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Functional Ecology

BRITISH ECOLOGICAL SOCIETY

Functional Ecology 2017 doi: 10.1111/1365-2435.12878

Towards a functional understanding of species coexistence: ecomorphological variation in relation to whole-organism performance in two sympatric lizards

Anamarija Žagar*[,1], Miguel A. Carretero[1], Al Vrezec[2], Katarina Drašler[3] and Antigoni Kaliontzopoulou[1]

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Antigoni Kaliontzopoulou

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Towards a functional understanding of species coexistence: ecomorphological variation in relation to whole-organism performance in two sympatric lizards

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In this context, the main aim of this work is to understand the functional relationships between morphology and factors involved in interspecific interactions that occur in cases of syntopy (coexistence) in studied sympatric lizards. Specifically, we focus on the functional traits promoting higher success in potential agonistic encounters. Firstly, in bite force we predict that if both species differ in bite force, the one previously known to have the dominant position over the other in agonistic encounters (*P. muralis*) is expected to have stronger bites. If coexisting occurrence (syntopy) is facilitated by differential microhabitat use, we should observe variation in morphological and performance traits that can enhance the use of various microhabitats in the study area. In particular, we would expect interspecific differences in climbing and running abilities and limb dimensions correlated with the use of different substrates and variability in head height, if head height determines the minimal size of the crevices accessible as refuges (e.g. Carretero *et al.* 2006). Using smaller refuges may also enhance escape from the most specialized common predator – saurophagous snakes for the flatter species. Thus, the studied species potentially differ in their ability to escape common predators, which is expected to have an indirect effect on their coexistence (Holt 1977). Finally, we also consider the variation between sexes to account for intraspecific differences.

02. PCM data preparation.R | 5.3. Showcase.R | data

Filter

	CODE	SP	SEX	MAXBITE	MAXRUN	MAXCLIMB	SVL	TRL	HL	PL	HW	HH	MO	FLL	HLL
1	20	IHOR	F	1.0260	161.8281	137.7114	60.4	39.8	19.2	12.2	7.3	4.8	10.5	18.6	28.4
2	21	IHOR	F	0.9120	132.1550	120.6082	58.9	41.0	18.9	12.4	7.5	4.9	10.7	19.1	26.6
3	22	IHOR	F	1.1020	150.2851	117.6548	64.3	42.9	19.4	12.6	7.7	4.8	10.9	19.4	29.2
4	23	IHOR	F	1.0355	158.3828	161.1837	62.6	44.6	19.7	13.0	7.4	4.7	10.8	19.2	27.1
5	24	IHOR	F	1.2255	293.2537	146.8594	66.1	47.9	20.5	12.7	7.7	5.4	10.3	19.0	29.2
6	26	IHOR	F	0.7220	1521.5744	112.8859	57.6	41.1	18.9	11.9	7.3	4.8	10.5	20.3	23.4
7	28	IHOR	F	0.8550	138.1386	125.5674	58.5	41.9	17.8	11.5	7.3	4.6	9.7	18.6	28.0
8	30	IHOR	F	1.3110	163.4215	163.4215	61.7	34.1	20.0	12.4	7.5	4.7	10.5	20.0	26.4
9	31	IHOR	F	0.7695	127.2870	114.0817	51.1	36.9	16.6	11.3	6.9	4.5	9.6	16.7	26.1
10	32	IHOR	F	0.7505	155.4925	132.4839	59.3	42.2	18.1	11.6	7.7	5.1	10.5	18.5	27.0
11	33	IHOR	F	1.3395	165.4863	128.8085	64.0	45.8	18.6	12.5	7.6	5.6	11.0	19.4	25.2
12	34	IHOR	F	0.2755	133.8815	143.0790	52.1	37.1	15.9	10.7	6.3	4.3	9.3	17.0	23.0
13	35	IHOR	F	0.7315	133.5465	119.6905	66.1	44.7	20.4	12.8	8.2	4.7	12.6	19.4	30.0
14	36	IHOR	F	0.8075	193.2613	150.3532	53.9	37.1	15.1	10.9	6.8	4.1	10.0	17.5	24.2

Showing 1 to 14 of 103 entries

Console ~/antigua/Collaborations/Anamarija/Ihor_Pmur_performance/

```
R is free software and comes with ABSOLUTELY NO WARRANTY.
You are welcome to redistribute it under certain conditions.
Type 'license()' or 'licence()' for distribution details.

  Natural language support but running in an English locale

R is a collaborative project with many contributors.
Type 'contributors()' for more information and
'citation()' on how to cite R or R packages in publications.

Type 'demo()' for some demos, 'help()' for on-line help, or
'help.start()' for an HTML browser interface to help.
Type 'q()' to quit R.

> setwd("/home/antigoni/antigua/Collaborations/Anamarija/Ihor_Pmur_performance/")
Error in setwd("/home/antigoni/antigua/Collaborations/Anamarija/Ihor_Pmur_performance/") :
  cannot change working directory
> setwd("/Users/antigoni/antigua/Collaborations/Anamarija/Ihor_Pmur_performance/")
> data <- read.table("data.csv", sep=",", header=T, na.strings="NA")
> data <- data[!is.na(data$MAXBITE),]
> colnames(data)[14:15] <- c("FLL", "HLL")
> View(data)
>
```

