Occupancy models – multi-species

Brett Skelly, Katharine Lewis, Reina Tyl, Gordon Dimmig & Christopher Rota
West Virginia University

Ecological communities are composed of multiple interacting species, and species occurrence can be influenced by environmental conditions and the presence of other species. For example, facilitation or competitive exclusion may lead to patterns of species occurrence in space that cannot be explained by environmental variables alone. Rota *et al.*'s (2016) multispecies occupancy model permits modelling detection/non-detection data simultaneously for 2 or more potentially interacting species, while accounting for the influence of environmental variables and imperfect detection.

The basic sampling protocols are identical to the single-species case (MacKenzie *et al.* 2006). A set of n sites is randomly selected from a population of interest, and each site i is surveyed for S focal species T_i times. During each survey, detections ($y_{sit} = 1$) and non-detections ($y_{sit} = 0$) of species s, at site i, during replicate survey t are recorded.

For species s at site i during replicate survey t, we model detection/non-detection as a Bernoulli random variable, conditional on the presence of species s ($z_{si} = 1$):

$$y_{sit} \mid z_{si} \sim Bernoulli(z_{si}\, p_{sit}),$$

where p_{sit} is the probability of detecting species s during replicate survey t, if present at site i. The latent occupancy state of all species at site i is modelled as a multivariate Bernoulli random variable:

$$\mathbf{Z}_i \sim \text{MVB}\left(\mathbf{\Psi}_i\right),$$

where $\mathbf{Z}_i = \{z_{1i}, z_{2i}, \dots, z_{Si}\}$ is an S-dimensional vector of 1's and 0's denoting the latent occupancy state of all S species and $\mathbf{\Psi}_i$ is a 2^S-dimensional vector denoting the probability of all possible sequences of 1's and 0's $\mathbf{Z}_i$ can attain. For example, when $S = 2$,

$$(z_{1i}, z_{2i}) \sim \text{MVB}(\psi_{11i}, \psi_{10i}, \psi_{01i}, \psi_{00i}).$$

When $S = 2$, we define the natural parameters f_1, f_2, f_{12} as

$$f_1 = \log\left(\frac{\psi_{10}}{\psi_{00}}\right)$$

$$f_2 = \log\left(\frac{\psi_{01}}{\psi_{00}}\right)$$

$$f_3 = \log\left(\frac{\psi_{11}\psi_{00}}{\psi_{01}\psi_{10}}\right).$$

Covariate information can be included by modeling the natural parameters as linear functions:

$$f_1 = \mathbf{x}'_{\alpha}\boldsymbol{\alpha}$$

$$f_2 = \mathbf{x}'_{\beta}\boldsymbol{\beta}$$

$$f_{12} = \mathbf{x}'_{\gamma}\boldsymbol{\gamma},$$

where $\mathbf{x}_{\alpha}$, $\mathbf{x}_{\beta}$ and $\mathbf{x}_{\gamma}$ are vectors of covariates and $\boldsymbol{\alpha}$, $\boldsymbol{\beta}$, and $\boldsymbol{\gamma}$ are conformable vectors of slope parameters (Dai *et al.* 2013). Note that there will always be $(2^S - 1)$ natural parameters, which are used to model the probability 1 species occurs in the absence of the others; the probability 2 species occur together in the absence of all others, etc. See Rota *et al.* (2016) for more details on interpretation. Finally, the natural parameters can be used to obtain the probability of each latent combination of presence / absence via the multinomial logit link:

$$\psi_{11} = \frac{\exp(f_1 + f_2 + f_{12})}{\left[1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})\right]}$$

$$\psi_{10} = \frac{\exp(f_1)}{\left[1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})\right]}$$

$$\psi_{01} = \frac{\exp(f_2)}{\left[1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})\right]}$$

$$\psi_{00} = \frac{1}{\left[1 + \exp(f_1) + \exp(f_2) + \exp(f_1 + f_2 + f_{12})\right]}.$$

