
```

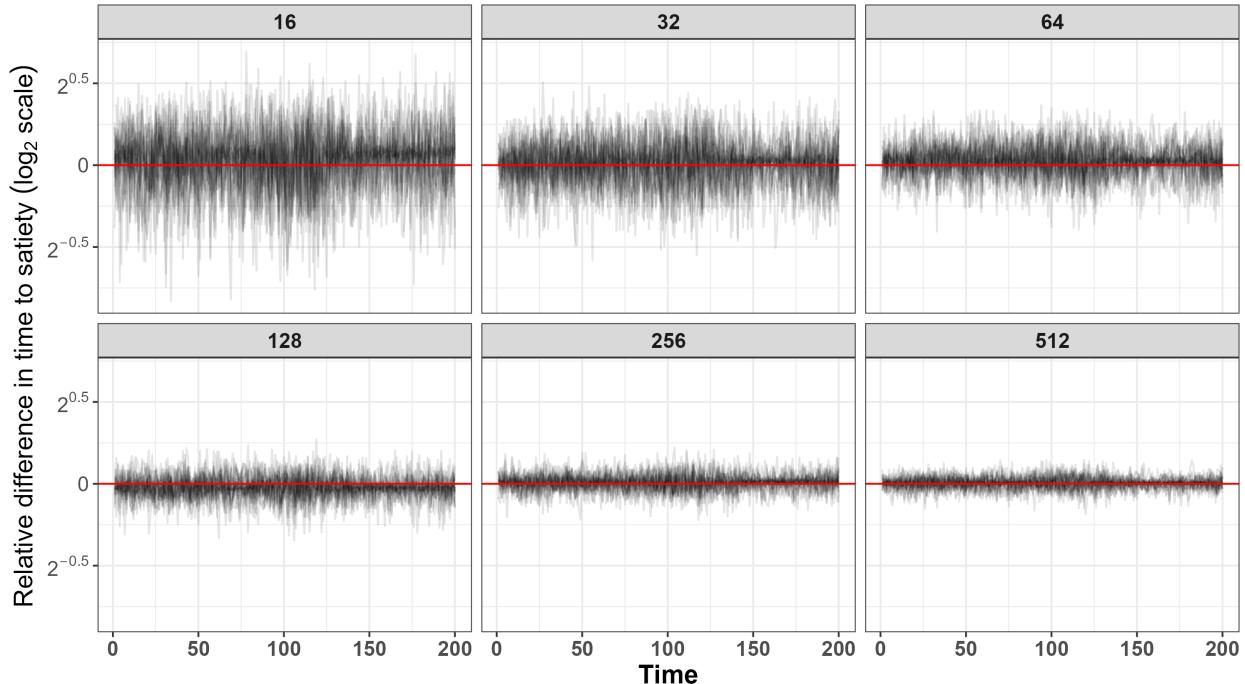


Figure 6: Ratios of average time required to reach satiety for each scenario in figure 1 (indicated by each line) and different amounts of tracks (indicated at the top of each facet). The ratios are relative to simulations with $2^{10} = 1024$ tracks for each time point on the x axis (and each scenario in fig. 1). The amount of time stabilizes for $\gtrsim 100$ tracks, which suggests that the home range estimates should also be stable with more than 100 tracks.

Script: `analysis/hr-simulation-extreme-scenarios.R`

In this script, we check how many tracks are necessary to produce stable and accurate estimates of the space-use requirements. We do so by estimating the home ranges of animals for varying numbers of track in the best-case scenario (highest $E(R)$ and lowest $\text{Var}(R)$) and worst-case scenario (lowest $E(R)$ and highest $\text{Var}(R)$).

```
set.seed(1) # for consistent results
tels <- readRDS('simulations/tracks.rds') # list of telemetry tracks
tracks <- readRDS('simulations/labelled-tracks.rds') # tibble of tracks
MAX_T <- max(tracks$t) # maximum amount of exploration time

WORST <- filter(d55, mu == min(mu)) %>% # lowest mean resources
  filter(sigma2 == max(sigma2)) %>% # with highest variance
  slice(1) # take the first row only
BEST <- filter(d55, mu == max(mu)) %>% # highest mean resources
  filter(sigma2 == min(sigma2)) %>% # with lowest variance
  slice(1) # take the first row only
```

```

days <-
  transmute(bind_rows(WORST, BEST),
            animal,
            mu,
            sigma2,
            d = list(tracks),
            scenario = c('Worst case', 'Best case')) %>%
  unnest(d) %>% # unnest the datasets so we have a single, large tibble
  select(-timestamp) %>%
  # generate the food for each row from a gamma distribution
  mutate(food = rgamma2(mu = mu, sigma2 = sigma2, N = n())),
  # the animal finds food if it visits a new cell, otherwise not
  food = if_else(new_cell, food, 0)) %>%
  # end the movement once the animal has reached satiety
  group_by(day, animal, scenario) %>%
  # calculate the total visits, total calories, and if animal is full
  mutate(satiety = cumsum(food), # for diagnostics if animals aren't full
         full = satiety >= REQUIRED) %>% # did the animal reach its needs?
  filter(cumsum(full) <= 1) %>% # full only once
  ungroup()