Environment | History

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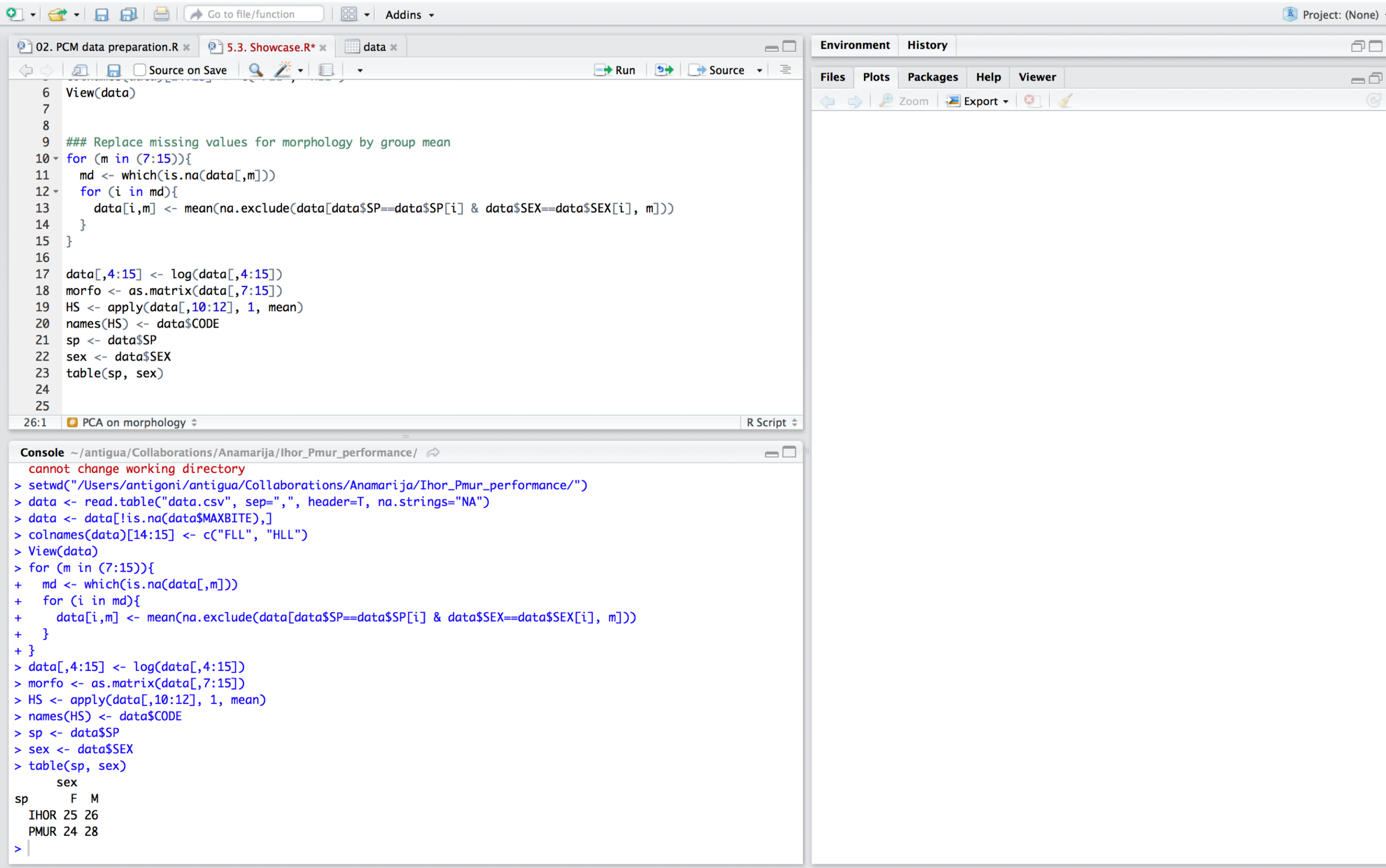
Addins | Go to file/function | Project: (None)



Go to file/function
Addins
Project: (None)
02. PCM data preparation.R
5.3. Showcase.R*
data
Source on Save
Run
Source
View(data)
Replace missing values for morphology by group mean
for (m in (7:15)){
md <- which(is.na(data[,m]))
for (i in md){
data[i,m] <- mean(na.exclude(data[data$SP==data$SP[i] & data$SEX==data$SEX[i], m]))
}
}
data[,4:15] <- log(data[,4:15])
morfo <- as.matrix(data[,7:15])
HS <- apply(data[,10:12], 1, mean)
names(HS) <- data$CODE
sp <- data$SP
sex <- data$SEX
table(sp, sex)
26:1
PCA on morphology
R Script
Console ~/antigua/Collaborations/Anamarija/Ihor_Pmur_performance/
cannot change working directory
> setwd("/Users/antigoni/antigua/Collaborations/Anamarija/Ihor_Pmur_performance/")
> data <- read.table("data.csv", sep=",", header=T, na.strings="NA")
> data <- data[!is.na(data$MAXBITE),]
> colnames(data)[14:15] <- c("FLL", "HLL")
> View(data)
> for (m in (7:15)){
+ md <- which(is.na(data[,m]))
+ for (i in md){
+ data[i,m] <- mean(na.exclude(data[data$SP==data$SP[i] & data$SEX==data$SEX[i], m]))
+ }
+ }
> data[,4:15] <- log(data[,4:15])
> morfo <- as.matrix(data[,7:15])
> HS <- apply(data[,10:12], 1, mean)
> names(HS) <- data$CODE
> sp <- data$SP
> sex <- data$SEX
> table(sp, sex)
sex
sp F M
IHOR 25 26
PMUR 24 28
>
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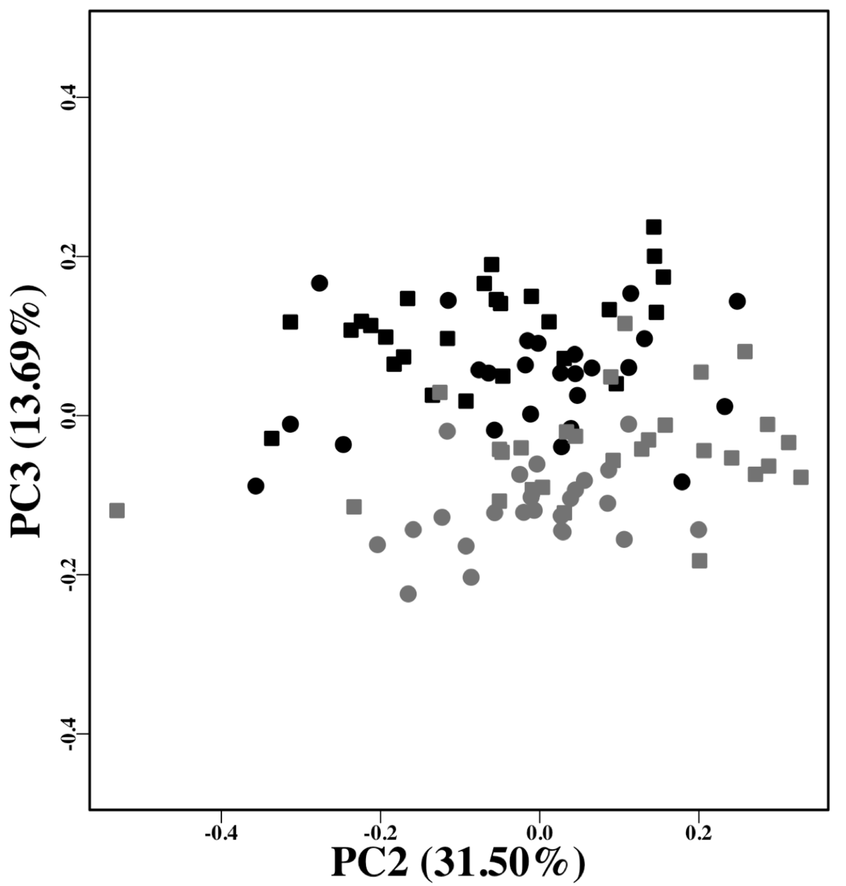
```r
cor(na.exclude(morfo), pcscores.all)

# Plot
ind.col <- ifelse(sp=="IHOR", "black", "grey45")
ind.symb <- ifelse(sex=="F", 21, 22)

par(family="Times", lwd=2, mgp=c(1.75, 0.35, 0))
plot(pcscores.all[,1:2], asp=1, xlab="PC1 (42.84%)", ylab="PC2 (31.50%)",
     cex.lab=2, font.lab=2, pch=ind.symb, col=ind.col, bg=ind.col, cex=1.5,
     font.axis=2)

par(family="Times", lwd=2, mgp=c(1.75, 0.35, 0))
plot(pcscores.all[,2:3], asp=1, xlab="PC2 (31.50%)", ylab="PC3 (13.69%)",
     cex.lab=2, font.lab=2, pch=ind.symb, col=ind.col, bg=ind.col, cex=1.5,
     font.axis=2)

#### AN(C)OVAs - morfo ####
library(vegan)
anova.svl <- adonis(morfo[,1]~sp*sex, method="euclidean")
anovas <- cbind(anova.svl$aov.tab, "svl")
```

