În drum spre speciație? Studii ecologice și evolutive asupra polimorfismului la vertebrate ectoterme

C.S. III Dr. Alexandru STRUGARIU

Do differential activity patterns and habitat use maintain color polymorphism in vipers from warmer environments?

Coloration

- the result of adaptation to different biotic or abiotic factors.

- Crucial roles in:

- Predator avoidance (through crypsis, mimetism or apposematism)
- Inter and intra-specific communication
- Sexual selection
- Thermoregulation (ectotherms)

Crypsis

Aposematic coloration (left)

and
Batesian mimicry (down)

Colour polymorphism

- the presence of two or more phenotypic morphs in the same population

Melanism

- one of the most well known examples of colour polymorphism in animals, being reported from all vertebrate groups.

Oecologia (Berl.) 43, 99–109 (1979)

Oecologia
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Thermal Biology of the Common Garter Snake *Thamnophis sirtalis* (L.)

II. The Effects of Melanism

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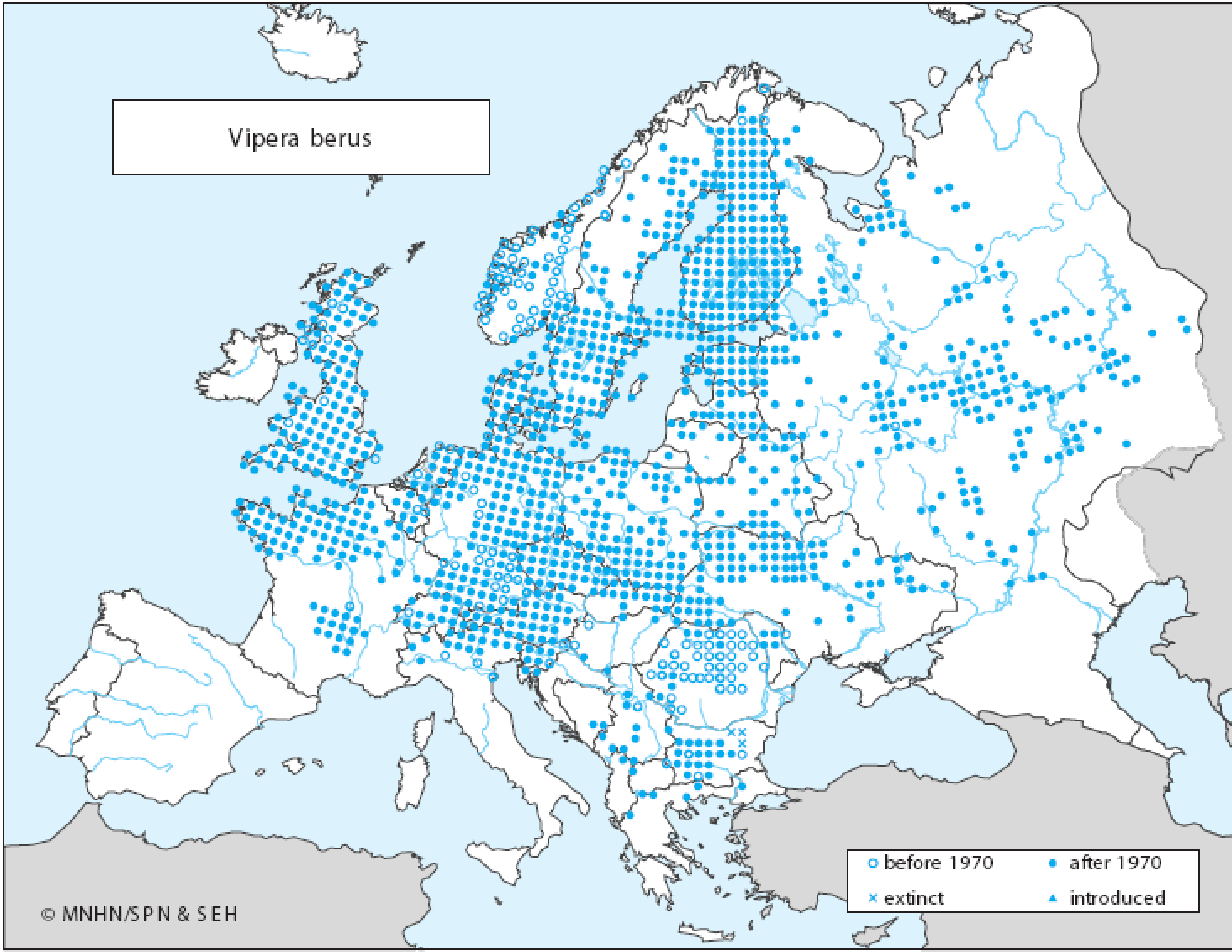
Summary. The thermoregulatory significance of a striped-melanic colour polymorphism in the common garter snake, *Thamnophis sirtalis*, was assessed through a combination of laboratory experimentation and field study. In experiments with living snakes the melanic morph maintained a higher body temperature than the striped morph, when exposed to natural insolation. Experiments with excised skin showed that this thermal advantage is attributable to some integumental difference between the two morphs. Body temperatures of snakes in the field revealed that, during the colder part of the active season, melanics were able to stay warmer than striped snakes by an amount (1.24 C°) approximating the difference observed in the laboratory. Some evidence and argument is presented to suggest that melanism also may confer protection against overheating in warm periods.