# single estimates that eventually converge to the asymptote ----
days_summarized <-
  days %>%
  # find how long it took to reach satiety
  group_by(scenario, day) %>%
  nest(tel_day = -c(scenario, day)) %>%
  mutate(t_expl = map_dbl(tel_day, \d) max(d$t))) %>%
  # add days sequentially
  group_by(scenario) %>%
  mutate(t_start = lag(2 * t_expl), # add the return time before next "day"
         t_start = if_else(is.na(t_start), 0, t_start), # start at 0
         t_start = cumsum(t_start), # make start times consecutive
         tel_day = map2(day, t_expl,
                       \i, te) tels$tel[[i]] %>% # extract day's tel
                       data.frame() %>% # for filtering
                       filter(t <= te))) %>% # end tracks at satiety
  unnest(tel_day) %>% # make one big dataset
  mutate(t = t + t_start, # make times consecutive
         individual.local.identifier = scenario, # ctmm identifier
         timestamp = as.POSIXct(t, origin = '2000-01-01')) %>% # new times
  ungroup() # remove grouping by scenario

```

```

# estimate saturation curve of home range size over number of days
saturation_days <-
  expand_grid(n_days = (2^seq(1, log2(1e3), by = 0.2)) %>%
    round() %>%
    unique(),
    case = unique(days_summarized$scenario)) %>%
  mutate(data = map2(n_days, case,
    \(.n, .case) filter(days_summarized,
      day <= .n,
      scenario == .case)),
  tel = map(data, as.telemetry), # convert to telemetry for modeling
  theta = map(tel, \(x) ctmm.guess(data = x, interactive = FALSE)),
  m = map(1:n(), \(i) {
    cat('Fitting model', i, '\n')
    ctmm.fit(tel[[i]], theta[[i]])
  }), # fit movement model
  sigma = map_dbl(m, \(.m) ctmm:::area.covm(.m$sigma)), # var(pos)
  hr = get_hr(.sigma = sigma, quantile = 0.95)) # Gaussian HR

saturation_days %>%
  select(case, n_days, sigma, hr) %>%
  readr::write_csv('simulations/hr-saturation-days.csv')