As an example, we model co-occurrence probability of bobcat (*Lynx rufus*; species 1), coyote (*Canis latrans*; species 2), and red fox (*Vulpes vulpes*; species 3) using camera trap data from 6 Mid-Atlantic states in the eastern United States (see Rota *et al.* 2016 for details). **MARK** uses a binary counting system to code detection / non-detection patterns for all S species. For example, when $S = 2$, values of '00' indicate neither species were detected; '01' indicates only species 1 was detected; '02' indicates only species 2 was detected; and '03' indicates both species were detected. The possible encounter histories to be included in the dataset when $S = 3$ are defined in the following table:

Encounter History	Species 1	Species 2	Species 3	N(Species Detected)
00	0	0	0	0
01	1	0	0	1
02	0	1	0	1
03	1	1	0	2
04	0	0	1	1
05	1	0	1	2
06	0	1	1	2
07	1	1	1	3

A general formula and additional examples for determining how to code detection histories is available at the "**Occupancy Estimation Multiple Species**" page in the **MARK** Program Help File (found under "**Occupancy Estimation Multiple Species**").

In the examples that follow, we start by modeling constant occupancy and detection probability for each of the 3 species (i.e., the equivalent of 3 independent intercept-only occupancy models). We then add complexity by including covariates to independent occupancy models, modeling dependence between species, and including time-varying detection probabilities.

22.1. Multi-species occupancy model - without covariates

Open a new **MARK** session and select "**Multi-Species Occupancy Estimation | Multi-species Occupancy Model**"; this denotes an occupancy model that incorporates ≥ 2 species.
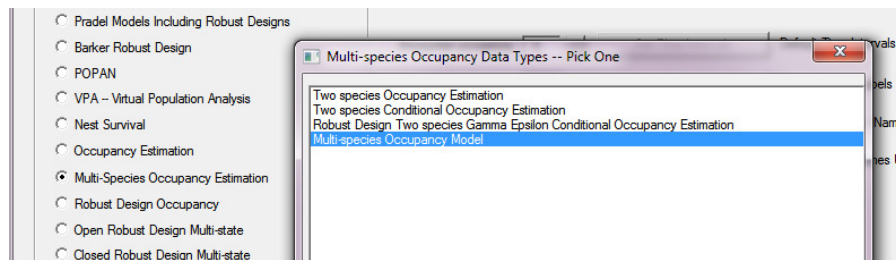
Select the "**Multispecies_Ex.inp**" file and view it – here are the first dozen or so lines:

```
/* Example Multispecies occupancy dataset without covariate data */
/* 3 survey occasions, 1 group */

000000 854;
000004 21;
040404 9;
000400 14;
040000 15;
040400 10;
000404 8;
040004 7;
020000 61;
000302 3;
010000 25;
000001 31;
010100 7;
000100 21;
020003 3;
```

This file contains 3 replicate surveys conducted simultaneously for 3 species. These data indicate, for example, that there were 9 sites where only red fox was detected during each of the 3 replicate surveys (row 3 above). Once the data has been loaded, add the appropriate information into the specification boxes (below) and click "**OK**":

First, let's build an intercept-only model for each of the 3 species using the parameter index matrix (PIM). In the multi-species occupancy model there are two PIMs created: one for the natural parameters (also called f parameters below) and another for the detection parameters (also called p parameters below). Click on "**PIM | Open Parameter Index Matrix**", and select both "**Natural Parameters (f) Group 1**" and "**Detection Probability (p) Group 1**":
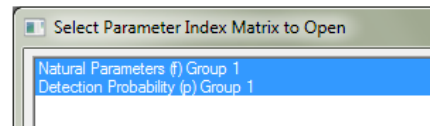
For 3 species, the f parameters are ordered within the PIM (from top to bottom) as follows:

$$f_1 \rightarrow f_2 \rightarrow f_{12} \rightarrow f_3 \rightarrow f_{13} \rightarrow f_{23} \rightarrow f_{123}$$

Pay close attention to the ordering of the f parameters – the ordering can be non-intuitive for some users. General guidance on default ordering of the f parameters is available in the **MARK** Program Help File (found under "**Index | Occupancy Estimation Multiple Species**").