Console ~/antigua/Collaborations/Anamarija/Ihor_Pmur_performance/

```
> pca.all <- prcomp(na.exclude(morfo))
> summary(pca.all)
Importance of components%s:
                          PC1    PC2    PC3     PC4     PC5     PC6     PC7     PC8     PC9
Standard deviation     0.1870 0.1603 0.1057 0.05233 0.04996 0.04270 0.03513 0.02771 0.02634
Proportion of Variance 0.4284 0.3150 0.1369 0.03356 0.03060 0.02235 0.01513 0.00941 0.00851
Cumulative Proportion  0.4284 0.7435 0.8804 0.91401 0.94461 0.96696 0.98208 0.99149 1.00000
> pcscores.all <- pca.all$x
> cor(na.exclude(morfo), pcscores.all)
             PC1       PC2         PC3         PC4          PC5          PC6         PC7         PC8
SVL -0.507512580 0.7252314 -0.06247276  0.02288562  0.175410276 -0.077681479  0.39359948 -0.13038104
TRL -0.942100718 0.3259448 -0.04096824 -0.01379322 -0.033202692  0.016385304 -0.04630923  0.02101759
HL   0.367282513 0.7499058  0.20553368  0.35167788 -0.007140944  0.342043931  0.03276189  0.11368818
PL   0.559174034 0.7508861  0.03666573  0.15321935 -0.032564539 -0.001253206 -0.01578704 -0.10349012
HW   0.272749614 0.8329139  0.25009102  0.03174392 -0.172487364 -0.060898072 -0.20645102 -0.25420143
HH   0.461194698 0.6398853 -0.55844543 -0.22247724  0.102591945  0.054118985 -0.04134039  0.03304121
MO   0.396124557 0.7708708  0.06081712  0.13913139 -0.146695719 -0.411564179  0.01346900  0.18326533
FLL -0.005189254 0.3244603  0.79092247 -0.09955578  0.492604005 -0.059336451 -0.10870655  0.03428554
HLL  0.250947242 0.3597267  0.71167771 -0.42784348 -0.299252843  0.109741611  0.11621836  0.04784663
             PC9
SVL -0.057626610
TRL  0.019503295
HL  -0.076026470
PL   0.294367853
```



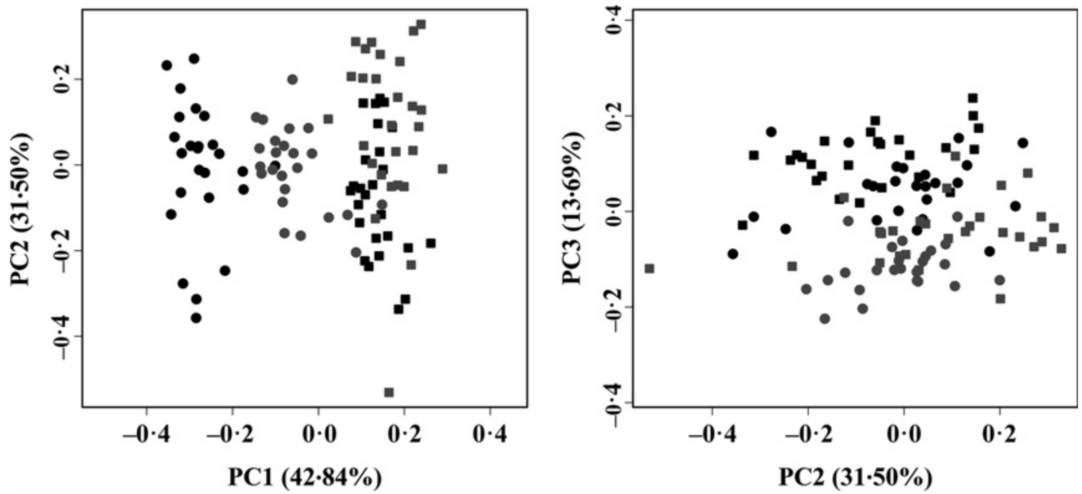


Fig. 2. Variation across species and sexes in morphological traits represented as principal component scores. Black: *Iberolacerta horvati*, grey: *Podarcis muralis*, circles: females, squares: males.