ggplot(saturation_days, aes(n_days, hr)) +
  facet_wrap(~ case, nrow = 1) +
  geom_vline(xintercept = 100, color = 'darkorange') +
  geom_smooth(method = 'gam', color = 'black',
    formula = y ~ s(x, bs = 'cs', k = 10),
    method.args = list(family = Gamma(link = 'log'))) +
  geom_point(alpha = 0.3) +
  scale_x_continuous(expression(Number~of~days~sampled~(log[2]~scale)),
    trans = 'log2', breaks = c(2, 16, 128, 1024),
    limits = c(2, 1100)) +
  scale_y_continuous(expression(atop(Estimated~'space-use',
    requirements~(log[2]~scale))),
    trans = 'log2')

```

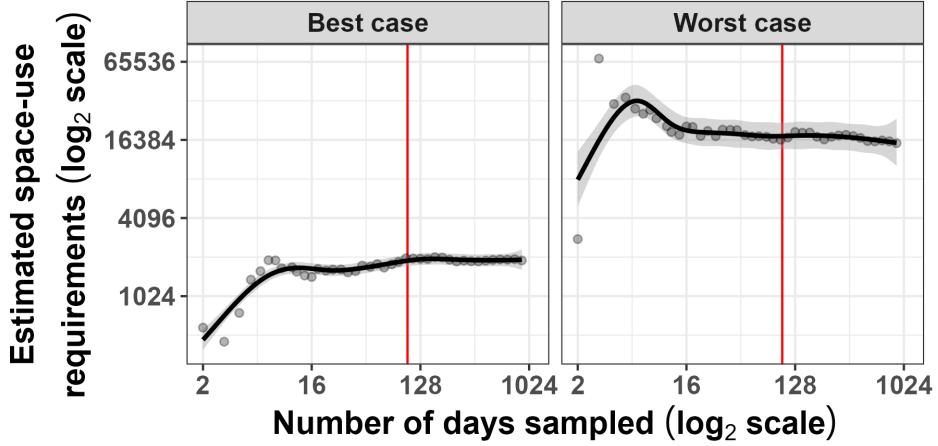


Figure 7: Estimated space-use requirements as a function of the number of days sampled for an animal in a habitat with the highest $E(R)$ and lowest $\text{Var}(R)$ (left) and an animal with the lowest $E(R)$ and highest $\text{Var}(R)$ (right). In both cases, 100 days are sufficient to produce stable estimates of space-use requirements.

3 Main scripts (to be run in the following order)

1. analysis/simulations/hr – mean – variance – simulations – days.R
2. analysis/simulations/hr – mean – variance – simulations – days – summarized.R
3. analysis/simulations/hr – mean – variance – simulations – modeling.R
4. analysis/simulations/hr – mean – variance – simulations – hrs.R
5. analysis/simulations/modeling – R – and – hr.R

4 Modeling the results from the simulations

This final section illustrates the location-scale GAM used to estimate the effects of resource abundance and stochasticity on the simulated space-use requirements. Although the model was fit to both the 95% and core (50%) home range estimates, the results were presented only for the 95% quantile for simplicity. The home range was calculated using a Gaussian approximation using the simulated organism's positional variance:

$$\widehat{h}_q = -2 \log(1 - q) \pi \sigma_{pos}^2,$$

where $\widehat{widehath}_q$ is the estimated home range for the q^{th} quantile and σ_{pos}^2 is the positional variance. Consequently, the estimated core home range estimate is simply a multiple of the 95% quantile:

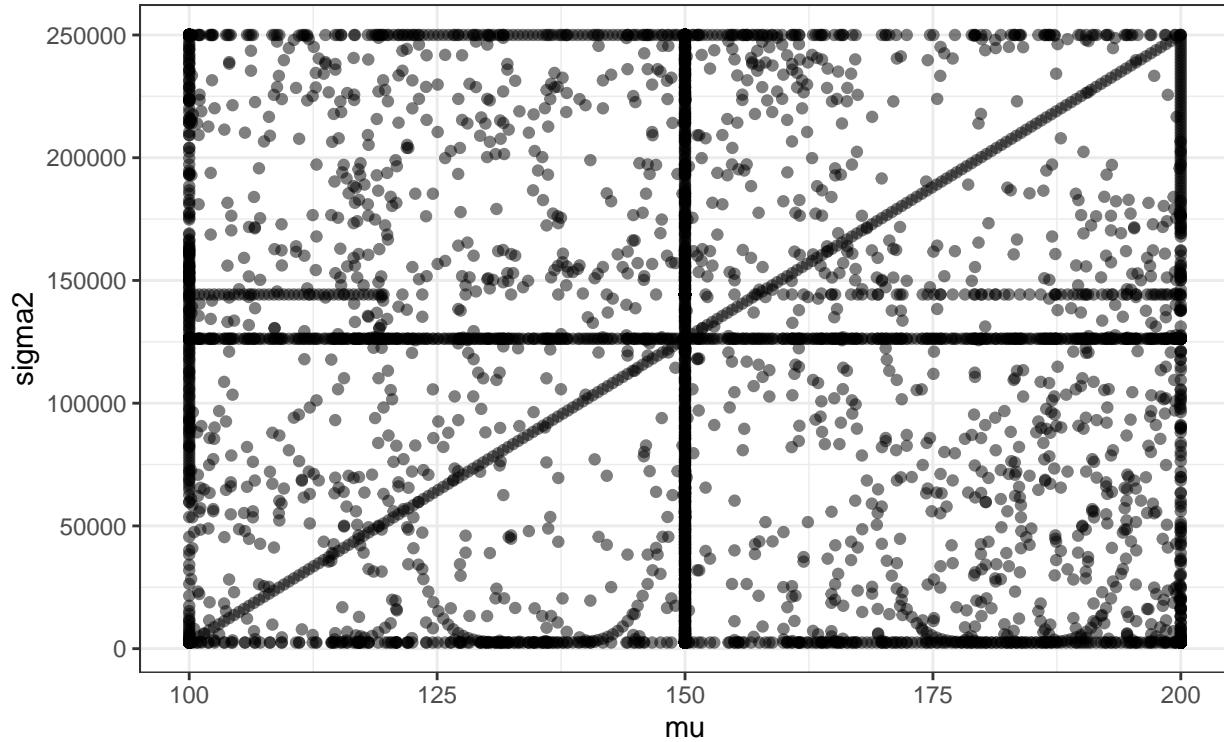
$$\widehat{h}_{0.95}/\widehat{h}_{0.5} = \frac{-2 \log(1 - 0.95) \pi \sigma_{pos}^2}{-2 \log(1 - 0.5) \pi \sigma_{pos}^2} = \frac{\log(1 - 0.95)}{\log(1 - 0.5)} = \frac{\log(0.05)}{\log(0.5)} = \log_{0.5}(0.05) \approx 4.322,$$

and therefore $E(R)$ and $\text{Var}(R)$ would have similar effects (but about 4.322 times weaker) on the core home range than they do on the 95% home range. Note that we used this approximation because, unlike real organisms, the simulated organism did not use the available space selectively (e.g., spending more time near cell boundaries), so the Gaussian approximation is appropriate. When estimating space-use requirements based on empirical data, we suggest estimating utilization distributions using methods such as Autocorrelated Kernel Density Estimation (see Appendix 3 on empirical modeling and Noonan et al. 2019; Alston et al. 2022; Silva et al. 2022).

