

An Analysis of Life History Data on the Purple Coneflower (*Echinacea angustifolia*) using the R Package Aster

Charles J. Geyer Ruth G. Shaw Stuart Wagenius

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1 Preliminaries

Load aster and data.

```
> library(aster)
> data(echinacea)
> names(echinacea)

[1] "hdct02" "hdct03" "hdct04" "site"   "ewloc"  "nsloc"
[7] "ld02"   "f102"   "ld03"   "f103"   "ld04"   "f104"
```

the variables with numbers in the names are the columns of the response matrix of the aster model. The variables `ld0x` (where x is a digit) are the survival indicator variables for year 200 x (one for alive, zero for dead). The variables `f10x` are the flowering indicator variables (one for any flowers, zero for none). The variables `hdct0x` are the inflorescence (flower head) count variables (number of flower heads). The variables without numbers are other predictors. The variables `ewloc` and `nsloc` are spatial predictions (east-west and north-south location, respectively). The variable `site` is the site of origin of the plant, so plants with different values of `site` may be more genetically diverse than those with the same values of `site`.

Make graph (of the graphical model, specified by a function p given by an R vector `pred`).

```
> pred <- c(0, 1, 2, 1, 2, 3, 4, 5, 6)
> fam <- c(1, 1, 1, 1, 1, 1, 3, 3, 3)
```

Reshape data.

```

> vars <- c("ld02", "ld03", "ld04", "fl02", "fl03",
+          "fl04", "hdct02", "hdct03", "hdct04")
> redata <- reshape(echinacea, varying = list(vars),
+                  direction = "long", timevar = "varb", times = as.factor(vars),
+                  v.names = "resp")
> redata <- data.frame(redata, root = 1)
> names(redata)

[1] "site" "ewloc" "nsloc" "varb" "resp" "id" "root"

```

2 Modeling

2.1 First Model

For our first model we try something simple (moderately simple). We have no site effects. We put in a mean and effect of north-south and east-west position for each of the nine variables. That gives us $3 \times 9 = 27$ parameters.

```

> out1 <- aster(resp ~ varb + varb:nsloc + varb:ewloc,
+              pred, fam, varb, id, root, data = redata)
> summary(out1, show.graph = TRUE)

```

Call:

```

aster.formula(formula = resp ~ varb + varb:nsloc + varb:ewloc,
              pred = pred, fam = fam, varvar = varb, idvar = id, root = root,
              data = redata)

```

Graphical Model:

variable	predecessor	family
ld02	root	bernoulli
ld03	ld02	bernoulli
ld04	ld03	bernoulli
fl02	ld02	bernoulli
fl03	ld03	bernoulli
fl04	ld04	bernoulli
hdct02	fl02	non.zero.poisson
hdct03	fl03	non.zero.poisson
hdct04	fl04	non.zero.poisson

Estimate Std. Error z value Pr(>|z|)

```

(Intercept)      -1.6418322  0.1928540  -8.513 < 2e-16 ***
varbfl03         -0.2585034  0.2961442  -0.873  0.38272
varbfl04         -0.3368137  0.2601966  -1.294  0.19551
varbhdct02       1.9661735  0.2675730   7.348 2.01e-13 ***
varbhdct03       1.9185775  0.2203482   8.707 < 2e-16 ***
varbhdct04       2.4696479  0.2001443  12.339 < 2e-16 ***
varbld02        -0.9772646  0.3502261  -2.790  0.00526 **
varbld03         1.0373523  0.4281242   2.423  0.01539 *
varbld04         4.1243999  0.3469256  11.888 < 2e-16 ***
varbfl02:nsloc   0.0838694  0.0265213   3.162  0.00157 **
varbfl03:nsloc   0.0655407  0.0302581   2.166  0.03031 *
varbfl04:nsloc   0.0698900  0.0244358   2.860  0.00423 **
varbhdct02:nsloc -0.0179987  0.0116776  -1.541  0.12324
varbhdct03:nsloc  0.0001156  0.0138761   0.008  0.99335
varbhdct04:nsloc -0.0034831  0.0074230  -0.469  0.63891
varbld02:nsloc  -0.0463586  0.0376371  -1.232  0.21805
varbld03:nsloc   0.0291040  0.0527152   0.552  0.58088
varbld04:nsloc   0.0339060  0.0405000   0.837  0.40249
varbfl02:ewloc   0.0460555  0.0267844   1.719  0.08553 .
varbfl03:ewloc  -0.0060486  0.0290874  -0.208  0.83527
varbfl04:ewloc  -0.0094399  0.0239818  -0.394  0.69385
varbhdct02:ewloc  0.0024187  0.0120993   0.200  0.84156
varbhdct03:ewloc  0.0230630  0.0135295   1.705  0.08826 .
varbhdct04:ewloc  0.0084179  0.0072661   1.159  0.24665
varbld02:ewloc   0.0149197  0.0357336   0.418  0.67629
varbld03:ewloc  -0.0285742  0.0517154  -0.553  0.58059
varbld04:ewloc   0.0048502  0.0409964   0.118  0.90582

```

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

2.2 Second Model

So now we put in site.

```
> levels(echinacea$site)
```

```
[1] "AA"      "Eriley" "Lf"      "Nessman" "NWLf"    "SPP"
[7] "Stevens"
```

Let us put `site` in only at the top level in this model (just to see what happens). In order to do that we have to add a predictor that “predicts” the top level.

```

> hdct <- grep("hdct", as.character(redata$varb))
> hdct <- is.element(seq(along = redata$varb), hdct)
> redata <- data.frame(redata, hdct = as.integer(hdct))
> names(redata)

[1] "site" "ewloc" "nsloc" "varb" "resp" "id" "root"
[8] "hdct"

> out2 <- aster(resp ~ varb + varb:nsloc + varb:ewloc +
+ hdct * site - site, pred, fam, varb, id, root,
+ data = redata)
> summary(out2)

Call:
aster.formula(formula = resp ~ varb + varb:nsloc + varb:ewloc +
hdct * site - site, pred = pred, fam = fam, varvar = varb,
idvar = id, root = root, data = redata)