Table 1. Variance explained by the three principal component axes (% exp.) and correlations of each to the measured morphological traits

	PC1	PC2	PC3
% exp.	0·428	0·315	0·137
SVL	**−0·508**	**0·725**	−0·062
TRL	**−0·942**	0·326	−0·041
HL	0·367	**0·750**	0·206
PL	**0·559**	**0·751**	0·037
HW	0·273	**0·833**	0·250
HH	0·461	**0·640**	**−0·558**
MO	0·396	**0·771**	0·061
FLL	−0·005	0·324	**0·791**
HLL	0·251	0·360	**0·712**

Correlations >0·5 are highlighted in bold.
SVL, snout-vent length; TRL, trunk length; HL, head length; PL, pileus length; HW, head width; HH, head height; FLL, fore limb length; HLL, hind limb length; MO, mouth opening.

absolute terms and relative to body size (Table 4). Remarkably, the interaction between species and sex was also significant in this case, where climbing speed differed between sexes in *I. horvathi*, but not in *P. muralis*. This resulted in a pattern where females of *I. horvathi* exhibited lower climbing speeds than respective males, or individuals of *P. muralis* of either sex (Fig. 4).

The observed variation across groups in whole-organism performance was in part attributable to their morphological differences. Interestingly, though, differences across species and sexes in biting and climbing performance remained after accounting for variation in head size and body size, respectively. As revealed by partial least squares analysis, once size effects are taken into account, there was still a significant association between morphology and performance. Specifically, we found a significant PLS vector of association between size-corrected bite force and relative head dimensions (r_{PLS} = 0·42, P = 0·002). This association

Go to file/function | Addins | Project: (None)

02. PCM data preparation.R | 5.3. Showcase.R* | data

Source on Save | Run | Source

```r
#### AN(C)OVAs - morfo ####
library(vegan)
anova.svl <- adonis(morfo[,1]~sp*sex, method="euclidean")
anovas <- cbind(anova.svl$aov.tab, "svl")
colnames(anovas)[7] <- "VAR"
anova.HS <- cbind(adonis(HS~morfo[,1]*sp*sex, method="euclidean")$aov.tab, "HS")
colnames(anova.HS)[7] <- "VAR"
anovas <- rbind(anovas, anova.HS)

for(i in 8:9){
  temp <- cbind(adonis(morfo[,i]~morfo[,1]*sp*sex, method="euclidean")$aov.tab,
                colnames(morfo)[i])
  colnames(temp)[7] <- "VAR"
  anovas <- rbind(anovas, temp)
}

for(i in 3:7){
  temp <- cbind(adonis(morfo[,i]~HS*sp*sex, method="euclidean")$aov.tab,
                colnames(morfo)[i])
  colnames(temp)[7] <- "VAR"
  anovas <- rbind(anovas, temp)
}
anovas
#write.table(anovas, "SEP2015/anovas.morpho.txt", sep=",")
```

102:1 | AN(C)OVAs - morfo | R Script

Console ~/antigua/Collaborations/Anamarija/Ihor_Pmur_performance/

```
> anovas
                 Df   SumsOfSqs     MeanSqs     F.Model           R2 Pr(>F) VAR
sp                1 3.287867e-03 3.287867e-03 8.523468e-01 6.332737e-03  0.377 svl
sex               1 1.265840e-01 1.265840e-01 3.281564e+01 2.438125e-01  0.001 svl
sp:sex            1 7.428423e-03 7.428423e-03 1.925745e+00 1.430784e-02  0.151 svl
Residuals        99 3.818854e-01 3.857429e-03           NA 7.355469e-01     NA svl
Total           102 5.191857e-01           NA           NA 1.000000e+00     NA svl
morfo[, 1]        1 6.243015e-02 6.243015e-02 4.811662e+01 1.085307e-01  0.001  HS
sp1               1 1.458960e-01 1.458960e-01 1.124460e+02 2.536305e-01  0.001  HS
sex1              1 2.338146e-01 2.338146e-01 1.802073e+02 4.064711e-01  0.001  HS
morfo[, 1]:sp     1 2.096372e-03 2.096372e-03 1.615731e+00 3.644404e-03  0.224  HS
morfo[, 1]:sex    1 1.315522e-03 1.315522e-03 1.013908e+00 2.286947e-03  0.327  HS
sp:sex1           1 4.941690e-05 4.941690e-05 3.808696e-02 8.590800e-05  0.847  HS
morfo[, 1]:sp:sex 1 6.368269e-03 6.368269e-03 4.908199e+00 1.107081e-02  0.026  HS
Residuals1       95 1.232602e-01 1.297476e-03           NA 2.142797e-01     NA  HS
Total1          102 5.752306e-01           NA           NA 1.000000e+00     NA  HS
morfo[, 1]1       1 3.089240e-02 3.089240e-02 1.001095e+01 5.270655e-02  0.002 FLL
sp2               1 1.512556e-01 1.512556e-01 4.901568e+01 2.580622e-01  0.001 FLL
sex2              1 1.053315e-01 1.053315e-01 3.413359e+01 1.797096e-01  0.001 FLL
```

Environment | History

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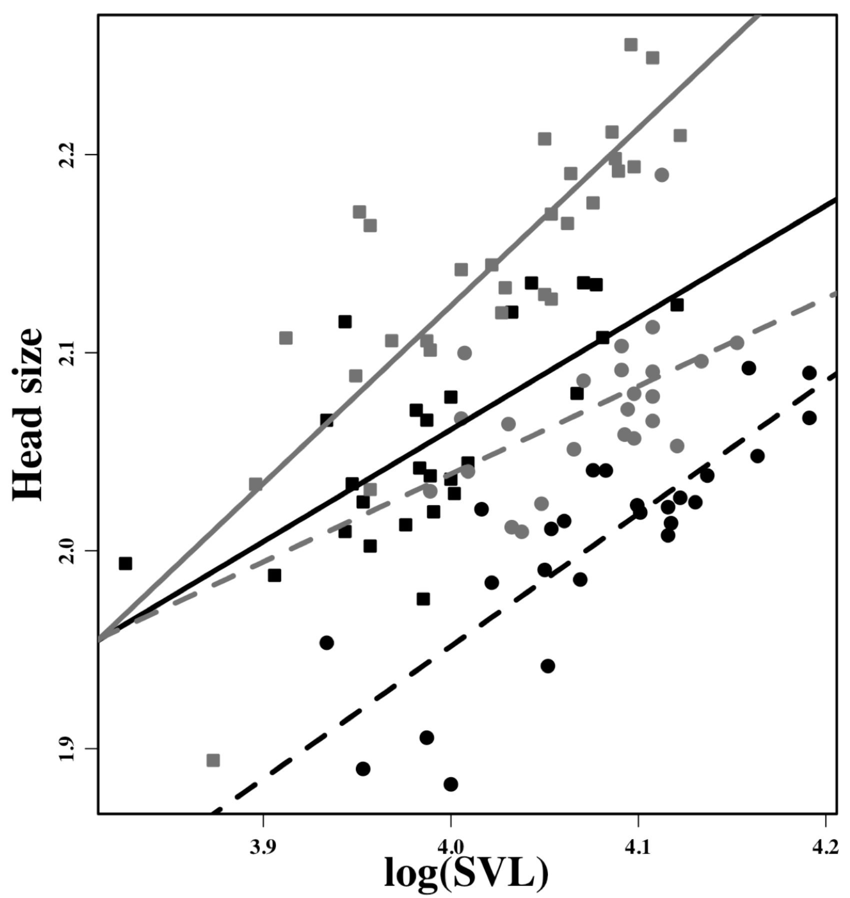