```
# switch data to long format with a column of quantile
sims <- readRDS('H:/GitHub/hr-resource-stoch/simulations/days-hrs.rds') %>%
  tibble() %>%
  pivot_longer(c(hr_50, hr_95), names_to = 'quantile', values_to = 'hr') %>%
  mutate(quantile = factor(quantile)) # necessary for GAMs
```

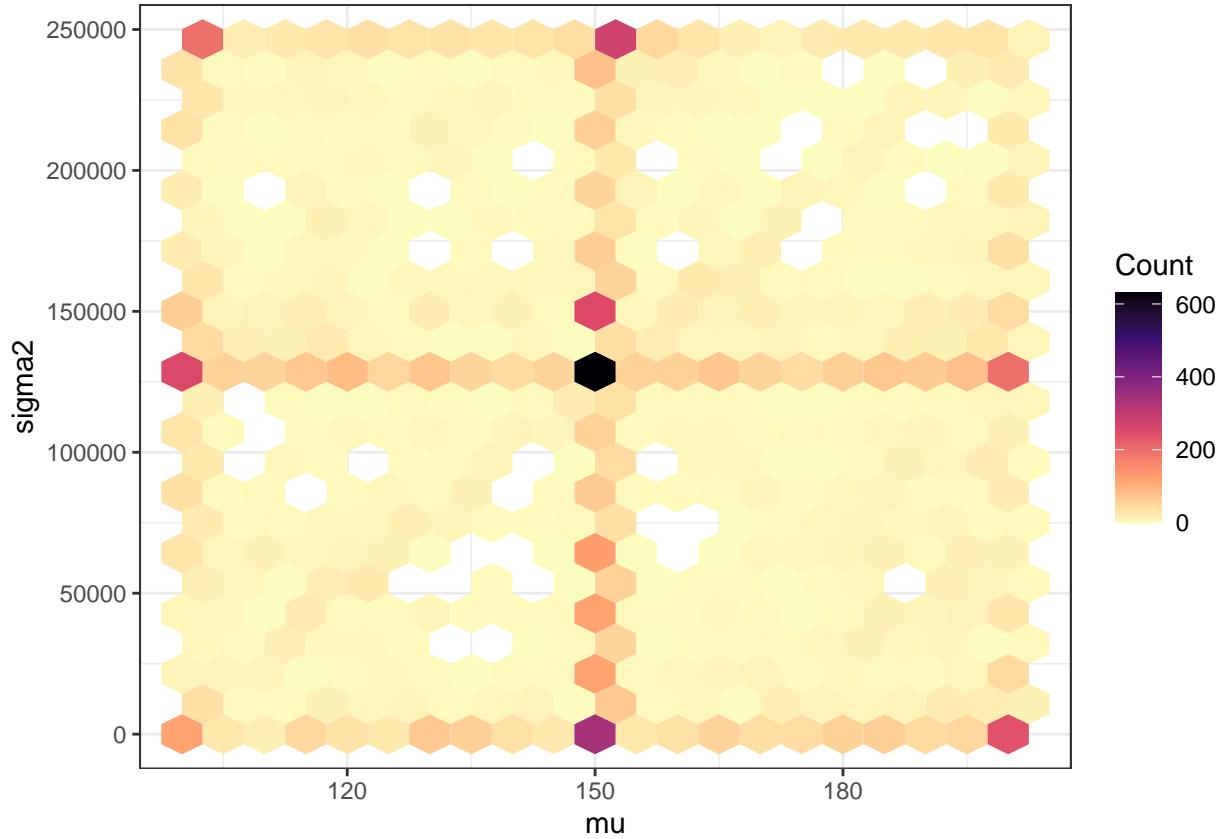
The sampling of the data is not uniform:

```
ggplot(sims, aes(mu, sigma2)) +
  geom_point(alpha = 0.3) +
  theme_bw() # Rmd only keeps theme_bw as default for a single plot
```



But it is not particularly problematic:

```
ggplot(sims, aes(mu, sigma2)) +
  geom_hex(bins = 20) +
  scale_fill_viridis_c('Count', limits = c(0, NA), option = 'A',
                      direction = -1) +
  theme_bw()
```



The abundance of data for the average $E(R)$ and $\text{Var}(R)$ did not create biases in the models, since removing such values had no appreciable effect on the model estimates (not shown). To estimate the effects of resource abundance and stochasticity on the simulated space-use requirements, we fit 3 location-scale GAMs (GAMLSs) with a location-scale gamma distribution (since home ranges are strictly positive) of increasing complexity. We hypothesized that the effect of $E(R)$ would depend on $\text{Var}(R)$ (and the effect of $\text{Var}(R)$ would depend on $E(R)$), since we expected organisms to respond to changes in $\mu(t)$ less in predictable environments than in stochastic ones. The three models are detailed below and compared using the Akaike Information Criterion and the Bayesian Information Criterion. Both information criteria demonstrate that the third model, which accounts for the interaction effects of $E(R)$ and $\text{Var}(R)$, is the best model.