European Adder (*Vipera berus*)


www.tomdyring.com

The “coolest” snake in the world

Foto: C. Strugariu (2008)


Vipera berus
before 1970
after 1970
extinct
introduced
© MNHN/SPN & SEH

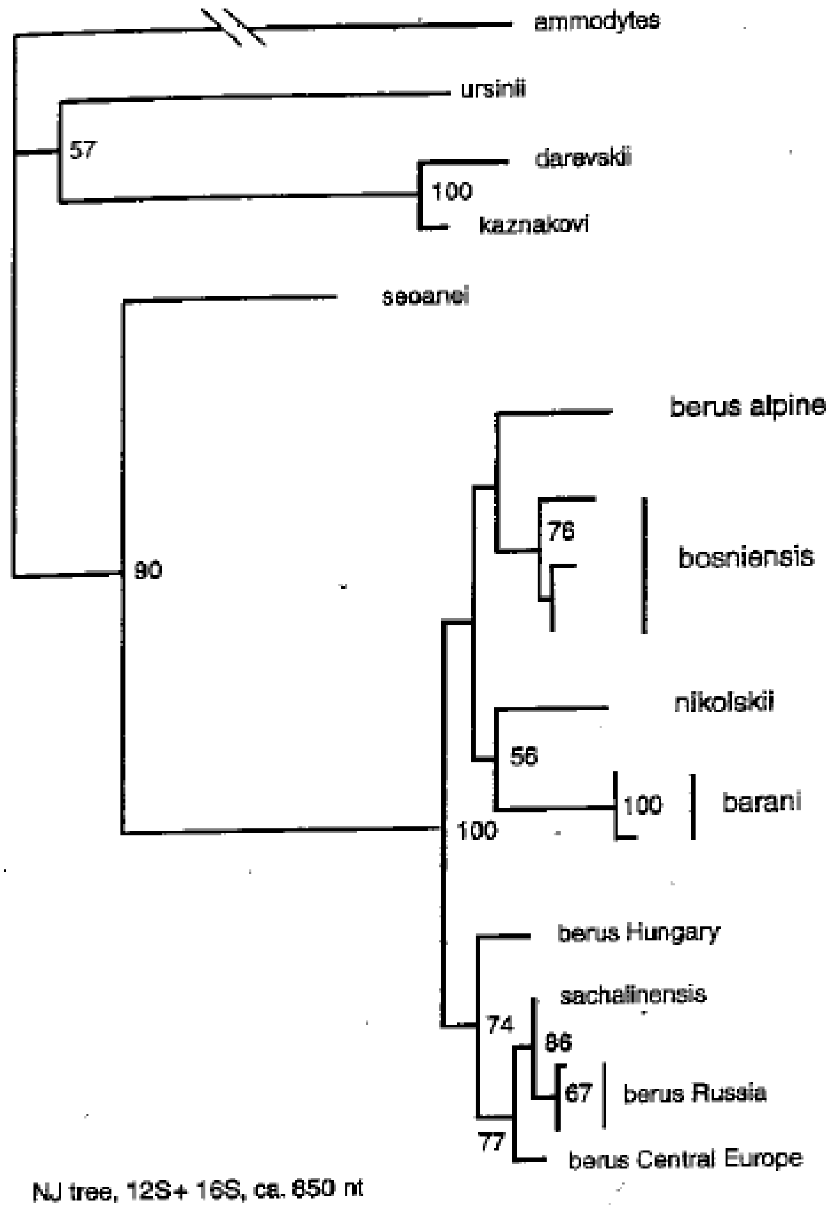


Fig. 3. Neighbor Joining tree of the *Vipera berus* group, derived from DNA sequences of ribosomal 12s and 16s genes (850 NT). Bootstrap values above 50 are indicated.

Neighbor-joining-Baum nach DNA der *Vipera berus*-Gruppe, erstellt nach DNA-Sequenzen der ribosomalen 12s- und 16s-Gene (850 Basenpaare). Bootstrap-Werte über 50 % werden angegeben.

The color morphs

Function of the zig-zag

- Predator avoidance:

-crypsis ?

-aposematism ?

-”flicker fusion” hypothesis ?

Advantages of melanism

- **Superior thermoregulation** – favoured in cooler areas (higher latitudes or altitudes)?
- Superior growth rate
- Larger size -> better reproductive success
- Superior post-partum survival

Foto: A. Strugariu (2009)

Disadvantages of melanism

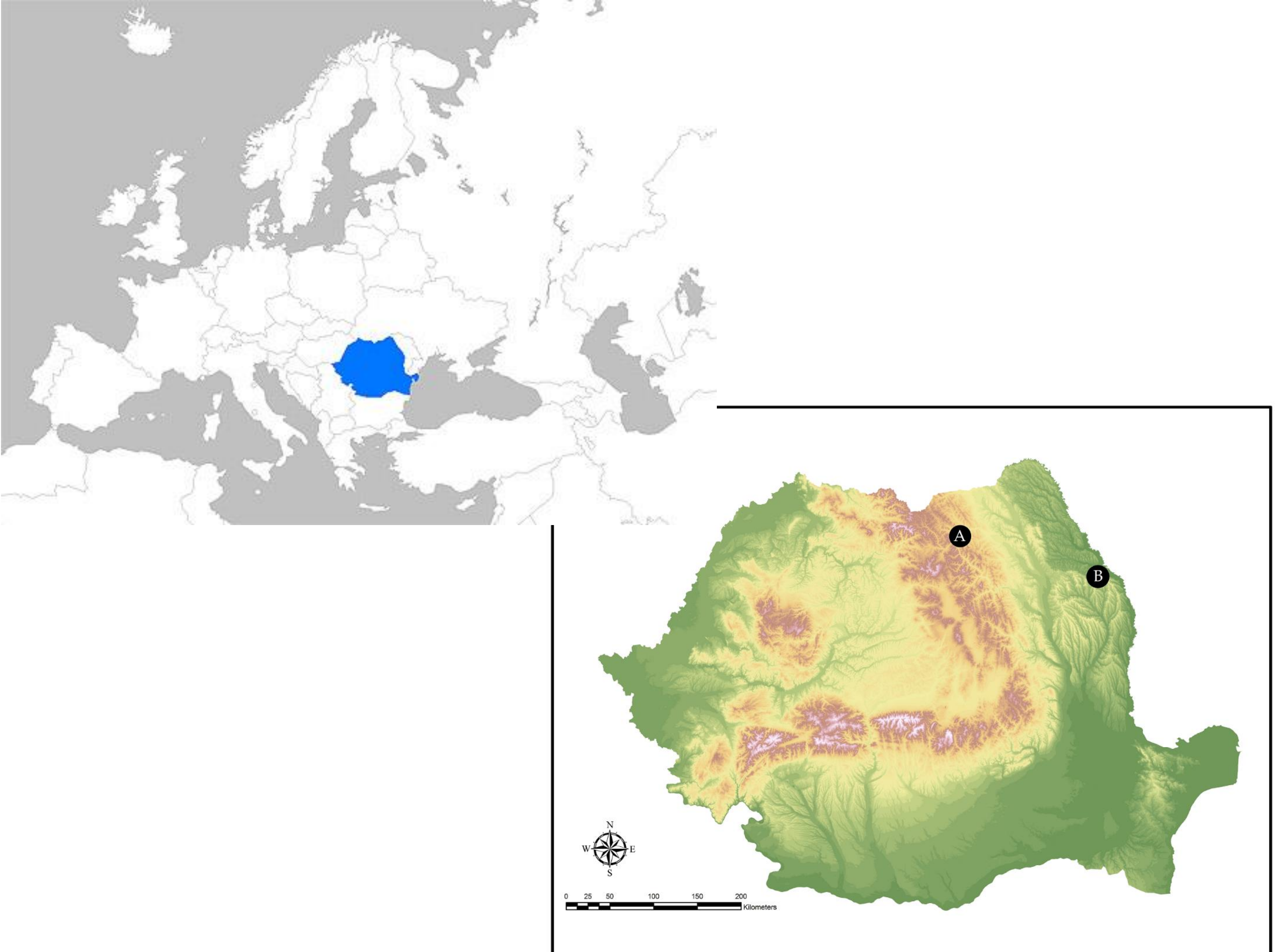
- Higher predation risk.
- Increased mortality in periods with low food availability.