Table 2. Results of AN(C)OVA comparisons on SVL (top), body parts in relation to SVL (middle) and head dimensions relative to head size (bottom), considering the effect of species (sp), sex and their interaction

	SVL		
	d.f.	*F*	*P*
sp	1	0·85	0·362
Sex	1	32·82	**0·001**
sp × sex	1	1·93	0·174
Residuals	99		
Total	102		

		HS		TRL		FLL		HLL	
	d.f.	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
SVL	1	48·12	**0·001**	396·47	**0·001**	10·01	**0·002**	0·59	0·429
sp	1	112·45	**0·001**	57·54	**0·001**	49·02	**0·001**	21·80	**0·001**
Sex	1	180·21	**0·001**	210·35	**0·001**	34·13	**0·001**	65·08	**0·001**
SVL × sp	1	1·62	0·209	7·75	**0·010**	0·02	0·906	0·03	0·882
SVL × sex	1	1·01	0·319	0·06	0·827	1·37	0·247	1·83	0·161
sp × sex	1	0·04	0·859	70·54	**0·001**	0·28	0·588	0·56	0·448
SVL × sp × sex	1	4·91	**0·038**	0·93	0·325	0·11	0·747	0·11	0·753
Residuals	95								
Total	102								

		HL		PL		HW		HH		MO	
	d.f.	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
HS	1	163·94	**0·001**	683·07	**0·001**	487·43	**0·001**	717·13	**0·001**	189·11	**0·001**
sp	1	27·00	**0·001**	6·85	**0·022**	132·67	**0·001**	94·06	**0·001**	8·60	**0·010**
Sex	1	1·58	0·207	30·03	**0·001**	5·33	**0·026**	4·97	**0·038**	1·38	0·243
HS × sp	1	0·13	0·702	2·41	0·122	9·98	**0·003**	10·49	**0·002**	0·16	0·696
HS × sex	1	5·35	**0·020**	0·14	0·725	0·43	0·516	0·49	0·472	2·06	0·167
sp × sex	1	7·45	**0·012**	1·20	0·266	0·95	0·291	0·01	0·928	0·33	0·541
HS × sp × sex	1	3·15	0·075	2·33	0·123	0·01	0·905	0·99	0·331	0·37	0·566
Residuals	95										

Significant effects are marked in bold.

d.f., degrees of freedom; *F*, *F*-statistic; *P*, corresponding *P*-value; PL, pileus length; SVL, snout-vent length; HL, head length; HW, head width; HH, head height; FLL, fore limb length; HLL, hind limb length; TRL, trunk length; HS, head shape; MO, mouth opening.