```

# marginal effects of mu and sigma only (linear on the log link scale)
m_1 <- gam(
  list(
    # predictor for the mean
    hr ~ quantile + mu + sigma2,
    # predictor for the scale (variance = scale * mean)
    ~ quantile + mu + sigma2),
  family = gammals(),
  data = sims)

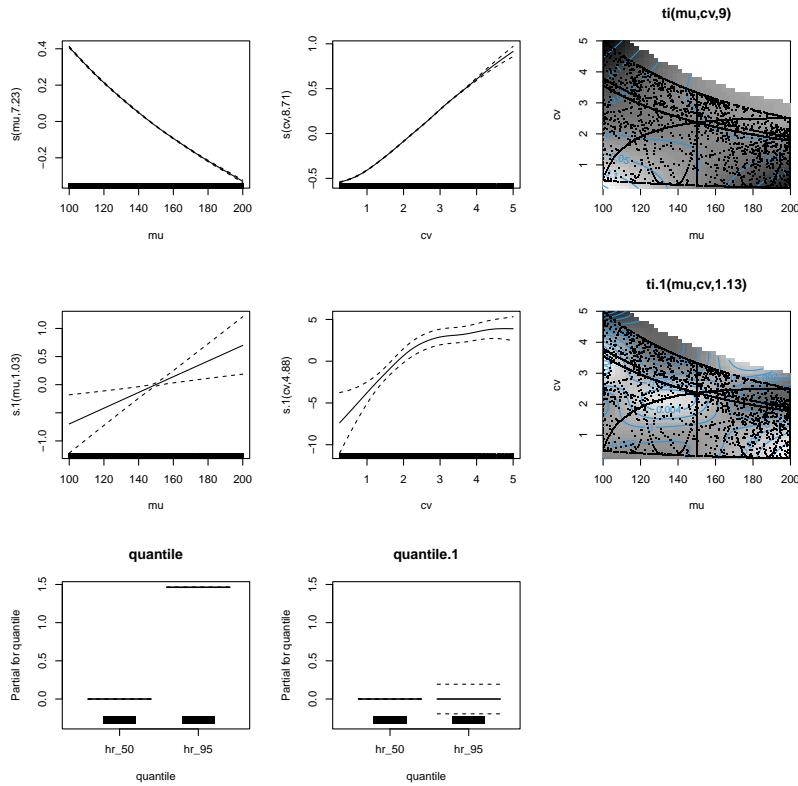
# marginal effects of mu and sigma only (nonlinear on the log link scale)
m_2 <- gam(
  list(
    hr ~ quantile + s(mu) + s(sigma2),
    ~ quantile + s(mu) + s(sigma2)),
  family = gammals(),
  data = sims)

# marginal and interaction effects (nonlinear on the log link scale)
m_3 <- gam(
  list(
    hr ~ quantile + s(mu) + s(sigma2) + ti(mu, sigma2, k = 5),
    ~ quantile + s(mu) + s(sigma2) + ti(mu, sigma2, k = 5)),
  family = gammals(),
  data = sims)

# check if CV = sigma/mu is better than sigma
m_4 <- gam(
  list(
    hr ~ quantile + s(mu) + s(cv) + ti(mu, cv, k = 5),
    ~ quantile + s(mu) + s(cv) + ti(mu, cv, k = 5)),
  family = gammals(),
  data = mutate(sims, cv = sqrt(sigma2) / mu))

# ti term of the scale parameter looks over-fit and too uncertain
plot(m_4, all.terms = TRUE, pages = 1, scheme = 3, scale = 0)

```



```
AIC(m_1, m_2, m_3, m_4) # not much of a difference between m_3 and m_4
```

	df	AIC
m_1	8.00000	133093.9
m_2	34.34593	120810.8
m_3	44.93047	115819.6
m_4	39.93244	115818.5

```
BIC(m_1, m_2, m_3, m_4) # not much of a difference between m_3 and m_4
```

	df	BIC
m_1	8.00000	133151.6
m_2	34.34593	121058.5
m_3	44.93047	116143.5
m_4	39.93244	116106.4

```
# the difference in df (and significance) is in the ti.1() term
summary(m_3)
```

Family: gammals
Link function: identity log

Formula:

```
hr ~ quantile + s(mu) + s(sigma2) + ti(mu, sigma2, k = 5)
~quantile + s(mu) + s(sigma2) + ti(mu, sigma2, k = 5)
```

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	7.097e+00	4.946e-04	14347.89	<2e-16 ***
quantilehr_95	1.464e+00	6.844e-04	2138.79	<2e-16 ***
(Intercept).1	-2.758e+00	3.057e-01	-9.02	<2e-16 ***
quantilehr_95.1	1.826e-14	9.709e-02	0.00	1

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Ref.df	Chi.sq	p-value
s(mu)	7.835	8.627	1.067e+06	< 2e-16 ***
s(sigma2)	8.426	8.900	7.735e+05	< 2e-16 ***
ti(mu,sigma2)	14.334	15.664	8.565e+03	< 2e-16 ***
s.1(mu)	1.199	1.363	2.701e+01	1.92e-06 ***
s.1(sigma2)	4.370	5.238	1.260e+02	< 2e-16 ***
ti.1(mu,sigma2)	1.073	1.139	9.511e+00	0.00253 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Deviance explained = 99.9%

-REML = 57975 Scale est. = 1 n = 10000

```
summary(m_4)
```

Family: gammals
Link function: identity log

Formula:

```
hr ~ quantile + s(mu) + s(cv) + ti(mu, cv, k = 5)  
~quantile + s(mu) + s(cv) + ti(mu, cv, k = 5)
```

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	7.122e+00	1.762e-03	4040.86	< 2e-16 ***
quantilehr_95	1.464e+00	6.837e-04	2140.92	< 2e-16 ***
(Intercept).1	-3.037e+00	4.658e-01	-6.52	7.03e-11 ***
quantilehr_95.1	1.324e-14	9.687e-02	0.00	1

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Approximate significance of smooth terms:

	edf	Ref.df	Chi.sq	p-value
s(mu)	7.228	8.215	4.445e+04	< 2e-16 ***
s(cv)	8.710	8.965	3.578e+05	< 2e-16 ***
ti(mu, cv)	9.005	10.649	1.148e+04	< 2e-16 ***
s.1(mu)	1.027	1.053	7.681e+00	0.00752 **
s.1(cv)	4.884	5.817	1.082e+02	< 2e-16 ***
ti.1(mu, cv)	1.126	1.235	1.000e-03	0.99757

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Deviance explained = 99.9%

-REML = 57967 Scale est. = 1 n = 10000

```
m <- m_3 # select the best model
```

Fig. 8 shows each of the terms from model 3. The estimated effect of `quantile` (see the output of `summary()` above) supports the relationship between the gaussian HR estimates detailed above, since $\exp(1.464) = 4.323218 \approx \log_{0.5}(0.05)$, but there is no differences in the scale parameter between the two quantiles. Additionally, the interaction term of $\mu(t)$ and $\sigma^2(t)$ on the mean HR indicates that the effect of $\sigma^2(t)$ is stronger at lower values of $\mu(t)$ (e.g., $\mu(t) = 100$), since the estimated effect is negative for low values of $\sigma^2(t)$ and positive for high values of $\sigma^2(t)$, which accentuates the effect of $\sigma^2(t)$ on the mean home range. The opposite is true for high values of $\mu(t)$, where the effect of $\sigma^2(t)$ becomes flatter, and thus weaker. Similar but opposite conclusions can be drawn from the interaction term for the scale parameter, since the effect of $\sigma^2(t)$ on the scale parameter is weaker when $\mu(t)$ is low and stronger when $\mu(t)$ is high.

Finally, we can use the model to recreate fig. 2 and visualize the marginal effects of $\mu(t)$ and $\sigma^2(t)$ on the 95% home range.

```
# effect of mu
newd_mu <-
  expand_grid(mu = seq(min(sims$mu), max(sims$mu), length.out = 400),
             sigma2 = mean(sims$sigma2),
             quantile = unique(sims$quantile))