In the PIM windows, specify each parameter group as below:

This gives all 1-way f parameters (f_1, f_2, f_3) a unique index (parameter index 1, 2, and 3 - one for each species); gives all 2-way and 3-way f parameters ($f_{12}, f_{13}, f_{23}, f_{123}$) the same index (parameter index 4);

and all detection probability parameters a unique index (parameter indices 5, 6, and 7 – one for each species).

Next we need to create a design matrix. We will fit an intercept-only model with 6 covariates: a constant term for each of the 1-way f parameters; and a constant term for each of the detection parameters. To do this click on "`Design | Reduced`":
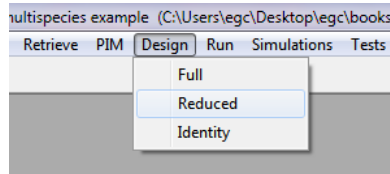
and specify 6 covariates:
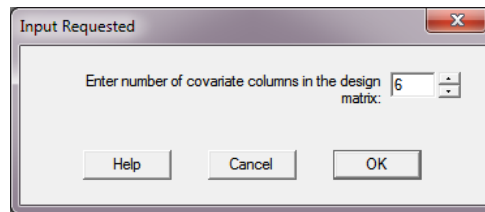
and fill in the design matrix as below (note that we label each column in the design matrix below, which will become more important for bookkeeping as the number of parameters grows):

B1 f1:bobcat	B2 f2:coyote	B3 f3:redfox	Parm	B4 p:bobcat	B5 p:coyote	B6 p:redfox
1	0	0	1:f	0	0	0
0	1	0	2:f	0	0	0
0	0	1	3:f	0	0	0
0	0	0	4:f	0	0	0
0	0	0	5:p	1	0	0
0	0	0	6:p	0	1	0
0	0	0	7:p	0	0	1

Note that we leave the `4:f` row empty because we wish to fix 2-way and 3-way f parameters at 0, which forces the model to assume independence between species (see Rota *et al*. 2016 for details). We also assume constant detection probability across space and time for all three species. This design matrix implies the following models for the natural (f) parameters:

$$f_1 = \beta_1$$
$$f_2 = \beta_2$$
$$f_3 = \beta_3$$
$$f_{12} = f_{13} = f_{23} = f_{123} = 0.$$

When you run this model, you may wish to change the link function from sin (the default) to logit.

Here are the β and real parameter estimates after fitting this model to the data:

```
                     LOGIT Link Function Parameters of {Intercept model}
                                                       95% Confidence Interval
       Parameter                 Beta        Standard Error      Lower            Upper
    ---------------------------  ---------------  ---------------  ---------------  ---------------
        1:f1:bobcat             -1.1713702       0.1327793        -1.4316176       -0.9111228
        2:f2:coyote             -0.6288249       0.0743686        -0.7745873       -0.4830625
        3:f3:redfox             -1.8460970       0.0943953        -2.0311118       -1.6610821
        4:p:bobcat              -1.1038668       0.1395677        -1.3774196       -0.8303140
        5:p:coyote              -0.3328908       0.0763581        -0.4825527       -0.1832288
        6:p:redfox              -0.2522156       0.1182469        -0.4839795       -0.0204516


                     Real Function Parameters of {Intercept model}
                                                       95% Confidence Interval
       Parameter                 Estimate     Standard Error      Lower            Upper
    ---------------------------  ---------------  ---------------  ---------------  ---------------
        1:f                     -1.1713702       0.1327793        -1.4316176       -0.9111228
        2:f                     -0.6288249       0.0743686        -0.7745873       -0.4830625
        3:f                     -1.8460970       0.0943953        -2.0311118       -1.6610821
        4:f                      0.0000000       0.0000000         0.0000000        0.0000000
        5:p                      0.2490161       0.0261002         0.2014237        0.3035787
        6:p                      0.4175374       0.0185703         0.3816495        0.4543205
        7:p                      0.4372782       0.0290965         0.3813129        0.4948873
```