Correlates of colour polymorphism in viper populations from contrasting environments

- Expectations:

- Frequency of melanistic individuals should be higher in the colder, montane environment.

- Ecological advantages should be greater for melanistic individuals in the cold environments, resulting in larger body size and fecundity.


A
B
N
W
E
S
0 25 50 100 150 200
Kilometers

Site A

Site B

Site A.

Melanistic snakes comprised 16% of the population (32% of males and 9% in females; $n = 77$).

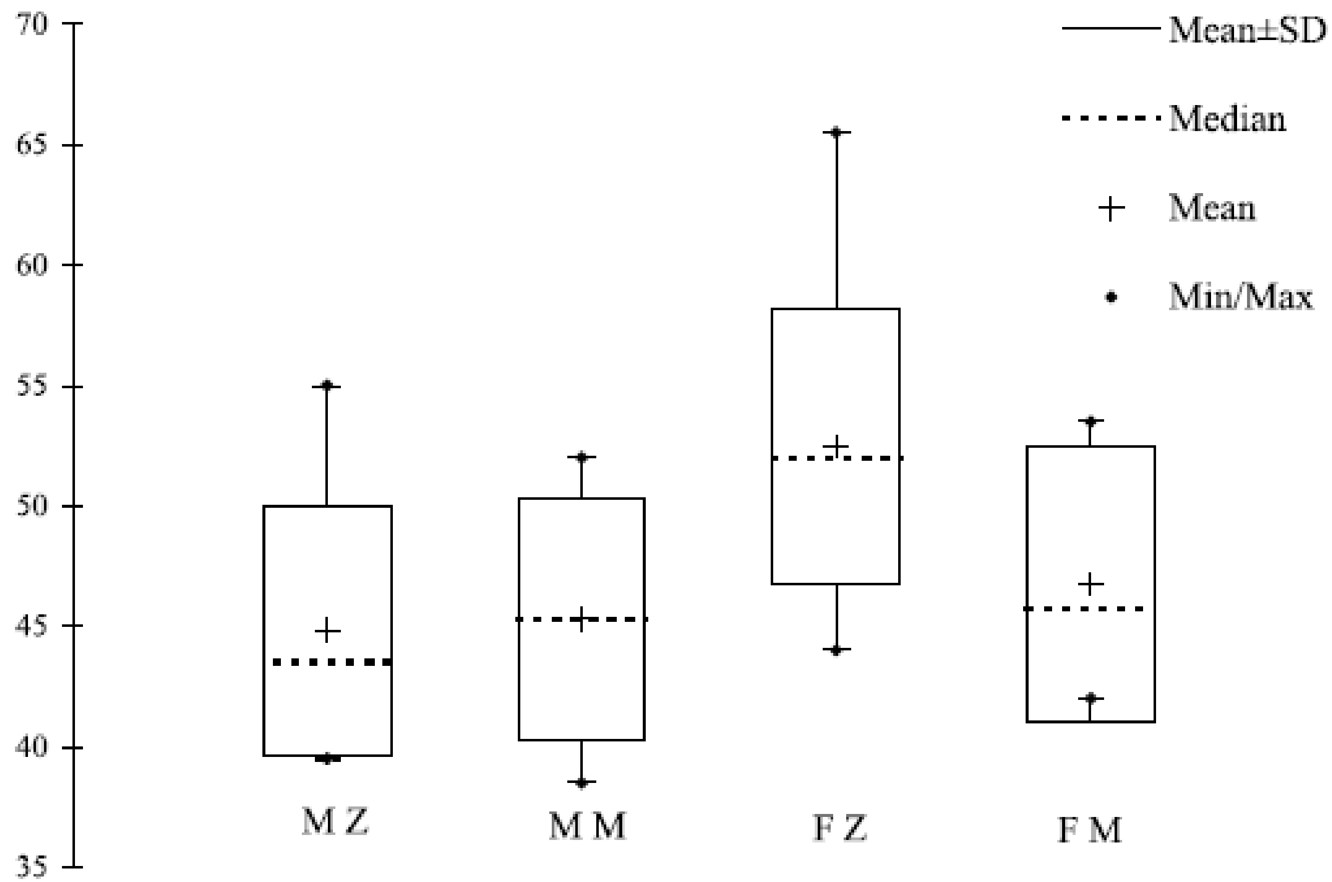


Figure 1. Descriptive statistics of the total lengths of zigzag male (M.Z.; n = 18), melanistic male (M.M.; n = 8), zigzag female (F.Z.; n = 35) and melanistic females (F.M.; n = 4).