```

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.6259835	0.1925029	-8.447	< 2e-16	***
varbfl03	-0.2591673	0.2953707	-0.877	0.38025	
varbfl04	-0.3272159	0.2594037	-1.261	0.20716	
varbhdct02	2.0516689	0.2751442	7.457	8.87e-14	***
varbhdct03	2.0032366	0.2298569	8.715	< 2e-16	***
varbhdct04	2.5544660	0.2106706	12.125	< 2e-16	***
varbld02	-0.9847880	0.3499238	-2.814	0.00489	**
varbld03	1.0268923	0.4279181	2.400	0.01641	*
varbld04	4.1086115	0.3467427	11.849	< 2e-16	***
varbfl02:nsloc	0.0835490	0.0264359	3.160	0.00158	**
varbfl03:nsloc	0.0655031	0.0301469	2.173	0.02980	*
varbfl04:nsloc	0.0698326	0.0243307	2.870	0.00410	**
varbhdct02:nsloc	-0.0184434	0.0116321	-1.586	0.11284	
varbhdct03:nsloc	-0.0004162	0.0138183	-0.030	0.97597	
varbhdct04:nsloc	-0.0038684	0.0073788	-0.524	0.60010	
varbld02:nsloc	-0.0459235	0.0376414	-1.220	0.22245	
varbld03:nsloc	0.0295182	0.0527428	0.560	0.57571	
varbld04:nsloc	0.0339706	0.0405350	0.838	0.40200	
varbfl02:ewloc	0.0462769	0.0267337	1.731	0.08345	.
varbfl03:ewloc	-0.0054404	0.0289865	-0.188	0.85112	
varbfl04:ewloc	-0.0089080	0.0239051	-0.373	0.70942	

```

varbhdct02:ewloc  0.0028066  0.0120847  0.232  0.81635
varbhdct03:ewloc  0.0231490  0.0134693  1.719  0.08568 .
varbhdct04:ewloc  0.0086106  0.0072716  1.184  0.23636
varbld02:ewloc    0.0153283  0.0357260  0.429  0.66789
varbld03:ewloc   -0.0283036  0.0517141  -0.547  0.58417
varbld04:ewloc    0.0048550  0.0409914  0.118  0.90572
hdct:siteEriley  -0.1782285  0.0893919  -1.994  0.04618 *
hdct:siteLf       -0.1617692  0.0960825  -1.684  0.09225 .
hdct:siteNessman -0.3152202  0.1387855  -2.271  0.02313 *
hdct:siteNWLf     -0.1076672  0.0832346  -1.294  0.19582
hdct:siteSPP      0.0198694  0.0862319  0.230  0.81777
hdct:siteStevens -0.1288083  0.0891936  -1.444  0.14870

```

```

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

```

```

Original predictor variables dropped (aliased)
      hdct

```

```
> anova(out1, out2)
```

```
Analysis of Deviance Table
```

```

Model 1: resp ~ varb + varb:nsloc + varb:ewloc
Model 2: resp ~ varb + varb:nsloc + varb:ewloc + hdct * site - site
  Model Df Model Dev Df Deviance P(>|Chi|)
1      27  2717.39
2      33  2701.26  6    16.13    0.01

```

Comment The last bit of the summary that the “original predictor” `hdct` was “dropped (aliased)” means just what it (tersely) says. The R formula mini-language as implemented in the R functions `model.frame` and `model.matrix` produces a model matrix that is not full rank. In order to estimate anything we must drop some dummy variable that it constructed. In this particular case the (dummy variable that is the indicator of) `hdct` is equal to the sum of the (dummy variables that are the indicators of) `varbhdct02`, `varbhdct03`, and `varbhdct04`. Thus we must drop one of these variables for the model to be identifiable. So `aster` does.

Comment The reason for the `- site` in the formula is not obvious. In fact, we originally did not write the formula this way and got the wrong

model (see “Tenth Model” in Section 2.10 below). It took some grovelling in various bits of R documentation to come up with this - `site` trick, but once you see it, the effect is clear.

We want site effects only at the “hdct” level. But the `hdct * site` crosses the `hdct` indicator variable, which has two values (zero and one) with the `site` variable, which has seven values (the seven sites), giving 14 parameters, one of which R drops (because it is aliased with the intercept). But that’s not what we want. We don’t want `site` effects at the “non-hdct” levels. The way the R formula mini-language allows us to specify that is - `site` which means to leave out the site main effects (7 fewer parameters, leaving 6) and we see that we do indeed have 6 degrees of freedom difference between models one and two.

2.3 Third Model

Let us now put `site` in at all levels in this model.

```
> level <- gsub("[0-9]", "", as.character(redata$varb))
> redata <- data.frame(redata, level = as.factor(level))
> out3 <- aster(resp ~ varb + varb:nsloc + varb:ewloc +
+   level * site, pred, fam, varb, id, root, data = redata)
> summary(out3)
```

Call:

```
aster.formula(formula = resp ~ varb + varb:nsloc + varb:ewloc +
  level * site, pred = pred, fam = fam, varvar = varb, idvar = id,
  root = root, data = redata)
```

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.937453	0.423538	-4.574	4.77e-06	***
varbfl03	-0.268508	0.293765	-0.914	0.36071	
varbfl04	-0.303001	0.257928	-1.175	0.24009	
varbhdct02	2.477882	0.546517	4.534	5.79e-06	***
varbhdct03	2.433586	0.525941	4.627	3.71e-06	***
varbhdct04	2.972531	0.516328	5.757	8.56e-09	***
varbld02	-0.739801	0.582421	-1.270	0.20401	
varbld03	1.256976	0.632563	1.987	0.04691	*
varbld04	4.322854	0.581362	7.436	1.04e-13	***
siteEriley	0.807390	0.451694	1.787	0.07386	.
siteLf	0.877245	0.481248	1.823	0.06833	.
siteNessman	-0.602180	0.681430	-0.884	0.37686	

siteNWLf	-0.111507	0.434671	-0.257	0.79754	
siteSPP	0.541625	0.450808	1.201	0.22958	
siteStevens	0.112023	0.465345	0.241	0.80976	
varbfl02:nsloc	0.083795	0.026329	3.183	0.00146	**
varbfl03:nsloc	0.066937	0.029982	2.233	0.02558	*
varbfl04:nsloc	0.070146	0.024162	2.903	0.00370	**
varbhdct02:nsloc	-0.018769	0.011491	-1.633	0.10240	
varbhdct03:nsloc	-0.001417	0.013619	-0.104	0.91715	
varbhdct04:nsloc	-0.004397	0.007261	-0.606	0.54477	
varbld02:nsloc	-0.044854	0.037640	-1.192	0.23340	
varbld03:nsloc	0.030181	0.052719	0.572	0.56699	
varbld04:nsloc	0.034831	0.040522	0.860	0.39003	
varbfl02:ewloc	0.035972	0.026717	1.346	0.17817	
varbfl03:ewloc	-0.015152	0.028934	-0.524	0.60050	
varbfl04:ewloc	-0.018685	0.023867	-0.783	0.43371	
varbhdct02:ewloc	0.006926	0.012016	0.576	0.56435	
varbhdct03:ewloc	0.026914	0.013389	2.010	0.04441	*
varbhdct04:ewloc	0.012554	0.007241	1.734	0.08298	.
varbld02:ewloc	0.013009	0.035812	0.363	0.71641	
varbld03:ewloc	-0.030830	0.051730	-0.596	0.55119	
varbld04:ewloc	0.002422	0.040976	0.059	0.95287	
levelhdct:siteEriley	-1.341288	0.587473	-2.283	0.02242	*
levelld:siteEriley	-0.560351	0.553094	-1.013	0.31100	
levelhdct:siteLf	-1.408221	0.631418	-2.230	0.02573	*
levelld:siteLf	-0.674658	0.588417	-1.147	0.25156	
levelhdct:siteNessman	0.418459	0.893928	0.468	0.63970	
levelld:siteNessman	0.922668	0.778683	1.185	0.23605	
levelhdct:siteNWLf	0.046822	0.553566	0.085	0.93259	
levelld:siteNWLf	0.140229	0.531548	0.264	0.79192	
levelhdct:siteSPP	-0.702929	0.573865	-1.225	0.22061	
levelld:siteSPP	-0.479659	0.561548	-0.854	0.39301	
levelhdct:siteStevens	-0.215472	0.593594	-0.363	0.71661	
levelld:siteStevens	-0.240029	0.569320	-0.422	0.67331	

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

Original predictor variables dropped (aliased)

levelhdct

levelld

```
> anova(out1, out2, out3)
```

Analysis of Deviance Table

```
Model 1: resp ~ varb + varb:nsloc + varb:ewloc
Model 2: resp ~ varb + varb:nsloc + varb:ewloc + hdct * site - site
Model 3: resp ~ varb + varb:nsloc + varb:ewloc + level * site
  Model Df Model Dev Df Deviance P(>|Chi|)
1      27  2717.39
2      33  2701.26  6    16.13    0.01
3      45  2663.55 12    37.71 0.0001715
```

Comment This would finish a sensible analysis, but we're really not sure we have dealt with the "geometry" (the variables `ewloc` and `nsloc`) correctly.