Additionally, here are the (derived) estimates of the probabilities of all combinations of latent presence/absence:

```
                           Estimates of Derived Parameters
                       Occupancy Estimates (psi) of {Intercept model}
                                                     95% Confidence Interval
       Grp. Parm.  Estimate        Standard Error      Lower            Upper
       ---- -----  ---------------  ---------------  ---------------  ---------------
         1  Psi000  0.4300223       0.0183532         0.3944789        0.4663020
         1  Psi001  0.1332819       0.0140478         0.1080711        0.1632972
         1  Psi010  0.2292956       0.0135757         0.2037757        0.2569800
         1  Psi011  0.0710683       0.0080382         0.0568377        0.0885276
         1  Psi100  0.0678799       0.0061851         0.0567156        0.0810530
         1  Psi101  0.0210388       0.0027903         0.0162120        0.0272629
         1  Psi110  0.0361948       0.0036170         0.0297364        0.0439922
         1  Psi111  0.0112183       0.0015574         0.0085425        0.0147198
```

The probabilities of latent presence / absence are obtained from estimates of f parameters. For example, the probability all 3 species occupy the same site (ψ_{111}) is calculated as:

$$\psi_{111} = \frac{\exp(f_1 + f_2 + f_3 + f_{12} + f_{13} + f_{23} + f_{123})}{1 + \exp(f_1) + \exp(f_2) + \exp(f_3) + \exp(f_1 + f_2 + f_{12}) + \exp(f_1 + f_3 + f_{13}) + \exp(f_2 + f_3 + f_{23}) + \exp(f_1 + f_2 + f_3 + f_{12} + f_{13} + f_{23} + f_{123})},$$

which we can check by plugging our estimates of f parameters into the above equation.

22.2. Multi-species occupancy model - with covariates

The above example demonstrates the care you must take when specifying an intercept-only model (i.e., just accepting all defaults in the PIM could lead to unexpected behavior!). We now build on this example

by modeling occupancy and detection probabilities as functions of covariates. First, we will continue to assume occupancy is independent among all 3 species, but now we will allow individual occupancy probabilities to vary as a function of environmental covariates.

Open a new **MARK** session, load the "`Multispecies_ex_cov.inp`" file, and view it. This file contains 3 replicate surveys for 3 species, but now includes site-level and detection-level covariates:

```
/* Multispecies occupancy modeling example data*/
/* 3 survey occasions for 3 species (bobcat, coyote, and red fox) */
/* 5 covariates (all centered and scaled), 1 detection covariate  */
/*   (temperature) for each survey occasion and 2 occupancy covariates */
/* Covariates 1-3 are the average temperature for each survey occasion */
/* Covariates 4-5 are the occupancy covariates, (4) disturbance within */
/*  5km of the camera site (Dist5km) */
/* and (5) Housing density within 5km of the camera site (HDen5km) */

000000 1 0.869 0.037 -0.179 1.165 0.021;
000000 1 0.85 0.925 1.302 0.706 0.026;
000004 1 0.856 0.92 0.193 0.706 0.031;
000000 1 0.856 0.92 0.198 0.706 0.029;
000000 1 0.855 0.92 0.197 0.706 0.03;
040404 1 -0.267 0.383 0.1 0.706 0.035;
000000 1 -0.268 0.383 0.1 0.706 0.033;
000000 1 -0.268 0.383 0.1 0.706 0.032;
000000 1 -1.442 -0.932 -1.769 1.165 0.01;
000000 1 -1.442 -0.932 -1.769 1.165 0.01;
000400 1 -1.581 -0.929 -1.179 0.706 0.025;
000000 1 0.836 0.891 0.129 0.706 0.034;
040000 1 -0.347 0.592 -0.059 0.706 0.032;
```

Enter model specifications as below, indicating there are 5 individual covariates:

and enter individual covariate names as follows:

In this case `Temp1`, `Temp2`, and `Temp3` represent the average temperature during replicate survey 1, 2, and 3, respectively; `Dist5km` represents the proportion of recent disturbance within 5 km of the sample unit; and `HDen5km` represents the housing density within 5 km of the sample unit.