Structura pe dimensiuni a populaţiei polimorfice de vipere

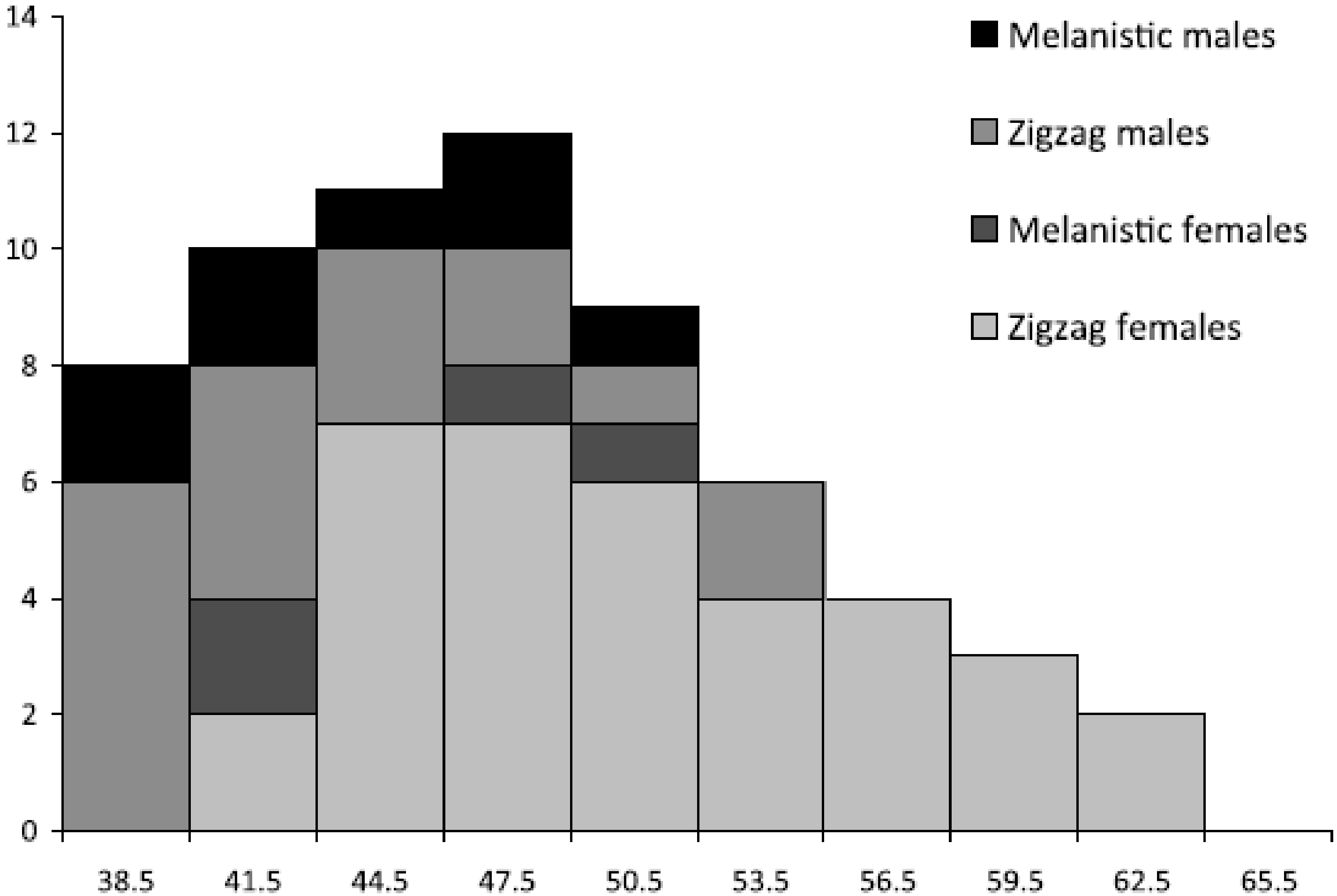
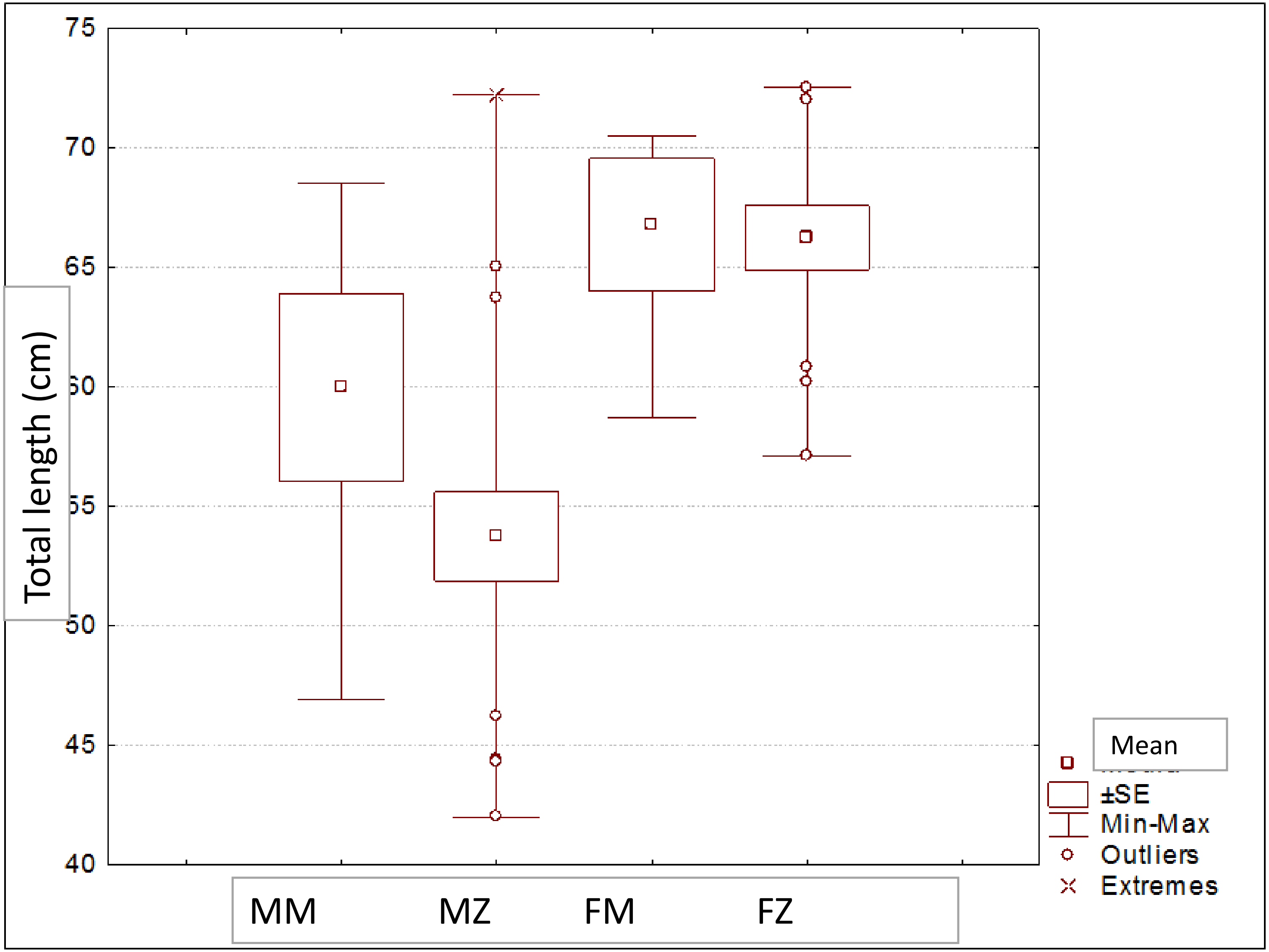