2.4 Fourth Model, Less Geometry

Thus we experiment with different ways to put in the spatial effects. First we reduce the geometry to a product, either year or level.

```
> year <- gsub("[a-z]", "", as.character(redata$varb))
> year <- paste("yr", year, sep = "")
> redata <- data.frame(redata, year = as.factor(year))
> out4 <- aster(resp ~ varb + (level + year):(nsloc +
+   ewloc) + level * site, pred, fam, varb, id, root,
+   data = redata)
> summary(out4)
```

Call:

```
aster.formula(formula = resp ~ varb + (level + year):(nsloc +
  ewloc) + level * site, pred = pred, fam = fam, varvar = varb,
  idvar = id, root = root, data = redata)
```

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.875208	0.419723	-4.468	7.91e-06	***
varbf103	-0.384991	0.268534	-1.434	0.15166	
varbf104	-0.373643	0.244457	-1.528	0.12640	
varbhdct02	2.387001	0.541799	4.406	1.05e-05	***
varbhdct03	2.399402	0.522036	4.596	4.30e-06	***
varbhdct04	2.913906	0.513754	5.672	1.41e-08	***
varbld02	-0.679149	0.562506	-1.207	0.22729	

varbld03	1.114165	0.611123	1.823	0.06828	.
varbld04	4.225862	0.573484	7.369	1.72e-13	***
siteEriley	0.809271	0.451391	1.793	0.07300	.
siteLf	0.878454	0.480895	1.827	0.06774	.
siteNessman	-0.600230	0.681076	-0.881	0.37816	.
siteNWLF	-0.111683	0.434221	-0.257	0.79702	.
siteSPP	0.540528	0.450468	1.200	0.23017	.
siteStevens	0.110291	0.464961	0.237	0.81250	.
levelfl:nsloc	0.068603	0.015126	4.535	5.75e-06	***
levelhdct:nsloc	-0.014500	0.007501	-1.933	0.05324	.
levelld:nsloc	0.001078	0.007299	0.148	0.88258	.
levelfl:ewloc	0.004590	0.015092	0.304	0.76102	.
levelhdct:ewloc	0.020550	0.007740	2.655	0.00793	**
levelld:ewloc	-0.001435	0.007502	-0.191	0.84825	.
yearyr03:nsloc	0.009125	0.007155	1.275	0.20224	.
yearyr04:nsloc	0.009184	0.006137	1.496	0.13453	.
yearyr03:ewloc	-0.001812	0.007242	-0.250	0.80241	.
yearyr04:ewloc	-0.011085	0.006324	-1.753	0.07965	.
levelhdct:siteEriley	-1.344673	0.587258	-2.290	0.02204	*
levelld:siteEriley	-0.561644	0.552345	-1.017	0.30923	.
levelhdct:siteLf	-1.410639	0.631143	-2.235	0.02541	*
levelld:siteLf	-0.674982	0.587591	-1.149	0.25067	.
levelhdct:siteNessman	0.416160	0.893648	0.466	0.64144	.
levelld:siteNessman	0.919968	0.777808	1.183	0.23690	.
levelhdct:siteNWLF	0.046781	0.553089	0.085	0.93259	.
levelld:siteNWLF	0.140718	0.530656	0.265	0.79087	.
levelhdct:siteSPP	-0.701296	0.573572	-1.223	0.22145	.
levelld:siteSPP	-0.477678	0.560739	-0.852	0.39429	.
levelhdct:siteStevens	-0.213370	0.593238	-0.360	0.71909	.
levelld:siteStevens	-0.237795	0.568455	-0.418	0.67571	.

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

Original predictor variables dropped (aliased)

levelhdct

levelld

> anova(out4, out3)

Analysis of Deviance Table

```

Model 1: resp ~ varb + (level + year):(nsloc + ewloc) + level * site
Model 2: resp ~ varb + varb:nsloc + varb:ewloc + level * site
  Model Df Model Dev Df Deviance P(>|Chi|)
1      37  2668.39
2      45  2663.55  8      4.83      0.78

```

So we have goodness of fit, and this can be our “big model”.

2.5 Fifth Model, Much Less Geometry

Now we reduce the geometry to just two predictors.

```

> out5 <- aster(resp ~ varb + nsloc + ewloc + level *
+   site, pred, fam, varb, id, root, data = redata)
> summary(out5)

```

Call:

```

aster.formula(formula = resp ~ varb + nsloc + ewloc + level *
  site, pred = pred, fam = fam, varvar = varb, idvar = id,
  root = root, data = redata)

```

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.740778	0.415402	-4.191	2.78e-05	***
varbfl03	-0.334899	0.264510	-1.266	0.205473	
varbfl04	-0.328208	0.240321	-1.366	0.172032	
varbhdct02	2.190026	0.536935	4.079	4.53e-05	***
varbhdct03	2.209167	0.516225	4.279	1.87e-05	***
varbhdct04	2.712799	0.509537	5.324	1.01e-07	***
varbld02	-0.769927	0.562247	-1.369	0.170882	
varbld03	0.982700	0.611052	1.608	0.107789	
varbld04	4.110627	0.573689	7.165	7.76e-13	***
nsloc	0.013506	0.001725	7.828	4.97e-15	***
ewloc	0.005965	0.001722	3.465	0.000531	***
siteEriley	0.755567	0.448815	1.683	0.092284	.
siteLf	0.809411	0.478696	1.691	0.090862	.
siteNessman	-0.721910	0.677652	-1.065	0.286735	
siteNWLf	-0.138061	0.433020	-0.319	0.749854	
siteSPP	0.516341	0.448626	1.151	0.249757	
siteStevens	0.080025	0.464014	0.172	0.863074	
levelhdct:siteEriley	-1.259136	0.585222	-2.152	0.031433	*
levelld:siteEriley	-0.548422	0.554771	-0.989	0.322881	

```

levelhdct:siteLf      -1.308189   0.629591  -2.078 0.037724 *
levelld:siteLf       -0.635814   0.590884  -1.076 0.281910
levelhdct:siteNessman 0.581044   0.890106   0.653 0.513898
levelld:siteNessman  1.048141   0.779258   1.345 0.178609
levelhdct:siteNWLf   0.072362   0.552482   0.131 0.895795
levelld:siteNWLf    0.183780   0.534492   0.344 0.730967
levelhdct:siteSPP   -0.662518   0.572464  -1.157 0.247147
levelld:siteSPP    -0.474797   0.564778  -0.841 0.400528
levelhdct:siteStevens -0.171288   0.593123  -0.289 0.772742
levelld:siteStevens -0.216441   0.572985  -0.378 0.705622