Specify the PIM exactly as the intercept-only model, then use the design matrix to specify covariate effects. We will model the effect of disturbance within 5 km on occupancy probabilities for each of the 3 species. This will require 9 parameters: an intercept and slope coefficient for each 1-way f parameter f_1, f_2, and f_3; and an intercept parameter for each detection parameter. Within the design matrix, you can right click on cells and select "**Individual Covariates**" from the dropdown box to add predictors into the design matrix as below:

B1 f1:bobcat	B2 bobcat_Dist5km	B3 f2:coyote	B4 coyote_Dist5km	B5 f3:redfox	B6 redfox_Dist5km	Parm	B7 p:bobcat	B8 p:coyote	B9 p:redfox
1	Dist5km	0	0	0	0	1:f	0	0	0
0	0	1	Dist5km	0	0	2:f	0	0	0
0	0	0	0	1	Dist5km	3:f	0	0	0
0	0	0	0	0	0	4:f	0	0	0
0	0	0	0	0	0	5:p	1	0	0
0	0	0	0	0	0	6:p	0	1	0
0	0	0	0	0	0	7:p	0	0	1

This design matrix implies the following models for the f parameters:

$$f_1 = \beta_1 + \beta_2(\texttt{Dist5km})$$

$$f_2 = \beta_3 + \beta_4(\texttt{Dist5km})$$

$$f_3 = \beta_5 + \beta_6(\texttt{Dist5km})$$

$$f_{12} = f_{13} = f_{23} = f_{123} = 0.$$

The following are parameter estimates from this model:

```
                  LOGIT Link Function Parameters of {M1}
                                            95% Confidence Interval
      Parameter              Beta        Standard Error      Lower           Upper
   ------------------   --------------   --------------   --------------   --------------
      1:f1:bobcat          -1.2484793      0.1358805       -1.5148051       -0.9821534
      2:bobcat_Dist5km     -0.4968829      0.1218956       -0.7357983       -0.2579674
      3:f2:coyote          -0.6288631      0.0743809       -0.7746496       -0.4830765
      4:coyote_Dist5km     -0.0018305      0.0663244       -0.1318264        0.1281654
      5:f3:redfox          -1.8784154      0.0969996       -2.0685345       -1.6882962
      6:redfox_Dist5km     -0.2906479      0.1109141       -0.5080396       -0.0732562
      7:p:bobcat           -1.0962115      0.1384530       -1.3675794       -0.8248437
      8:p:coyote           -0.3328899      0.0763581       -0.4825519       -0.1832280
      9:p:redfox           -0.2529214      0.1183254       -0.4848391       -0.0210036
```

Because we are assuming independence between all 3 species, this model shows that marginal occupancy probabilities of bobcat and red fox declines as the amount of recent disturbance within 5 km increases (because slope coefficients for parameters 2 and 6 are significantly different from 0), but that there is no relationship between coyote marginal occupancy probability and recent disturbance (because slope coefficient 4 is not significantly different from 0).

Next, let's incorporate constant pairwise dependence between each of the 3 species. Specify the PIM for both the f and p parameters as below
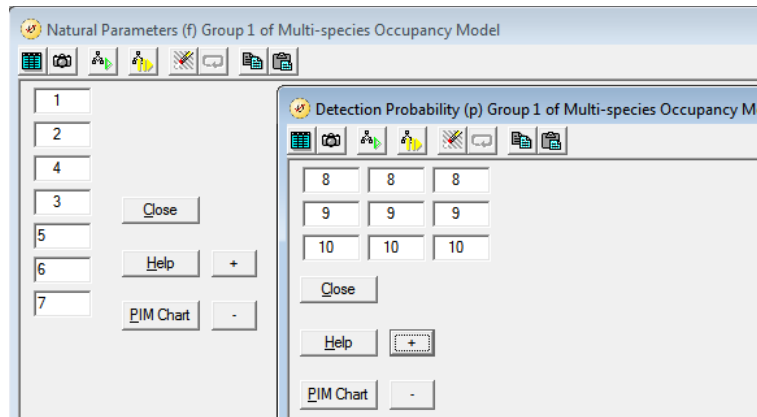
Within the design matrix, we now specify 12 covariates: an intercept and slope coefficient for each of the 1-way f parameters f_1, f_2, and f_3; an intercept parameter for 2-way f parameters f_{12}, f_{13}, and f_{23}; and intercept parameters for each of the detection models. Note that we are not interested in modeling 3-way interactions, and keep 7:f fixed at 0:

B1 f1:bobcat	B2 bobcat_Dist5km	B3 f2:coyote	B4 coyote_Dist5km	B5 f3:redfox	B6 redofx_Dist5km	B7 f12:bobcat-coyote	B8 f13:bobcat-redfox	B9 f23: coyote-redfox	Parm	B10 p:bobcat	B11 p:coyote	B12 p:redfox
1	Dist5km	0	0	0	0	0	0	0	1:f	0	0	0
0	0	1	Dist5km	0	0	0	0	0	2:f	0	0	0
0	0	0	0	1	Dist5km	0	0	0	3:f	0	0	0
0	0	0	0	0	0	1	0	0	4:f	0	0	0
0	0	0	0	0	0	0	1	0	5:f	0	0	0
0	0	0	0	0	0	0	0	1	6:f	0	0	0
0	0	0	0	0	0	0	0	0	7:f	0	0	0
0	0	0	0	0	0	0	0	0	8:p	1	0	0
0	0	0	0	0	0	0	0	0	9:p	0	1	0
0	0	0	0	0	0	0	0	0	10:p	0	0	1

This design matrix implies the following model for the 2-way and 3-way f parameters:

$$f_{12} = \beta_7$$

$$f_{13} = \beta_8$$

$$f_{23} = \beta_9$$

$$f_{123} = 0.$$

The parameter estimates from this model are shown at the top of the next page. This model suggests that bobcats are more likely to occur at sites where coyotes occur, bobcats are less likely to occur at sites where red fox occur, and coyotes are more likely to occur at sites where red fox occur (and vice versa for each pairwise association), since 2-way f-parameters (f_{12}, f_{13}, and f_{23}) are all significantly different from 0.

However, the slope coefficients associated with 1-way f-parameters now no longer have interpretations in terms of marginal probabilities of occurrence. Instead, they must now be interpreted in terms of covariate effects for each species when all other species are absent (i.e., conditional probabilities of

```
                        LOGIT Link Function Parameters of {M2}
                                                 95% Confidence Interval
          Parameter              Beta         Standard Error      Lower           Upper
   -------------------------  -------------   --------------  --------------  --------------
       1:f1:bobcat            -1.8524407       0.1825010      -2.2101427      -1.4947388
       2:bobcat_Dist5km       -0.5830310       0.1308089      -0.8394166      -0.3266455
       3:f2:coyote            -1.3173339       0.1379411      -1.5876984      -1.0469693
       4:coyote_Dist5km        0.1691281       0.0783650       0.0155326       0.3227235
       5:f3:redfox            -2.2417855       0.1554881      -2.5465422      -1.9370288
       6:redofx_Dist5km       -0.3955546       0.1182094      -0.6272450      -0.1638642
       7:f12:bobcat-coyote     1.7614248       0.2661261       1.2398177       2.2830319
       8:f13:bobcat-redfox    -1.5045668       0.3825343      -2.2543341      -0.7547995
       9:f23: coyote-redfox    1.4582497       0.2535426       0.9613062       1.9551931
      10:p:bobcat             -1.0934347       0.1373740      -1.3626878      -0.8241816
      11:p:coyote             -0.3296068       0.0760044      -0.4785754      -0.1806383
      12:p:redfox             -0.2514909       0.1181557      -0.4830761      -0.0199057
```

occurrence). Marginal and conditional occupancy probabilities can then be calculated as function of Ψ_i – see Rota *et al.* (2016) for details of calculation.

Although the above model assumes constant pairwise interactions between species, we can also model the probability two species occur together as a function of covariates. We will next examine how pairwise interactions are influenced by housing density within 5 km of each site. Specify the f and p parameters within the PIM as in the previous step. This time, we specify the design matrix to have 15 covariate columns: an intercept and slope for each of the 1-way and 2-way f parameters, and an intercept parameter for each detection model (note, the design matrix below still contains columns for the detection parameters, but they have been omitted from the screen shot for clarity):