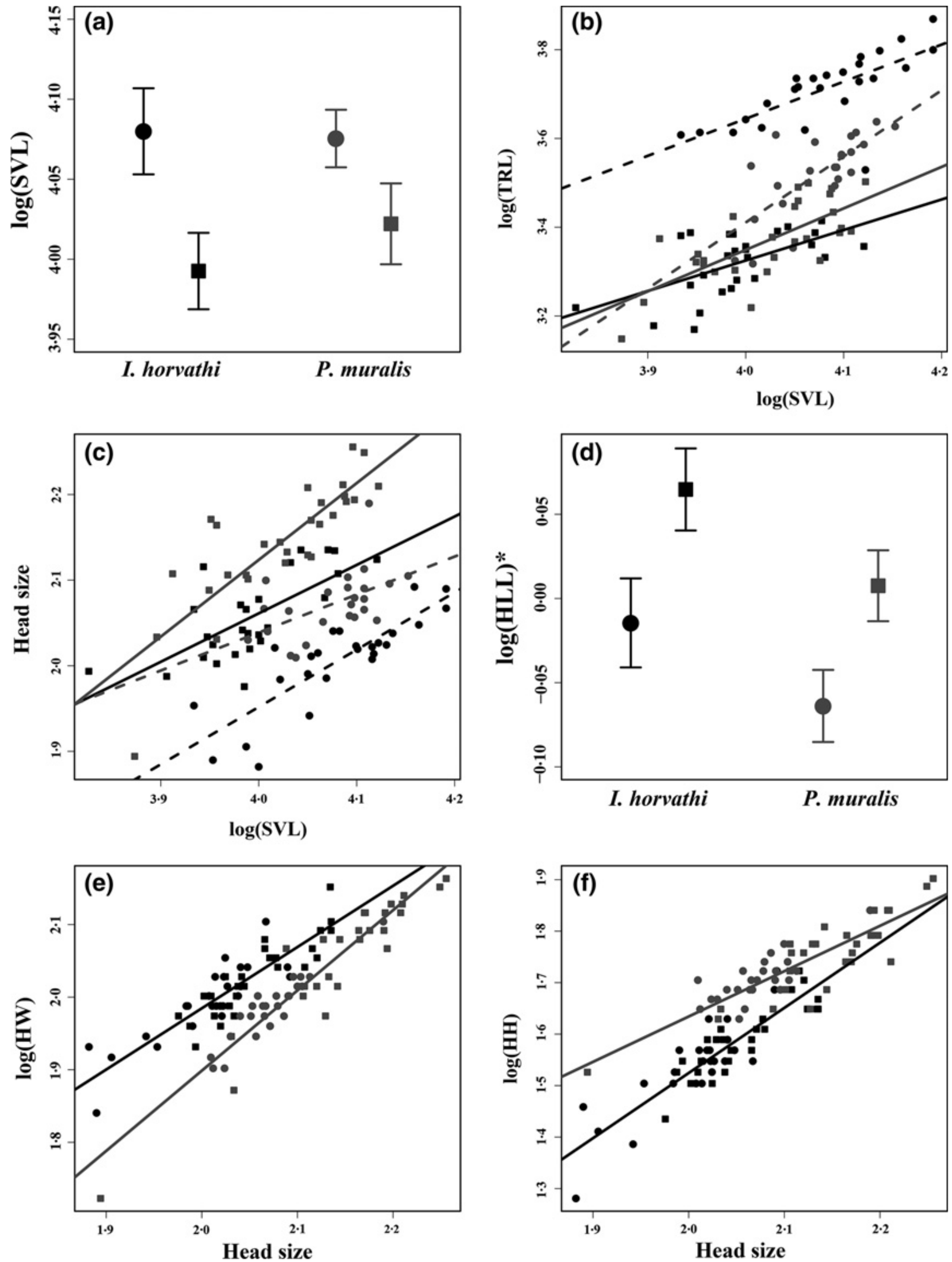
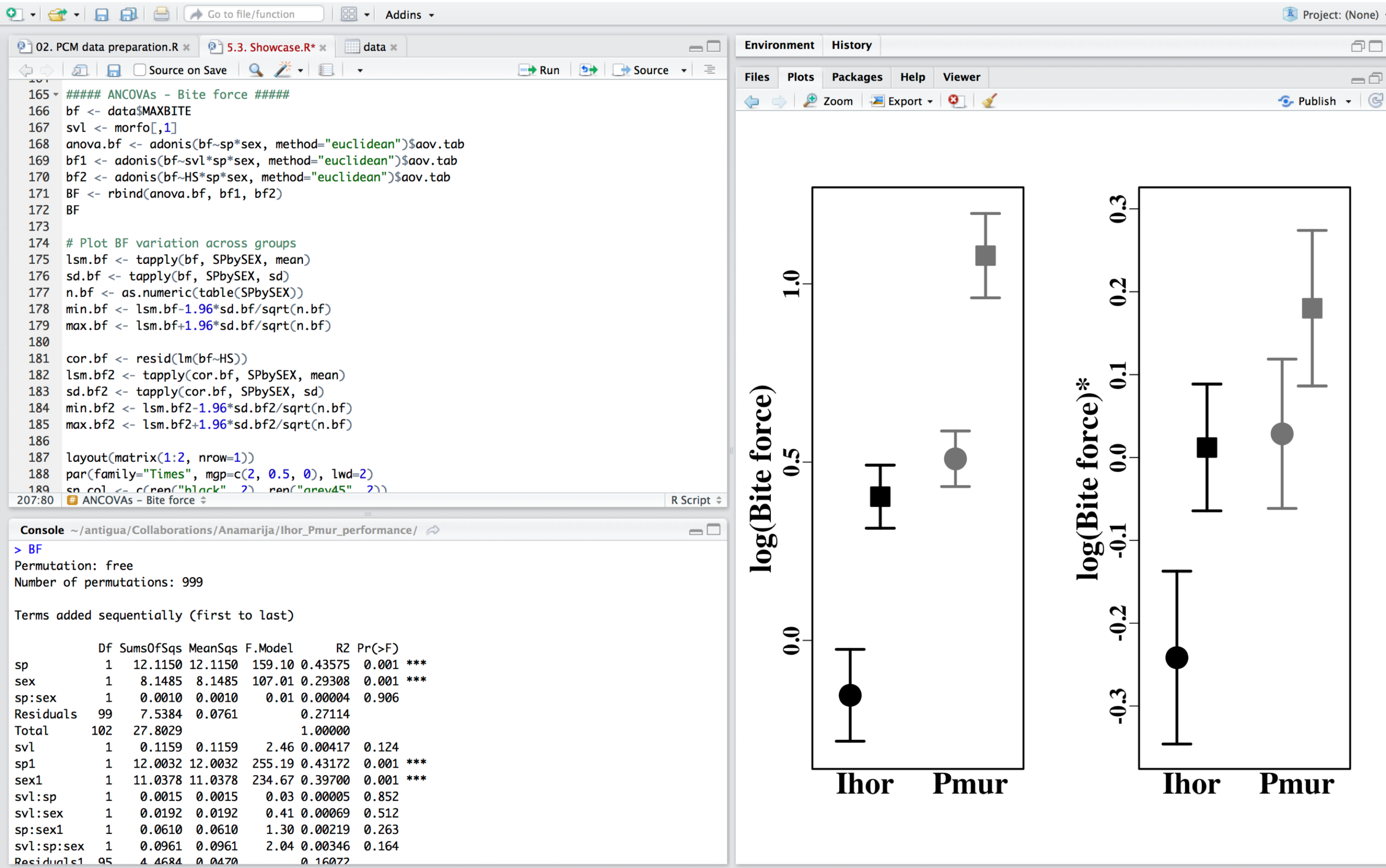


Fig. 3. Variation across species and sexes in morphological traits. (a) Means and 95% confidence intervals for snout-vent length (SVL); (b, c) Relationship of trunk length (TRL) and head size with SVL in different groups; (d) Means and 95% confidence intervals for hind limb length, after correction for SVL effects; (e, f) Relationship of head width (HW) and head height (HH) with head size in different groups; Black: *Iberolacerta horvati*, grey: *Podarcis muralis*, circles: females, squares: males.