```

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

Original predictor variables dropped (aliased)

```

levelhdct
levelld

```

```
> anova(out5, out4, out3)
```

Analysis of Deviance Table

```

Model 1: resp ~ varb + nsloc + ewloc + level * site
Model 2: resp ~ varb + (level + year):(nsloc + ewloc) + level * site
Model 3: resp ~ varb + varb:nsloc + varb:ewloc + level * site

```

Model	Df	Model Dev	Df	Deviance	P(> Chi)
1	29	2696.56			
2	37	2668.39	8	28.18	0.0004416
3	45	2663.55	8	4.83	0.78

So we do not have goodness of fit, and this cannot be our “big model”.

2.6 Sixth Model, Intermediate Geometry, Levels

So we try again with the geometry.

```

> out6 <- aster(resp ~ varb + level:(nsloc + ewloc) +
+ level * site, pred, fam, varb, id, root, data = redata)
> summary(out6)

```

Call:

```
aster.formula(formula = resp ~ varb + level:(nsloc + ewloc) +
```

```

level * site, pred = pred, fam = fam, varvar = varb, idvar = id,
root = root, data = redata)

```

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.907186	0.420138	-4.539	5.64e-06	***
varbfl03	-0.354186	0.266796	-1.328	0.1843	
varbfl04	-0.319952	0.242895	-1.317	0.1878	
varbhdct02	2.424075	0.542402	4.469	7.85e-06	***
varbhdct03	2.447742	0.521950	4.690	2.74e-06	***
varbhdct04	2.945476	0.514751	5.722	1.05e-08	***
varbl02	-0.626114	0.562017	-1.114	0.2653	
varbl03	1.128493	0.611062	1.847	0.0648	.
varbl04	4.254223	0.573494	7.418	1.19e-13	***
siteEriley	0.812524	0.451595	1.799	0.0720	.
siteLf	0.882088	0.481103	1.833	0.0667	.
siteNessman	-0.593161	0.680863	-0.871	0.3837	
siteNWLF	-0.110570	0.434822	-0.254	0.7993	
siteSPP	0.543515	0.450805	1.206	0.2280	
siteStevens	0.114072	0.465336	0.245	0.8063	
levelfl:nsloc	0.070763	0.014568	4.857	1.19e-06	***
levelhdct:nsloc	-0.006425	0.005465	-1.176	0.2398	
levelld:nsloc	0.008036	0.005924	1.356	0.1749	
levelfl:ewloc	0.007768	0.014546	0.534	0.5933	
levelhdct:ewloc	0.011689	0.005561	2.102	0.0356	*
levelld:ewloc	-0.007240	0.006114	-1.184	0.2363	
levelhdct:siteEriley	-1.350424	0.587897	-2.297	0.0216	*
levelld:siteEriley	-0.563945	0.552117	-1.021	0.3071	
levelhdct:siteLf	-1.416802	0.631793	-2.243	0.0249	*
levelld:siteLf	-0.678297	0.587394	-1.155	0.2482	
levelhdct:siteNessman	0.405845	0.893667	0.454	0.6497	
levelld:siteNessman	0.912760	0.777262	1.174	0.2403	
levelhdct:siteNWLF	0.044673	0.554325	0.081	0.9358	
levelld:siteNWLF	0.139453	0.530726	0.263	0.7927	
levelhdct:siteSPP	-0.705876	0.574445	-1.229	0.2191	
levelld:siteSPP	-0.481472	0.560611	-0.859	0.3904	
levelhdct:siteStevens	-0.218838	0.594180	-0.368	0.7126	
levelld:siteStevens	-0.242044	0.568322	-0.426	0.6702	

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

Original predictor variables dropped (aliased)

levelhdct
levelld

```
> anova(out5, out6, out4, out3)
```

Analysis of Deviance Table

Model 1: resp ~ varb + nsloc + ewloc + level * site
Model 2: resp ~ varb + level:(nsloc + ewloc) + level * site
Model 3: resp ~ varb + (level + year):(nsloc + ewloc) + level * site
Model 4: resp ~ varb + varb:nsloc + varb:ewloc + level * site

Model	Df	Model Dev	Df	Deviance	P(> Chi)
1	29	2696.56			
2	33	2674.70	4	21.87	0.000213
3	37	2668.39	4	6.31	0.18
4	45	2663.55	8	4.83	0.78

So we have goodness of fit, and this can be our “big model”. But why drop year rather than level?

2.7 Seventh Model, Intermediate Geometry, Years

So we try again with the geometry.

```
> out7 <- aster(resp ~ varb + year:(nsloc + ewloc) +  
+ level * site, pred, fam, varb, id, root, data = redata)  
> summary(out7)
```

Call:

```
aster.formula(formula = resp ~ varb + year:(nsloc + ewloc) +  
level * site, pred = pred, fam = fam, varvar = varb, idvar = id,  
root = root, data = redata)
```

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.737420	0.416050	-4.176	2.97e-05	***
varbf103	-0.316825	0.265066	-1.195	0.231981	
varbf104	-0.337380	0.241251	-1.398	0.161973	
varbhdct02	2.193871	0.538051	4.077	4.55e-05	***
varbhdct03	2.168558	0.517159	4.193	2.75e-05	***
varbhdct04	2.713968	0.510169	5.320	1.04e-07	***

varbld02	-0.778587	0.562724	-1.384	0.166480	
varbld03	0.992898	0.611831	1.623	0.104625	
varbld04	4.099985	0.574053	7.142	9.19e-13	***
siteEriley	0.741522	0.449483	1.650	0.099000	.
siteLf	0.799687	0.479291	1.668	0.095221	.
siteNessman	-0.727352	0.678773	-1.072	0.283914	
siteNWLF	-0.128513	0.433273	-0.297	0.766765	
siteSPP	0.507401	0.449178	1.130	0.258636	
siteStevens	0.075879	0.464452	0.163	0.870225	
yearyr02:nsloc	0.009909	0.004372	2.266	0.023441	*
yearyr03:nsloc	0.019664	0.004995	3.937	8.27e-05	***
yearyr04:nsloc	0.012311	0.003276	3.758	0.000172	***
yearyr02:ewloc	0.010774	0.004435	2.430	0.015116	*
yearyr03:ewloc	0.008521	0.004798	1.776	0.075742	.
yearyr04:ewloc	0.001578	0.003246	0.486	0.626836	
levelhdct:siteEriley	-1.239189	0.585903	-2.115	0.034429	*
levelld:siteEriley	-0.532712	0.555127	-0.960	0.337246	
levelhdct:siteLf	-1.294188	0.630147	-2.054	0.039996	*
levelld:siteLf	-0.624375	0.591157	-1.056	0.290881	
levelhdct:siteNessman	0.587678	0.891330	0.659	0.509686	
levelld:siteNessman	1.055395	0.779991	1.353	0.176028	
levelhdct:siteNWLF	0.059302	0.552518	0.107	0.914526	
levelld:siteNWLF	0.174231	0.534494	0.326	0.744444	
levelhdct:siteSPP	-0.650145	0.572908	-1.135	0.256452	
levelld:siteSPP	-0.463775	0.564970	-0.821	0.411712	
levelhdct:siteStevens	-0.165745	0.593407	-0.279	0.780007	
levelld:siteStevens	-0.211556	0.573114	-0.369	0.712028	