B1 f1:bobcat	B2 bobcat_Dist5km	B3 f2:coyote	B4 coyote_Dist5km	B5 f3:redfox	B6 redfox_Dist5km	B7 f12:bobcat-coyote	B8 bobcatcoyote_HDens	B9 f13:bobcat-redfox	B10 bobcatredfox_HDen	B11 f23:coyote-redfox	B12 coyoteredfox_HDen	Parm
1	Dist5km	0	0	0	0	0	0	0	0	0	0	1:f
0	0	1	Dist5km	0	0	0	0	0	0	0	0	2:f
0	0	0	0	1	Dist5km	0	0	0	0	0	0	3:f
0	0	0	0	0	0	1	HDen5km	0	0	0	0	4:f
0	0	0	0	0	0	0	0	1	HDen5km	0	0	5:f
0	0	0	0	0	0	0	0	0	0	1	HDen5km	6:f
0	0	0	0	0	0	0	0	0	0	0	0	7:f
0	0	0	0	0	0	0	0	0	0	0	0	8:p
0	0	0	0	0	0	0	0	0	0	0	0	9:p
0	0	0	0	0	0	0	0	0	0	0	0	10:p

This design matrix implies the following models for the 2-way f parameters:

$$f_{12} = \beta_7 + \beta_8(\text{HDens5km})$$

$$f_{13} = \beta_9 + \beta_{10}(\text{HDens5km})$$

$$f_{23} = \beta_{11} + \beta_{12}(\text{HDens5km}).$$

The f parameter estimates from this model are shown at the top of the next page. This model suggests that bobcats and coyotes are less likely to occur together at sites with high housing density; while both bobcat and red fox, and coyote and red fox, are more likely to occur together at sites with high housing density.

```
                         LOGIT Link Function Parameters of {M3}
                                                         95% Confidence Interval
          Parameter                Beta       Standard Error      Lower           Upper
        ------------------------  ---------------  ---------------  ---------------  ---------------
           1:f1:bobcat            -1.9742531       0.2086447       -2.3831968       -1.5653095
           2:bobcat_Dist5km       -0.6133402       0.1335555       -0.8751090       -0.3515715
           3:f2:coyote            -1.3668612       0.1544098       -1.6695043       -1.0642181
           4:coyote_Dist5km        0.2019524       0.0835053        0.0382821        0.3656228
           5:f3:redfox            -2.3299546       0.1652129       -2.6537720       -2.0061372
           6:redfox_Dist5km       -0.2806017       0.1164679       -0.5088789       -0.0523246
           7:f12:bobcat-coyote     1.6808418       0.3210028        1.0516762        2.3100073
           8:bobcatcoyote_HDens   -1.7110137       0.5864057       -2.8603689       -0.5616585
           9:f13:bobcat-redfox    -1.3216698       0.3977406       -2.1012415       -0.5420982
          10:bobcatredfox_HDen     0.6343162       0.2079745        0.2266862        1.0419461
          11:f23:coyote-redfox     1.4910223       0.2815331        0.9392173        2.0428273
          12:coyoteredfox_HDen     0.5766354       0.0804574        0.4189389        0.7343319
          13:p:bobcat             -1.1180296       0.1382356       -1.3889714       -0.8470878
          14:p:coyote             -0.3919947       0.0792814       -0.5473863       -0.2366031
          15:p:redfox             -0.2498783       0.1147784       -0.4748440       -0.0249126
```

22.2.1. Detection Model

Finally, we usually wish to make detection probability vary across sites and replicate surveys. To do so, specify the f parameter PIM as above. However, detection probability is now specified with each row representing one of the three species and each column representing each survey occasion as below:
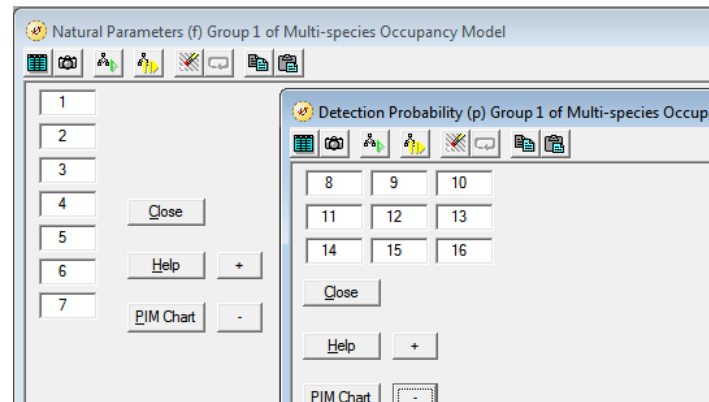
Next, specify a design matrix with 18 parameters: an intercept and slope parameter for each of the 1-way and 2-way f parameters; and an intercept and slope parameter for each detection model. Note that you must pay careful attention to which detection parameter index specified in the PIM is associated with each replicate survey for each species, to properly specify the detection model shown at the top of the next page (note, the design matrix below still contains f-parameters, but they have been omitted from the screen shot for clarity).