Go to file/function
Addins
Project: (None)
02. PCM data preparation.R
5.3. Showcase.R*
data
Source on Save
Run
Source
165 ##### ANCOVAs - Bite force #####
166 bf <- data$MAXBITE
167 svl <- morfo[,1]
168 anova.bf <- adonis(bf~sp*sex, method="euclidean")$aov.tab
169 bf1 <- adonis(bf~svl*sp*sex, method="euclidean")$aov.tab
170 bf2 <- adonis(bf~HS*sp*sex, method="euclidean")$aov.tab
171 BF <- rbind(anova.bf, bf1, bf2)
172 BF
174 # Plot BF variation across groups
175 lsm.bf <- tapply(bf, SPbySEX, mean)
176 sd.bf <- tapply(bf, SPbySEX, sd)
177 n.bf <- as.numeric(table(SPbySEX))
178 min.bf <- lsm.bf-1.96*sd.bf/sqrt(n.bf)
179 max.bf <- lsm.bf+1.96*sd.bf/sqrt(n.bf)
181 cor.bf <- resid(lm(bf~HS))
182 lsm.bf2 <- tapply(cor.bf, SPbySEX, mean)
183 sd.bf2 <- tapply(cor.bf, SPbySEX, sd)
184 min.bf2 <- lsm.bf2-1.96*sd.bf2/sqrt(n.bf)
185 max.bf2 <- lsm.bf2+1.96*sd.bf2/sqrt(n.bf)
187 layout(matrix(1:2, nrow=1))
188 par(family="Times", mgp=c(2, 0.5, 0), lwd=2)
207:80
ANCOVAs - Bite force
R Script
Console ~/antigua/Collaborations/Anamarija/Ihor_Pmur_performance/
> BF
Permutation: free
Number of permutations: 999
Terms added sequentially (first to last)
Df SumsOfSqs MeanSqs F.Model R2 Pr(>F)
sp 1 12.1150 12.1150 159.10 0.43575 0.001 ***
sex 1 8.1485 8.1485 107.01 0.29308 0.001 ***
sp:sex 1 0.0010 0.0010 0.01 0.00004 0.906
Residuals 99 7.5384 0.0761 0.27114
Total 102 27.8029 1.00000
svl 1 0.1159 0.1159 2.46 0.00417 0.124
sp1 1 12.0032 12.0032 255.19 0.43172 0.001 ***
sex1 1 11.0378 11.0378 234.67 0.39700 0.001 ***
svl:sp 1 0.0015 0.0015 0.03 0.00005 0.852
svl:sex 1 0.0192 0.0192 0.41 0.00069 0.512
sp:sex1 1 0.0610 0.0610 1.30 0.00219 0.263
svl:sp:sex 1 0.0961 0.0961 2.04 0.00346 0.164
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log(Bite force)
0.0
0.5
1.0
Ihor
Pmur
log(Bite force)*
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
Ihor
Pmur

Table 3. Results of AN(C)OVA comparisons on bite force considering the effect of species (sp), sex and their interaction, using SVL (middle) or head size (bottom) as a covariate

	BITE FORCE		
	d.f.	*F*	*P*
sp	1	159·10	**0·001**
Sex	1	107·01	**0·001**
sp × sex	1	0·01	0·906
Residuals	99		
Total	102		
	d.f.	*F*	*P*
SVL	1	2·46	0·116
sp	1	255·19	**0·001**
sex	1	234·67	**0·001**
SVL × sp	1	0·03	0·874
SVL × sex	1	0·41	0·545
sp × sex	1	1·30	0·266
SVL × sp × sex	1	2·04	0·161
Residuals	95		
Total	102		
	d.f.	*F*	*P*
HS	1	510·54	**0·001**
sp	1	45·53	**0·001**
Sex	1	62·65	**0·001**
HS × sp	1	0·76	0·421
HS × sex	1	0·03	0·880
sp × sex	1	0·20	0·652
HS × sp × sex	1	1·43	0·233
Residuals	95		
Total	102		

Significant effects are marked in bold.
d.f., degrees of freedom; *F*, *F*-statistic; *P*, corresponding *P*-value; SVL, snout-vent length; HS, head shape.

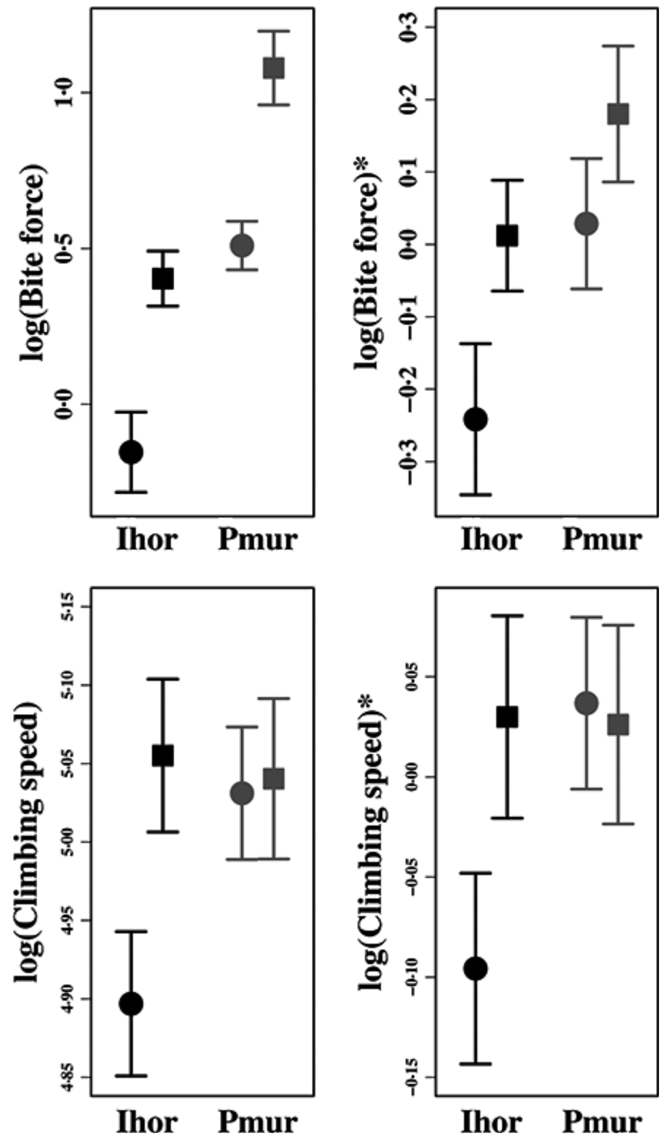

Fig. 4. Variation across species and sexes in bite force (top) and climbing speed (bottom) before (left) and after (right) correction for effects of the covariate (head size in the case of bite force and snout-vent length in the case of climbing speed). Black: *Iberolacerta horvati*, grey: *Podarcis muralis*, circles: females, squares: males.