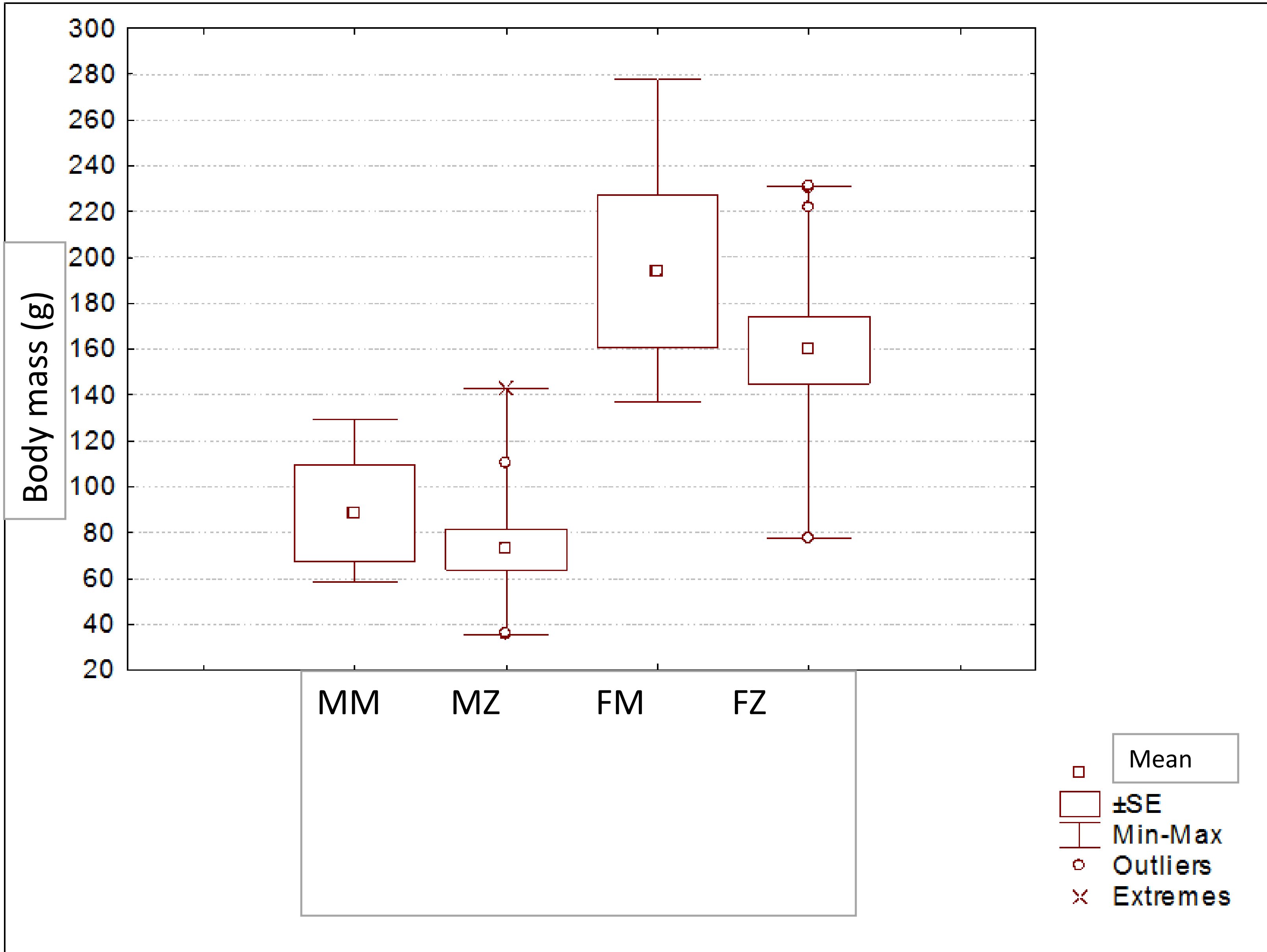
Figure 2. Combined observed size structure of the colour polymorphic adder population (horizontal axis: total length in cm; vertical axis: number of individuals).