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

Original predictor variables dropped (aliased)

levelhdct

levelld

> anova(out5, out7, out4, out3)

Analysis of Deviance Table

Model 1: resp ~ varb + nsloc + ewloc + level * site

Model 2: resp ~ varb + year:(nsloc + ewloc) + level * site

Model 3: `resp ~ varb + (level + year):(nsloc + ewloc) + level * site`
 Model 4: `resp ~ varb + varb:nsloc + varb:ewloc + level * site`

	Model	Df	Model Dev	Df	Deviance	P(> Chi)
1	29	2696.56				
2	33	2691.95	4	4.61	0.33	
3	37	2668.39	4	23.57	9.761e-05	
4	45	2663.55	8	4.83	0.78	

And we do not have goodness of fit! So Model Six is our “big model” and we have been logical in our model selection. Note that it is not valid to compare Models Six and Seven because they are not nested, but both fit between Models Five and Four, so Six and Seven can each be compared to both Five and Four (and this tells us what we want to know).

2.8 Eighth Model, Like Models Two and Six

We need to make a model with the structure of Model Two with respect to variables and like Model Six with respect to geometry.

```
> out8 <- aster(resp ~ varb + level:(nsloc + ewloc) +
+   hdct * site - site, pred, fam, varb, id, root,
+   data = redata)
> summary(out8)
```

Call:

```
aster.formula(formula = resp ~ varb + level:(nsloc + ewloc) +
  hdct * site - site, pred = pred, fam = fam, varvar = varb,
  idvar = id, root = root, data = redata)
```

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.591968	0.184332	-8.636	< 2e-16 ***
varbfl03	-0.349096	0.267919	-1.303	0.19258
varbfl04	-0.344222	0.243899	-1.411	0.15815
varbhdct02	1.991976	0.265192	7.511	5.85e-14 ***
varbhdct03	2.013936	0.219375	9.180	< 2e-16 ***
varbhdct04	2.521890	0.205048	12.299	< 2e-16 ***
varbld02	-0.874272	0.315703	-2.769	0.00562 **
varbld03	0.895081	0.396189	2.259	0.02387 *
varbld04	4.036755	0.334266	12.076	< 2e-16 ***
levelfl:nsloc	0.070102	0.014652	4.785	1.71e-06 ***
levelhdct:nsloc	-0.005804	0.005550	-1.046	0.29564

```

levelld:nsloc      0.007165    0.005867    1.221    0.22196
levelfl:ewloc      0.017977    0.014413    1.247    0.21229
levelhdct:ewloc    0.007606    0.005561    1.368    0.17138
levelld:ewloc     -0.004787    0.005919   -0.809    0.41863
hdct:siteEriley   -0.178799    0.089411   -2.000    0.04553 *
hdct:siteLf       -0.162516    0.096116   -1.691    0.09087 .
hdct:siteNessman  -0.315507    0.138823   -2.273    0.02304 *
hdct:siteNWLf     -0.108209    0.083110   -1.302    0.19292
hdct:siteSPP       0.019942    0.086198    0.231    0.81704
hdct:siteStevens -0.129238    0.089129   -1.450    0.14706

```

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

Original predictor variables dropped (aliased)

hdct

```
> anova(out8, out6)
```

Analysis of Deviance Table

Model 1: resp ~ varb + level:(nsloc + ewloc) + hdct * site - site

Model 2: resp ~ varb + level:(nsloc + ewloc) + level * site

	Model	Df	Model Dev	Df	Deviance	P(> Chi)
1	21	2712.54				
2	33	2674.70	12	37.84	0.0001632	

2.9 Ninth Model, Like Models One and Eight

We need to make a model with the structure of Model Eight except no sites.

```

> out9 <- aster(resp ~ varb + level:(nsloc + ewloc),
+   pred, fam, varb, id, root, data = redata)
> summary(out9)

```

Call:

```

aster.formula(formula = resp ~ varb + level:(nsloc + ewloc),
  pred = pred, fam = fam, varvar = varb, idvar = id, root = root,
  data = redata)

```

Estimate Std. Error z value Pr(>|z|)

```

(Intercept)      -1.607690    0.184593   -8.709 < 2e-16 ***
varbfl03         -0.349426    0.268532   -1.301  0.1932
varbfl04         -0.353847    0.244529   -1.447  0.1479
varbhdct02       1.906022    0.257183    7.411 1.25e-13 ***
varbhdct03       1.929506    0.209331    9.217 < 2e-16 ***
varbhdct04       2.436417    0.194176   12.547 < 2e-16 ***
varbld02        -0.866520    0.315991   -2.742  0.0061 **
varbld03         0.905229    0.396379    2.284  0.0224 *
varbld04         4.052121    0.334412   12.117 < 2e-16 ***
levelfl:nsloc    0.070281    0.014705    4.779 1.76e-06 ***
levelhdct:nsloc -0.005378    0.005578   -0.964  0.3350
levelld:nsloc    0.006855    0.005868    1.168  0.2427
levelfl:ewloc    0.017686    0.014441    1.225  0.2207
levelhdct:ewloc  0.007312    0.005542    1.320  0.1870
levelld:ewloc   -0.005027    0.005932   -0.847  0.3968

```

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

```
> anova(out9, out8, out6)
```

Analysis of Deviance Table

```

Model 1: resp ~ varb + level:(nsloc + ewloc)
Model 2: resp ~ varb + level:(nsloc + ewloc) + hdct * site - site
Model 3: resp ~ varb + level:(nsloc + ewloc) + level * site
  Model Df Model Dev Df Deviance P(>|Chi|)
1      15  2728.72
2      21  2712.54  6    16.18    0.01
3      33  2674.70 12    37.84 0.0001632

```

2.10 Tenth Model, Between Models Six and Eight

We accidentally created a new tenth model by not understanding the “minus site” stuff in the formulae for Models Two and Eight.

```

> out10 <- aster(resp ~ varb + level:(nsloc + ewloc) +
+   hdct * site, pred, fam, varb, id, root, data = redata)
> summary(out10)

```

Call:

```
aster.formula(formula = resp ~ varb + level:(nsloc + ewloc) +
```

```
hdct * site, pred = pred, fam = fam, varvar = varb, idvar = id,
root = root, data = redata)
```