locomotor abilities, i.e. negatively influence the climbing speed. Ecological implication of lower performance in climbing ability is that it may lower anti-predator escape abilities on steep surfaces, but on the other hand allow

Go to file/function | Addins | Project: (None)

02. PCM data preparation.R | 5.3. Showcase.R | data

Source on Save | Run | Source

```r
##### BF and head shape #####
source("pls.AK.R")
head <- NULL
for (i in 3:7){
  temp <- resid(lm(morfo[,i]~HS))
  head <- cbind(head, temp)
}
colnames(head) <- colnames(morfo)[3:7]

pls.bf <- pls.AK(head, cor.bf)
pls.bf$obs.cor; pls.bf$p.perm

corsX <- cor(head, pls.bf$Xscores)
corsX

# Plot
layout(matrix(1:2, nrow=2, byrow=T), heights=c(3.5, 1.5))

par(family="Times", mgp=c(0.5, 0, 0), pin=c(4.25, 4.25), lwd=2, xpd=T)
plot(pls.bf$Yscores~pls.bf$Xscores, pch=ind.symb, bg=ind.col, col=ind.col,
     cex=1.25, xlab="PLS Scores - Head shape", ylab="PLS Scores - Bite force",
     cex.lab=1.75, font.lab=2, xaxt="n", yaxt="n", lwd=2)

par(mgp=c(2, 0.5, 0), mar=c(3, 8, 1, 8)+0.1)
barplot(corsX, horiz=T, beside=T, space=0.2, names.arg=rownames(corsX),family="Times",
```

234:1 | BF and head shape | R Script

Console ~/antigua/Courses/BIODIV/2017-2018/Intro2R/AK lectures/5.3. Showcase/

```
[1] 0.001
> corsX <- cor(head, pls.bf$Xscores)
> corsX
          [,1]
HL -0.46598734
PL  0.02892826
HW -0.95794757
HH  0.69719805
MO -0.38029298
> layout(matrix(1:2, nrow=2, byrow=T), heights=c(3.5, 1.5))
> par(family="Times", mgp=c(0.5, 0, 0), pin=c(4.25, 4.25), lwd=2, xpd=T)
> plot(pls.bf$Yscores~pls.bf$Xscores, pch=ind.symb, bg=ind.col, col=ind.col,
+      cex=1.25, xlab="PLS Scores - Head shape", ylab="PLS Scores - Bite force",
+      cex.lab=1.75, font.lab=2, xaxt="n", yaxt="n", lwd=2)
> par(mgp=c(2, 0.5, 0), mar=c(3, 8, 1, 8)+0.1)
> barplot(corsX, horiz=T, beside=T, space=0.2, names.arg=rownames(corsX),family="Times",
+         font=2, lwd=2, xlim=c(-1, 1), col="snow3", las=1, cex.axis=1, cex.names=1.25,
+         xlab="Correlations with variables", cex.lab=1.5, font.lab=2, bg="transparent")
>
```

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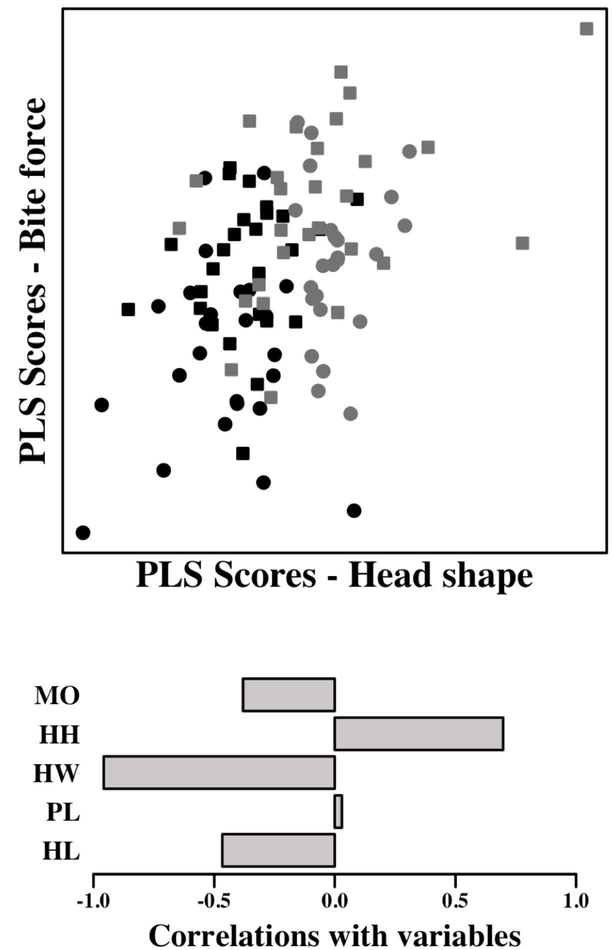

STATISTICAL ANALYSIS

To obtain a general view of morphological variation in our dataset we first performed a principal components analysis (PCA) of all morphological measurements (Klingenberg & Monteiro 2005; Mitteroecker & Bookstein 2011). To examine whether both species differed in their morphological properties and in whole-organism performance traits, we first conducted AN(C)OVA comparisons with species, sex and their interaction as categorical predictors. Two-way ANOVA comparisons were conducted in the case of total body size, as represented by SVL. To examine variation across both species and sexes in relative head size, TRL and fore and hind limb length, we performed ANCOVA comparisons using SVL as the covariate. Furthermore, we examined differences across species × sex groups in relative head dimensions using ANCOVA comparisons where head size was treated as the covariate. For bite force, we examined AN(C)OVA models with species, sex and their interaction as categorical predictors, and in addition including either SVL or head size as covariates. Finally, to investigate variation across species and sexes in locomotor performance, we performed AN(C)OVA comparisons with or without SVL as a covariate.

To investigate the association between morphological and performance traits, and examine how differences in morphology between species and sexes may translate into differences in whole-organism performance, we used two-block partial least squares (PLS). Specifically, we examined the association of maximal bite force with relative head dimensions, after correcting both blocks of traits for the effect of head size variation. In terms of locomotor performance, we only investigated climbing speed and examined its association to trunk and limb length, after correcting both sets of traits for variation due to SVL. As a measure of the association between blocks of traits we used the Pearson correlation between individual scores of the PLS vectors, and we tested the significance of this association using a permutation procedure with 1000 permutations (Rohlf & Corti 2000).