Site B.

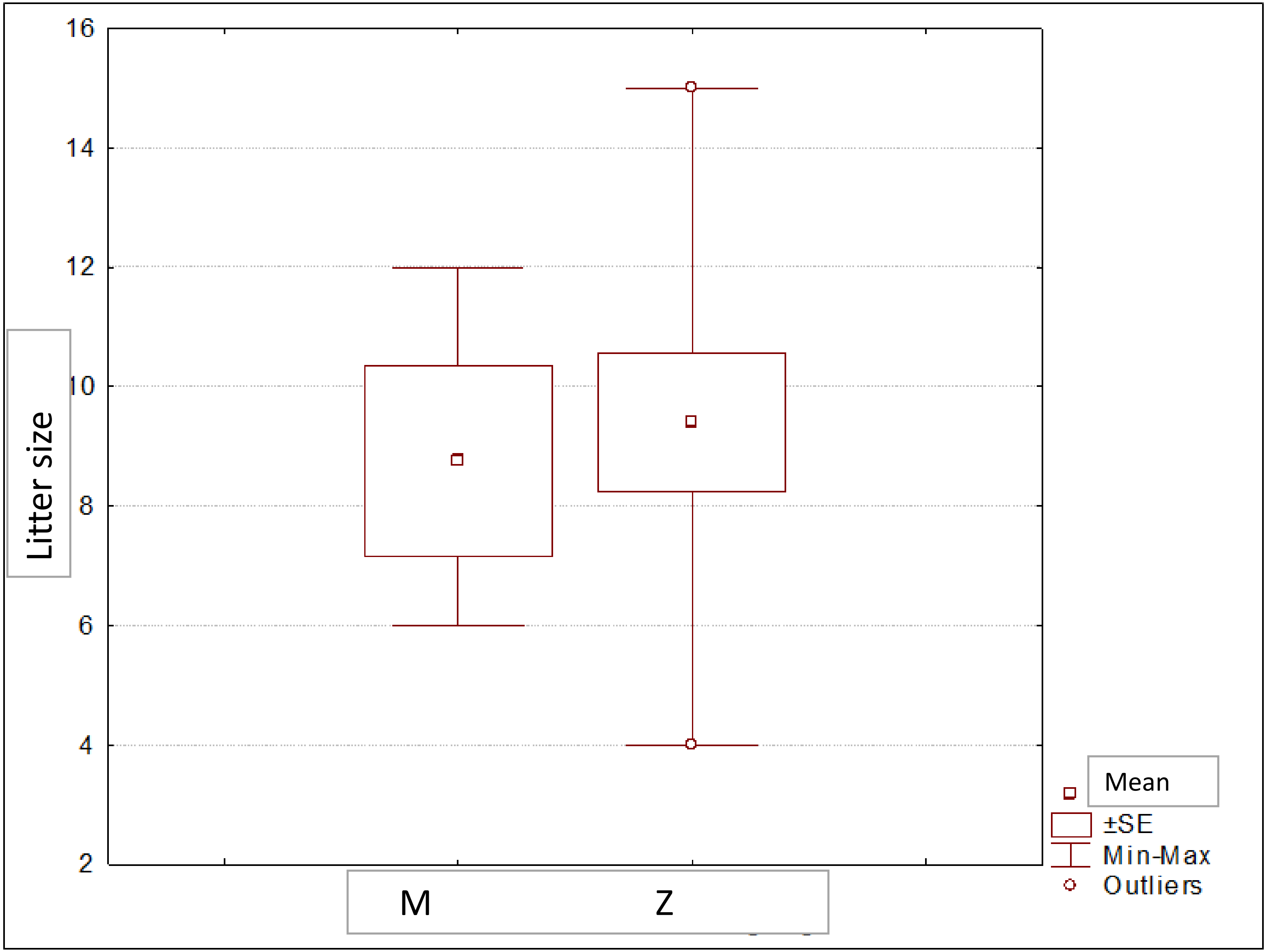
Melanistic snakes comprised 28% of the population, with melanistic females comprising just 17%.