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-1.726122	0.223462	-7.724	1.12e-14	***
varbfl03	-0.349106	0.266693	-1.309	0.19053	
varbfl04	-0.330903	0.242658	-1.364	0.17268	
varbhdct02	2.203913	0.331242	6.653	2.86e-11	***
varbhdct03	2.226234	0.296256	7.515	5.71e-14	***
varbhdct04	2.732111	0.285814	9.559	< 2e-16	***
varbld02	-0.861178	0.316060	-2.725	0.00644	**
varbld03	0.888715	0.396388	2.242	0.02496	*
varbld04	4.008350	0.334436	11.985	< 2e-16	***
siteEriley	0.375414	0.154884	2.424	0.01536	*
siteLf	0.355237	0.164870	2.155	0.03119	*
siteNessman	0.231430	0.189693	1.220	0.22245	
siteNWLf	0.012016	0.145094	0.083	0.93400	
siteSPP	0.185498	0.158948	1.167	0.24319	
siteStevens	-0.069680	0.153063	-0.455	0.64894	
levelfl:nsloc	0.070918	0.014584	4.863	1.16e-06	***
levelhdct:nsloc	-0.006532	0.005504	-1.187	0.23528	
levelld:nsloc	0.007901	0.005959	1.326	0.18488	
levelfl:ewloc	0.014308	0.014359	0.996	0.31904	
levelhdct:ewloc	0.010083	0.005557	1.814	0.06961	.
levelld:ewloc	-0.009182	0.006100	-1.505	0.13231	
hdct:siteEriley	-0.794844	0.264102	-3.010	0.00262	**
hdct:siteLf	-0.744006	0.282716	-2.632	0.00850	**
hdct:siteNessman	-0.705433	0.355627	-1.984	0.04730	*
hdct:siteNWLf	-0.114923	0.245244	-0.469	0.63935	
hdct:siteSPP	-0.270775	0.262750	-1.031	0.30276	
hdct:siteStevens	0.003604	0.260305	0.014	0.98895	

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

Original predictor variables dropped (aliased)

hdct

```
> anova(out9, out8, out10, out6)
```

Analysis of Deviance Table

```

Model 1: resp ~ varb + level:(nsloc + ewloc)
Model 2: resp ~ varb + level:(nsloc + ewloc) + hdct * site - site
Model 3: resp ~ varb + level:(nsloc + ewloc) + hdct * site
Model 4: resp ~ varb + level:(nsloc + ewloc) + level * site
  Model Df Model Dev Df Deviance P(>|Chi|)
1      15  2728.72
2      21  2712.54 6    16.18    0.01
3      27  2684.86 6    27.67 0.0001083
4      33  2674.70 6    10.17    0.12

```

So this says that Model Ten (which only has 12 d. f. for “site”) can be the big model.

```

> save(redata, out6, out8, out9, out10, pred, fam,
+      file = "coneflr.RData")

```

3 Mean Value Parameters

3.1 Unconditional

As argued in *Aster Models*, canonical parameters are “meaningless.” Only mean value parameters have real world, scientific interpretability.

So in this section we compare predicted values for a typical individual (say zero-zero geometry) in each site under both Models Six and Eight. The functional of mean value parameters we want is *total head count*, since this has the biological interpretation of the component of fitness measured in this data set. A biologist (at least an evolutionary biologist) is interested in the “predecessor variables” of head count only insofar as they contribute to head count. Two sets of parameter values that “predict” the same expected total head count (over the three years the data were collected) have the same contribution to fitness. So that is the “prediction” (really functional of mean value parameters) we “predict.”

To do this we must construct “newdata” for these hypothetical individuals.

```

> newdata <- data.frame(site = levels(echinacea$site))
> for (v in vars) newdata[[v]] <- 1
> newdata$root <- 1
> newdata$ewloc <- 0
> newdata$nsloc <- 0
> renewdata <- reshape(newdata, varying = list(vars),

```

```

+     direction = "long", timevar = "varb", times = as.factor(vars),
+     v.names = "resp")
> names(redata)

[1] "site" "ewloc" "nsloc" "varb" "resp" "id" "root"
[8] "hdct" "level" "year"

> names(renewdata)

[1] "site" "root" "ewloc" "nsloc" "varb" "resp" "id"

> hdct <- grep("hdct", as.character(renewdata$varb))
> hdct <- is.element(seq(along = renewdata$varb), hdct)
> renewdata$hdct <- as.integer(hdct)
> level <- gsub("[0-9]", "", as.character(renewdata$varb))
> renewdata$level <- as.factor(level)
> year <- gsub("[a-z]", "", as.character(renewdata$varb))
> year <- paste("yr", year, sep = "")
> renewdata$year <- as.factor(year)
> setequal(names(redata), names(renewdata))

[1] TRUE

```

We are using bogus data $x_{ij} = 1$ for all i and j because unconditional mean value parameters do not depend on x . We have to have an x argument because that's the way the aster package functions work (ultimately due to limitations of the R formula mini-language). So it doesn't matter what we make it. In the following section, the predictions will depend on x , but then (as we shall argue), this is the x we want.

```

> nind <- nrow(newdata)
> nnode <- length(vars)
> amat <- array(0, c(nind, nnode, nind))
> for (i in 1:nind) amat[i, grep("hdct", vars), i] <- 1
> pout6 <- predict(out6, varvar = varb, idvar = id,
+   root = root, newdata = renewdata, se.fit = TRUE,
+   amat = amat)
> pout8 <- predict(out8, varvar = varb, idvar = id,
+   root = root, newdata = renewdata, se.fit = TRUE,
+   amat = amat)

```

Figure 1 is produced by the following code

```

> conf.level <- 0.95
> crit <- qnorm((1 + conf.level)/2)

> sitenames <- as.character(newdata$site)
> fit8 <- pout8$fit
> i <- seq(along = sitenames)
> ytop <- fit8 + crit * pout8$se.fit
> ybot <- fit8 - crit * pout8$se.fit
> plot(c(i, i), c(ytop, ybot), type = "n", axes = FALSE,
+      xlab = "", ylab = "")
> segments(i, ybot, i, ytop)
> foo <- 0.1
> segments(i - foo, ybot, i + foo, ybot)
> segments(i - foo, ytop, i + foo, ytop)
> segments(i - foo, fit8, i + foo, fit8)
> axis(side = 2)
> title(ylab = "unconditional mean value parameter")
> axis(side = 1, at = i, labels = sitenames)
> title(xlab = "site")

```

and appears on p. 22.