preds_mu <- bind_cols( # bind new data and predictions
  newd_mu,
  predict(m, newdata = newd_mu, type = 'link', se.fit = TRUE) %>%
  data.frame() %>% # convert list to data frame
  # 95% CIs assuming Gaussian credible intervals on the link scale
  transmute(hr = exp(fit.1),
            hr_lwr = exp(fit.1 - se.fit.1 * 1.96),
            hr_upr = exp(fit.1 + se.fit.1 * 1.96)))
```

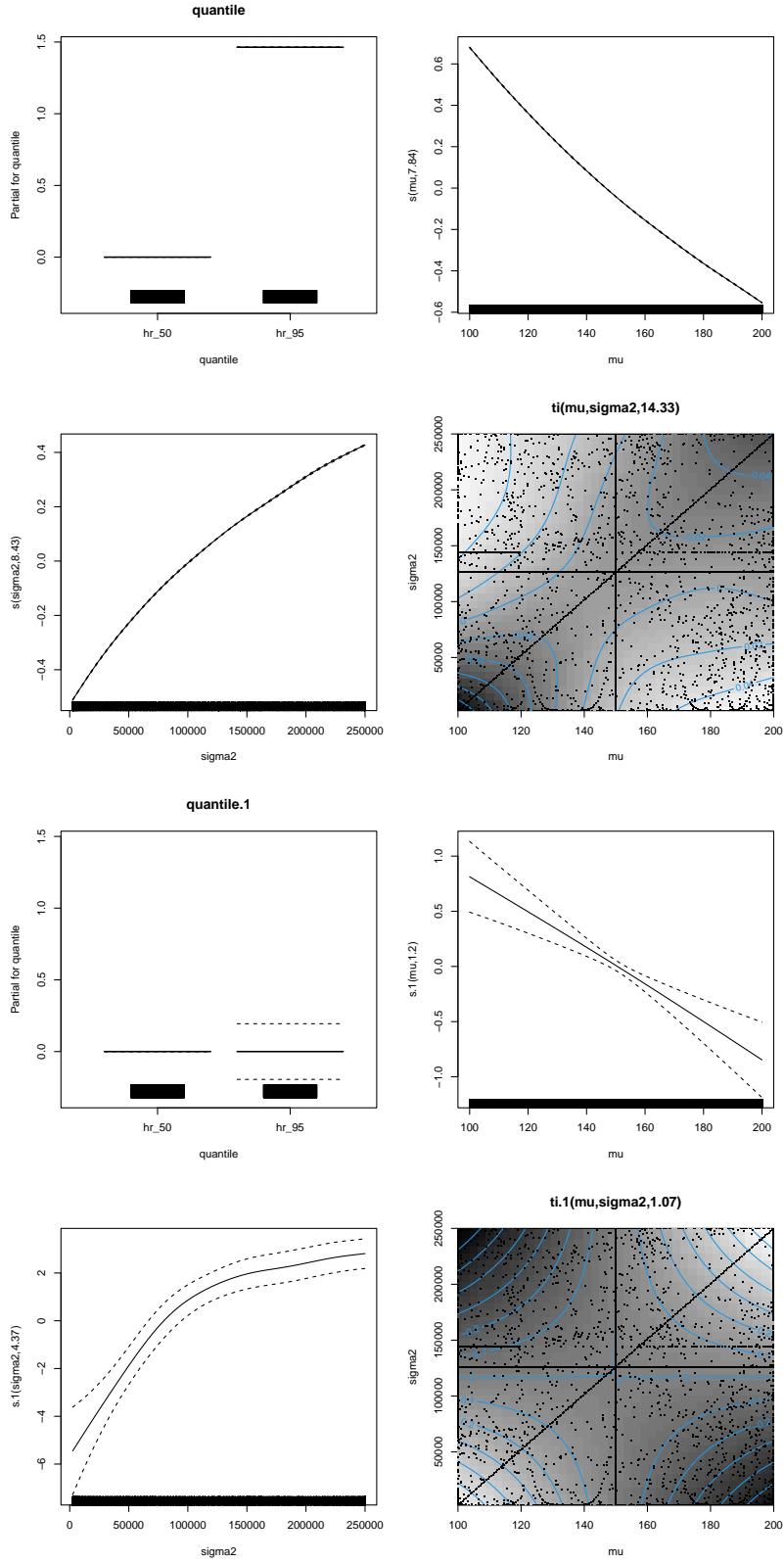


Figure 8: Marginal and interaction effects of each of the terms present in the final GAMLSS (on the log link scales). The dashed lines indicate the 95% Bayesian credible intervals. The data points are included as rug plots in all marginal terms and as points in the interaction terms.

```

# effect of sigma2
newd_sigma2 <-
  expand_grid(mu = mean(sims$mu),
             sigma2 = seq(min(sims$sigma2), max(sims$sigma2),
                           length.out = 400),
             quantile = unique(sims$quantile))

preds_sigma2 <- bind_cols(
  newd_sigma2,
  predict(m, newdata = newd_sigma2, type = 'link', se.fit = TRUE) %>%
    data.frame() %>%
    transmute(hr = exp(fit.1),
              hr_lwr = exp(fit.1 - se.fit.1 * 1.96),
              hr_upr = exp(fit.1 + se.fit.1 * 1.96)))

# final figure (Rmd throws and error with label_bquote)
e_r <- 'paste(bold("Resource abundance, E("), bolditalic("R"), bold(")"))'
v_r <-
  'paste(bold("Resource stochasticity, Var("), bolditalic("R"), bold(")"))'

preds <- bind_rows(mutate(preds_mu, x = e_r) %>%
  rename(value = mu) %>%
  select(-sigma2),
  mutate(preds_sigma2, x = v_r) %>%
  rename(value = sigma2) %>%
  select(-mu))