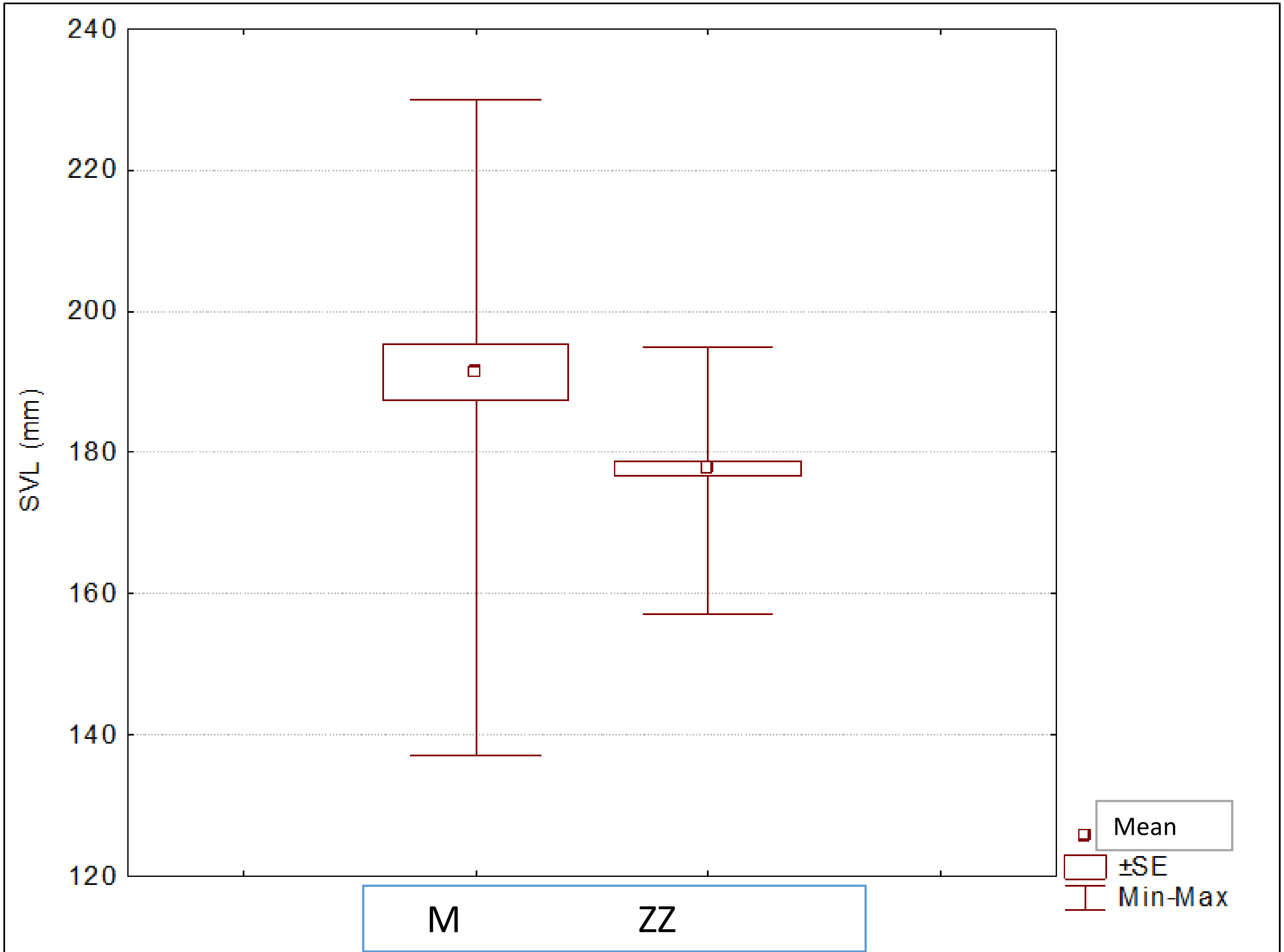
Body mass


300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
Body mass (g)
MM
MZ
FM
FZ
Mean
±SE
Min-Max
Outliers
Extremes

Litter size



Offspring size



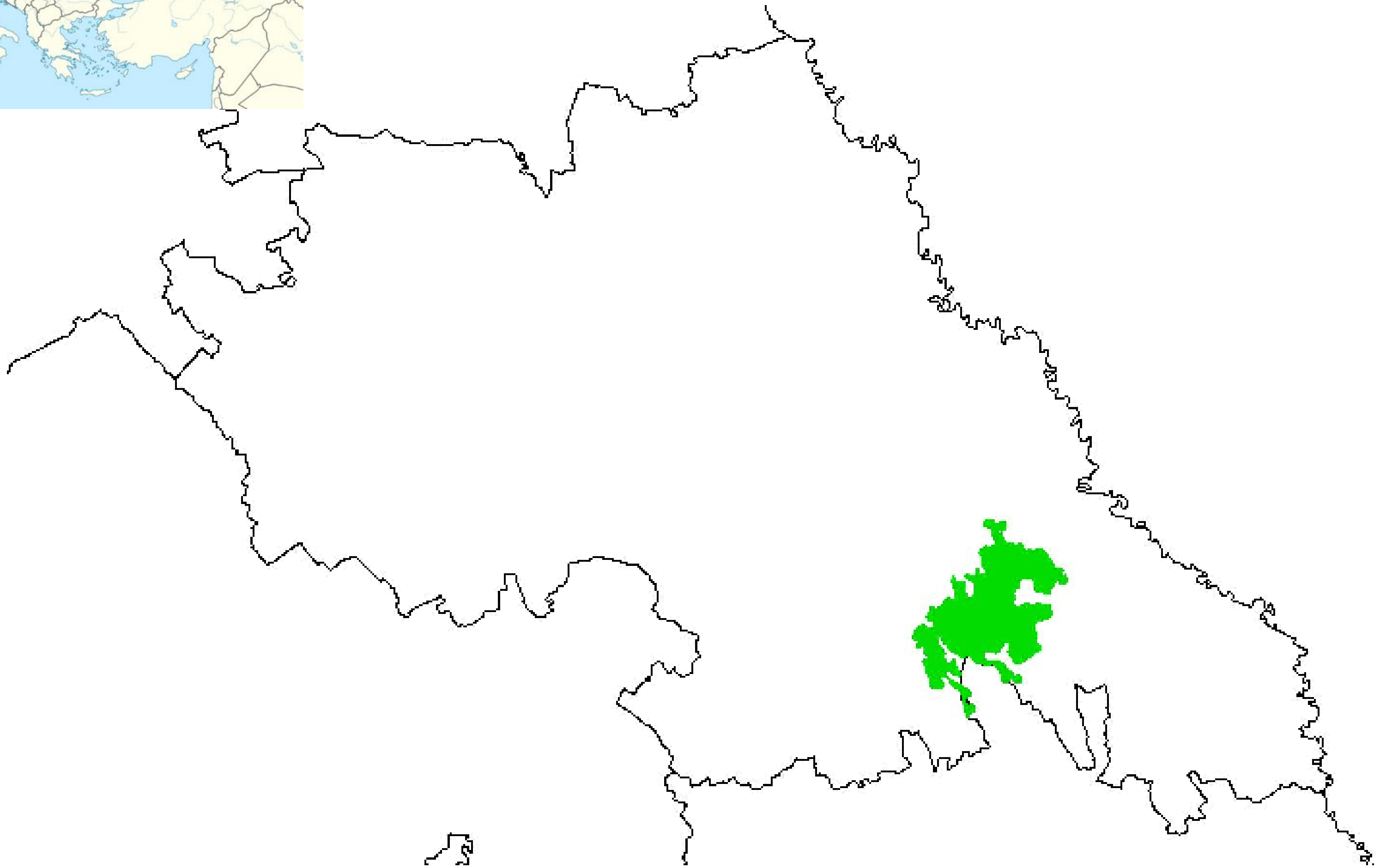
Aim

- We tested the hypothesis that differential habitat use and activity patterns could explain the maintenance of colour polymorphism in viper populations from warmer environment.