Figure 2 is produced by the following code

```

> fit6 <- pout6$fit
> i <- seq(along = sitenames)
> foo <- 0.1
> y8top <- fit8 + crit * pout8$se.fit
> y8bot <- fit8 - crit * pout8$se.fit
> y6top <- fit6 + crit * pout6$se.fit
> y6bot <- fit6 - crit * pout6$se.fit
> plot(c(i - 1.5 * foo, i - 1.5 * foo, i + 1.5 * foo,
+      i + 1.5 * foo), c(y8top, y8bot, y6top, y6bot),
+      type = "n", axes = FALSE, xlab = "", ylab = "")
> segments(i - 1.5 * foo, y8bot, i - 1.5 * foo, y8top)
> segments(i - 2.5 * foo, y8bot, i - 0.5 * foo, y8bot)
> segments(i - 2.5 * foo, y8top, i - 0.5 * foo, y8top)
> segments(i - 2.5 * foo, fit8, i - 0.5 * foo, fit8)
> segments(i + 1.5 * foo, y6bot, i + 1.5 * foo, y6top,
+      lty = 2)
> segments(i + 2.5 * foo, y6bot, i + 0.5 * foo, y6bot)
> segments(i + 2.5 * foo, y6top, i + 0.5 * foo, y6top)

```

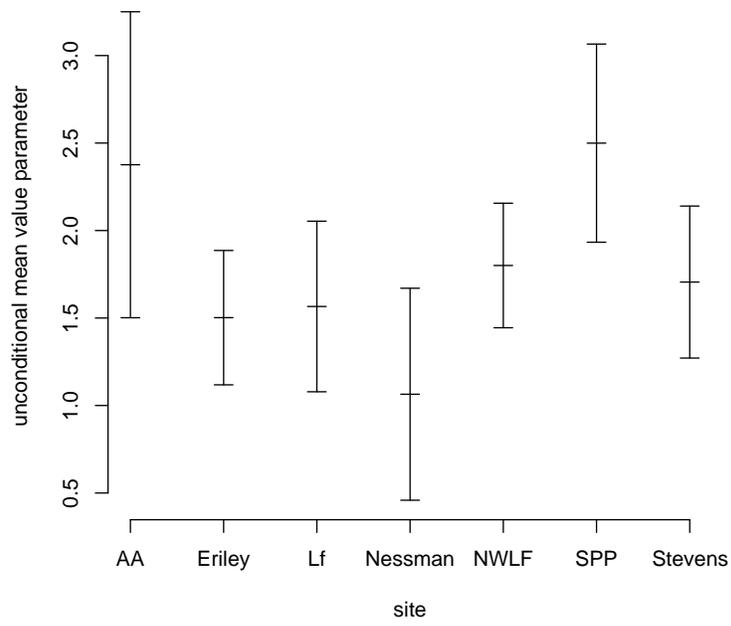


Figure 1: 95% confidence intervals for unconditional mean value parameter for fitness (sum of head count for all years) at each site for a “typical” individual having position zero-zero and having the parameterization of Model Eight. Tick marks in the middle of the bars are the center (the MLE).

```

> segments(i + 2.5 * foo, fit6, i + 0.5 * foo, fit6)
> axis(side = 2)
> title(ylab = "unconditional mean value parameter")
> axis(side = 1, at = i, labels = sitenames)
> title(xlab = "site")

```

and appears on p. 24.

3.2 Conditional

This section is very incomplete. We don't redo everything using conditional models. That's not the point. We only want to show that conditional models and conditional mean value parameters just don't do the same thing as unconditional models (which is obvious, but some people like examples, and in any case, this gives us an opportunity to show some options of aster model fitting).

3.2.1 Conditional Models

Let us redo Figure 2 based on conditional models with the same model matrices (a dumb idea, since the meaning of the models is entirely different despite the similarity in algebra, but we want to hammer the point home).

```

> cout6 <- aster(resp ~ varb + level:(nsloc + ewloc) +
+   level * site, pred, fam, varb, id, root, data = redata,
+   type = "conditional")
> cout8 <- aster(resp ~ varb + level:(nsloc + ewloc) +
+   hdct * site - site, pred, fam, varb, id, root,
+   data = redata, type = "conditional")
> pcout6 <- predict(cout6, varvar = varb, idvar = id,
+   root = root, newdata = renewdata, se.fit = TRUE,
+   amat = amat)
> pcout8 <- predict(cout8, varvar = varb, idvar = id,
+   root = root, newdata = renewdata, se.fit = TRUE,
+   amat = amat)

```

Note that these are exactly like the analogous statements making the analogous objects without the "c" in their names except for the `type = "conditional"` arguments in the two `aster` function calls. Then we make Figure 3 just like Figure 2 except for using `pcout6` and `pcout8` instead of `pout6` and `pout8`. It appears on p. 25.

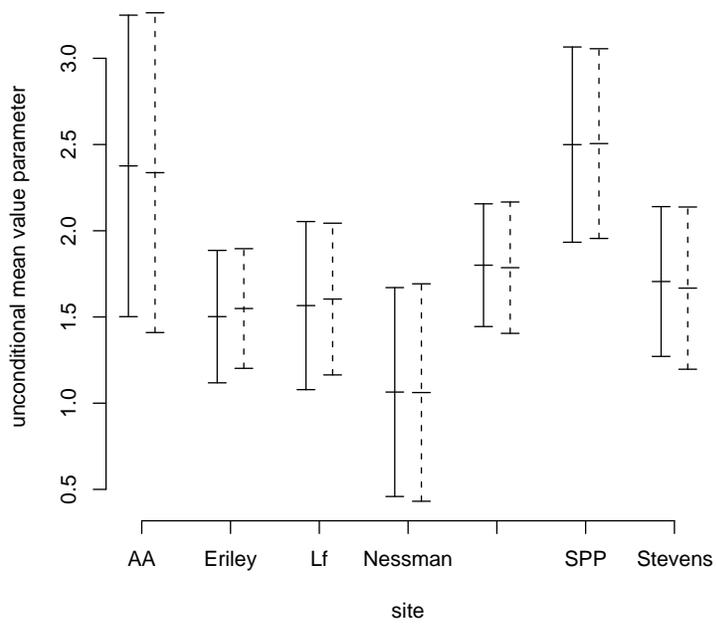


Figure 2: 95% confidence intervals for unconditional mean value parameter for fitness (sum of head count for all years) at each site for a “typical” individual having position zero-zero and having the parameterization of Model Eight (solid bar) or Model Six (dashed bar). Tick marks in the middle of the bars are the center (the MLE).

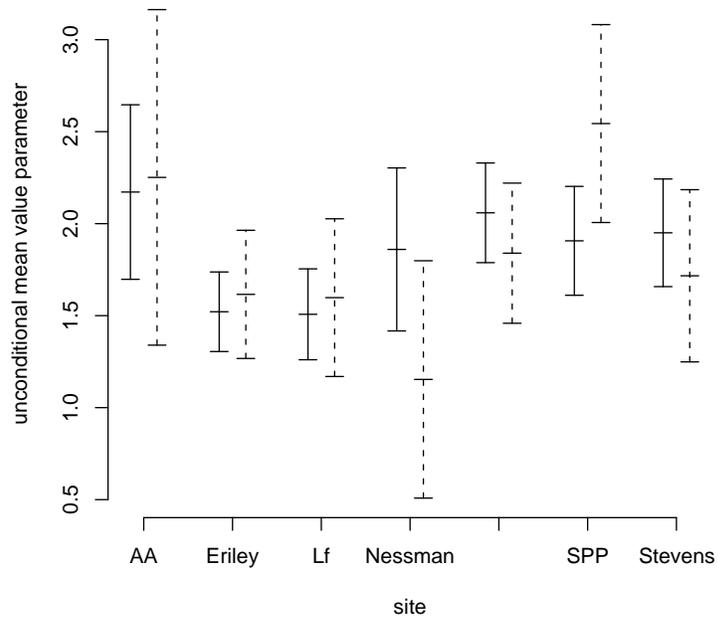


Figure 3: 95% confidence intervals for unconditional mean value parameter for fitness (sum of head count for all years) at each site for a “typical” individual having position zero-zero and having the parameterization of Model Eight (solid bar) or Model Six (dashed bar). Tick marks in the middle of the bars are the center (the MLE). The difference between this figure and Figure 2 is that the models fitted are *conditional* rather than *unconditional*.