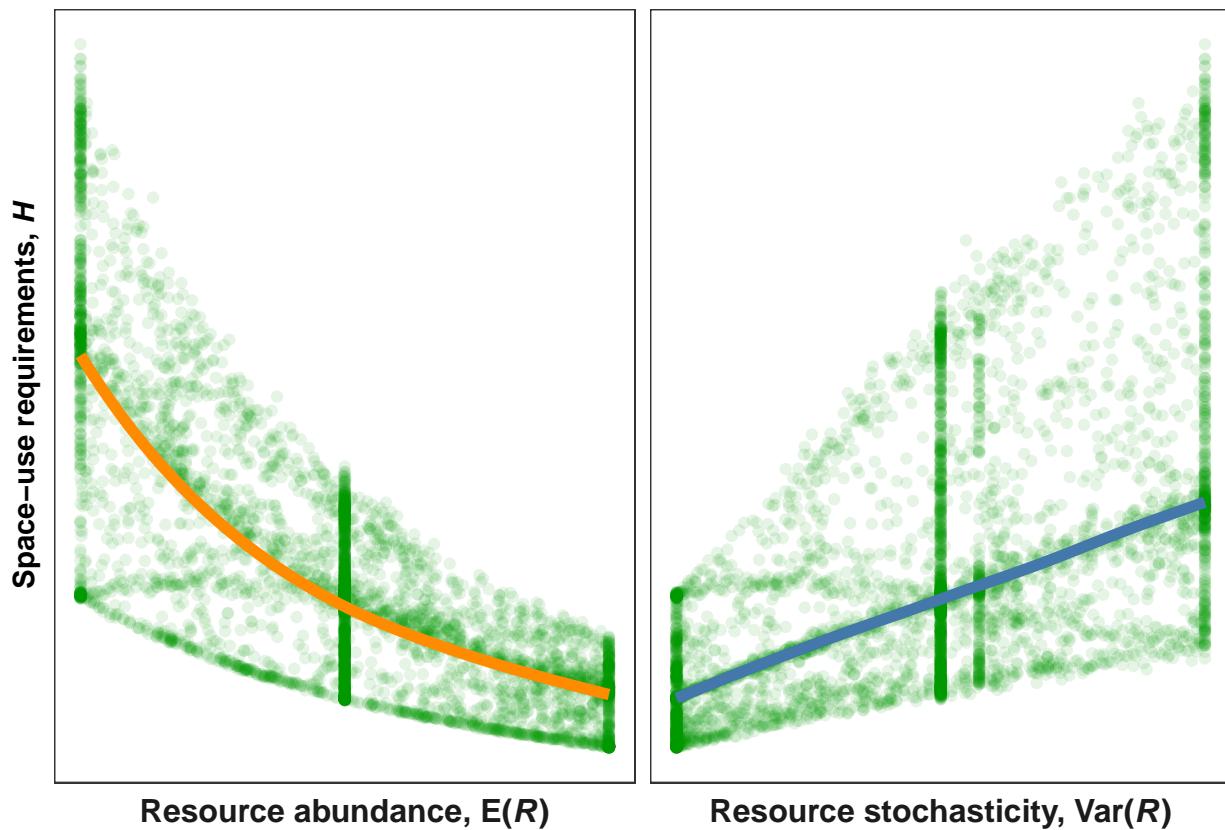
sims_l <- sims %>%
  mutate(e = hr - predict(m, newdata = sims, type = 'response')[, 1]) %>%
  pivot_longer(c(mu, sigma2)) %>%
  mutate(x = if_else(name == 'mu', e_r, v_r))

```

```

ggplot() +
  facet_grid(. ~ x, scales = 'free', switch = 'x',
             labeller = label_parsed) # label below x axis
  geom_point(aes(value, hr), filter(sims_l, quantile == 'hr_95'),
             alpha = 0.1, color = pal[3]) +
  # 95% CIs are present but hidden under the estimates
  geom_ribbon(aes(value, ymin = hr_lwr, ymax = hr_upr, fill = x),
              filter(preds, quantile == 'hr_95'), alpha = 0.5) +
  geom_line(aes(value, hr, color = x),
            filter(preds, quantile == 'hr_95'), linewidth = 2) +
  scale_color_manual(values = pal) +
  scale_x_continuous(NULL, breaks = NULL) +
  scale_y_continuous(bquote(paste(bold('Space-use requirements,'),
                                 bolditalic('H')))), breaks = NULL) +
  theme_bw() +
  # to make facet strip look like the x axis
  theme(legend.position = 'none',
        strip.background = element_blank(),
        strip.text = element_text(size = 12))

```



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