This design matrix implies the following detection model for each species (where b_{it}, c_{it}, and r_{it} indicates detection probability at site i and survey t for bobcat, coyote, and red fox, respectively):

$$\text{logit}(b_{it}) = \beta_{13} + \beta_{14}(\text{Temp}_{it})$$

$$\text{logit}(c_{it}) = \beta_{15} + \beta_{16}(\text{Temp}_{it})$$

$$\text{logit}(r_{it}) = \beta_{17} + \beta_{18}(\text{Temp}_{it}).$$

The following are the parameter estimates from this model:

```
             LOGIT Link Function Parameters of {M4}

                                               95% Confidence Interval
  Parameter                Beta      Standard Error    Lower          Upper
  --------------------   ------------  -------------  -------------  -------------
    1:f1:bobcat          -1.9215350    0.2103663      -2.3338530     -1.5092170
    2:bobcat_Dist5km     -0.6009057    0.1348201      -0.8651530     -0.3366584
    3:f2:coyote          -1.4200410    0.1665758      -1.7465296     -1.0935523
    4:coyote_Dist5km      0.2153348    0.0861658       0.0464499      0.3842197
    5:f3:redfox          -2.3324387    0.1668279      -2.6594214     -2.0054561
    6:redfox_Dist5km     -0.2850435    0.1173689      -0.5150866     -0.0550004
    7:f12:bobcat-coyote   1.7344094    0.3324873       1.0827342      2.3860845
    8:bobcatcoyote_HDens -1.7679987    0.5940844      -2.9324041     -0.6035933
    9:f13:bobcat-redfox  -1.3445714    0.4089191      -2.1460529     -0.5430899
   10:bobcatredfox_HDen   0.6438511    0.2061005       0.2398941      1.0478081
   11:f23:coyote-redfox   1.5402918    0.2913497       0.9692464      2.1113373
   12:coyoteredfox_HDen   0.5830677    0.0814602       0.4234057      0.7427298
   13:p:bobcat          -1.2157382    0.1374481      -1.4851365     -0.9463399
   14:p:bobcatTemp      -0.2998594    0.0851157      -0.4666861     -0.1330326
   15:p:coyote          -0.3956715    0.0795179      -0.5515266     -0.2398164
   16:coyoteTemp        -0.0675922    0.0645724      -0.1941540      0.0589696
   17:p:redfox          -0.2471444    0.1155182      -0.4735601     -0.0207286
   18:redfoxTemp        -0.0411816    0.1087036      -0.2542407      0.1718775
```

which suggests bobcats are less detectable at higher temperatures.

We can use model selection to discriminate among competing models. By appending each model's output to the database each time we run it, we obtain the following model selection table:

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{M4}	6525.3849	0.0000	0.97167	1.0000	18	6488.9025
{M3}	6532.4553	7.0704	0.02833	0.0292	15	6502.1175
{M2}	6600.1885	74.8036	0.00000	0.0000	12	6575.9694
{M1}	6687.6234	162.2385	0.00000	0.0000	9	6669.4973

These results suggest that the model assuming all first-order f parameters are a function of distur-bance within 5km, all second-order f parameters are a function of housing density, and all detection parameters are a function of temperature, is the top model. In fact, there is little model selection

uncertainty relative to the 2nd-ranked model (Δ AIC > 7). This seems like a sensible result: we found evidence that all of first-order and second-order f parameters were affected by disturbance and housing density within 5km, and that bobcat detection probability was influenced by temperature.

22.3. References

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