Note the huge difference between Figure 2 and Figure 3. The same model matrices are used in both cases. The linear predictor satisfies $\boldsymbol{\eta} = \mathbf{M}\boldsymbol{\beta}$, but in one case (Figure 2) the linear predictor is the unconditional canonical parameter ($\boldsymbol{\eta} = \boldsymbol{\varphi}$) and in the other case (Figure 3) the linear predictor is the conditional canonical parameter ($\boldsymbol{\eta} = \boldsymbol{\theta}$). In one case (Figure 2) the predictions of a linear functional of the unconditional mean value parameter ($\boldsymbol{\tau}$) are nearly the same for the two models and in the other case (Figure 3) the predictions of the same linear functional of $\boldsymbol{\tau}$ are wildly different.

Conclusion: conditional models and unconditional models are different. That’s the whole point. That’s why unconditional models were invented, because conditional models can’t be made to do the same thing.

3.2.2 Conditional Parameter

Let us redo Figure 2 now not changing the model (we still use the fits `out6` and `out8`) but changing the thingummy we “predict”. In Figure 2 we “predict” a linear functional $\mathbf{A}'\boldsymbol{\tau}$ of the unconditional mean value parameter (the sum of three components of $\boldsymbol{\tau}$, those for flower head count). In Figure 4 we predict the same linear functional $\mathbf{A}'\boldsymbol{\xi}$ of the *conditional* mean value parameter $\boldsymbol{\xi}$.

```
> pxout6 <- predict(out6, varvar = varb, idvar = id,
+   root = root, newdata = renewdata, se.fit = TRUE,
+   amat = amat, model.type = "conditional")
> pxout8 <- predict(out8, varvar = varb, idvar = id,
+   root = root, newdata = renewdata, se.fit = TRUE,
+   amat = amat, model.type = "conditional")
```

Note that these are exactly like the analogous statements making the analogous objects without the “x” in their names except for the `model.type = "conditional"` arguments in the two `predict` function calls. Then we make Figure 4 just like Figure 2 except for using `pxout6` and `pxout8` instead of `pout6` and `pout8`. It appears on p. 27.

Note the huge difference between Figure 2 and Figure 4. The same models are used in both cases but in one case (Figure 2) we “predict” a linear functional $\mathbf{A}'\boldsymbol{\tau}$ of the unconditional mean value parameter ($\boldsymbol{\tau}$) and in the other case (Figure 4) we “predict” the *same* linear functional $\mathbf{A}'\boldsymbol{\xi}$ of the conditional mean value parameter ($\boldsymbol{\xi}$).

Conclusion: conditional expectations and unconditional expectations are different. (Duh!) The two sorts of predictions can’t be made to do the same thing.

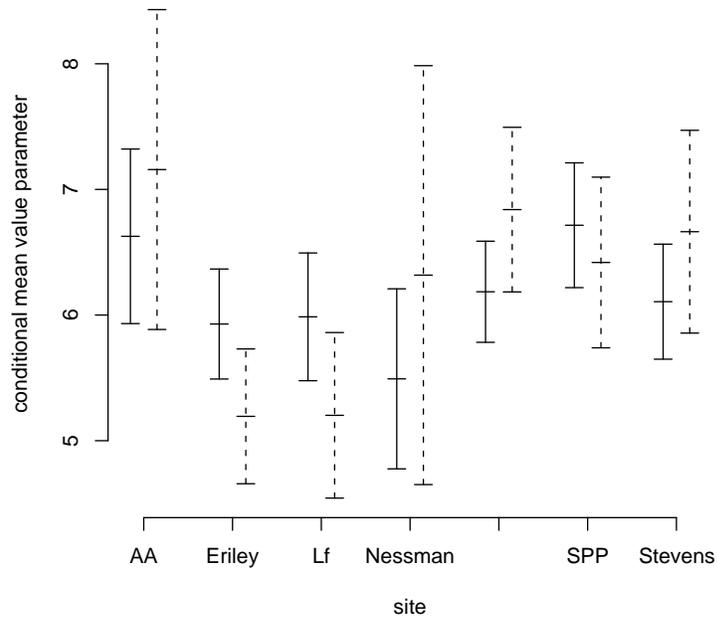


Figure 4: 95% confidence intervals for conditional mean value parameter for fitness (sum of head count for all years) at each site for a “typical” individual having position zero-zero and having the parameterization of Model Eight (solid bar) or Model Six (dashed bar). Tick marks in the middle of the bars are the center (the MLE). The difference between this figure and Figure 2 is that the parameters “predicted” are *conditional* rather than *unconditional*.

A Plot for the Paper

We redo Figure 2 changing the models compared to Model 8 and Model 10 (fits in `out8` and `out10`).

```
> pout10 <- predict(out10, varvar = varb, idvar = id,  
+   root = root, newdata = renewdata, se.fit = TRUE,  
+   amat = amat)
```

It appears on p. 29.

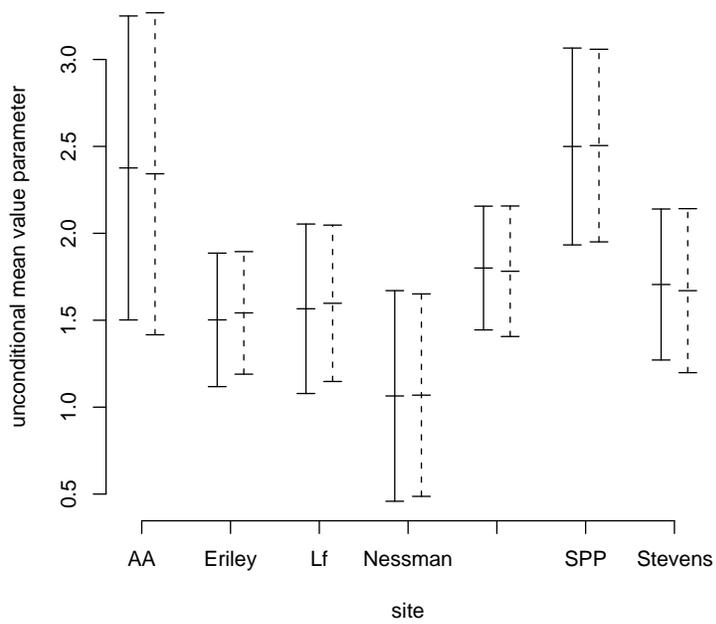


Figure 5: 95% confidence intervals for unconditional mean value parameter for fitness (sum of head count for all years) at each site for a “typical” individual having position zero-zero and having the parameterization of Model Eight (solid bar) or Model Ten (dashed bar). Tick marks in the middle of the bars are the center (the MLE).