- According to the thermal melanism hypothesis, we would expect melanistic vipers to favour less open habitats and/or be more active at cooler temperatures.



Study area



Methods

- Visual field surveys were conducted along random and pre-determined paths during April-2009-May 2016 (usually April-October), on randomly chosen dates.

- We recorded the following biological and ecological variables: sex, age (adult or immature), color morph, time of capture, habitat type (within the forest, forest edge, meadow, or bushes in open areas), substrate type (litter, grass, wood or rocky), microhabitat exposure, weather conditions (clear, cloudy, partly cloudy or rain), behavior (basking, partly hidden, moving, hiding) temperature and relative humidity at substrate level.

- Each viper caught was also marked by scale clipping.

Data Analysis

- Patterns of activity and habitat use were investigated using Correspondence Analysis (CA), Multiple Correspondence Analysis (MCA) - for categorical variables.
- Substrate temperature and relative humidity were compared using two-way ANOVA, with sex and morph as factors.

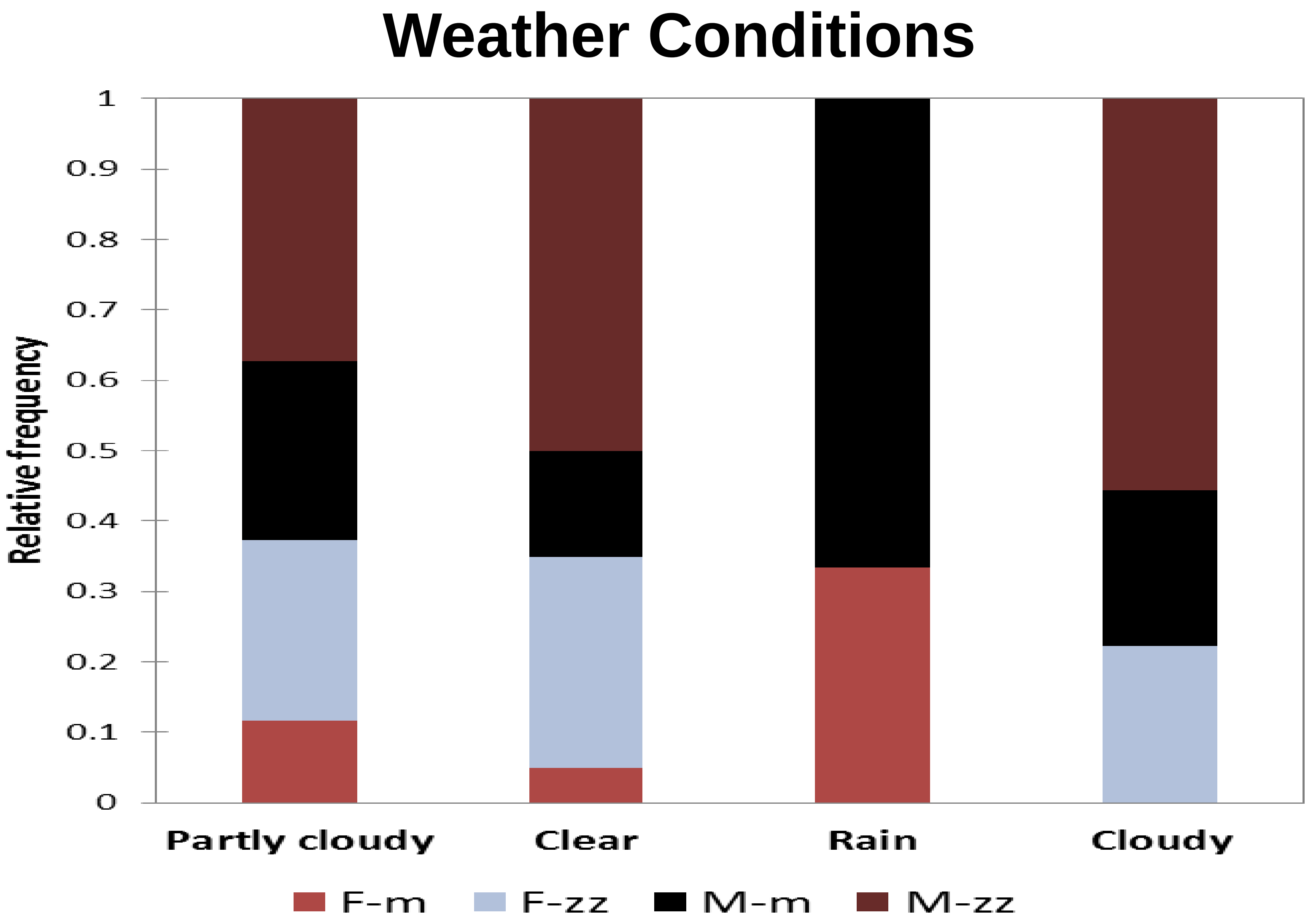
Results

CA: sexes pooled (left) & just females (right)

Morph vs.	χ^2	DF	p
Season	0.095	2	0.953
Time of day	5.991	2	0.375
Exposure	4.743	6	0.577
Substrate	0.731	3	0.866
Habitat	1.913	3	0.591
Weather	8.391	3	0.039*

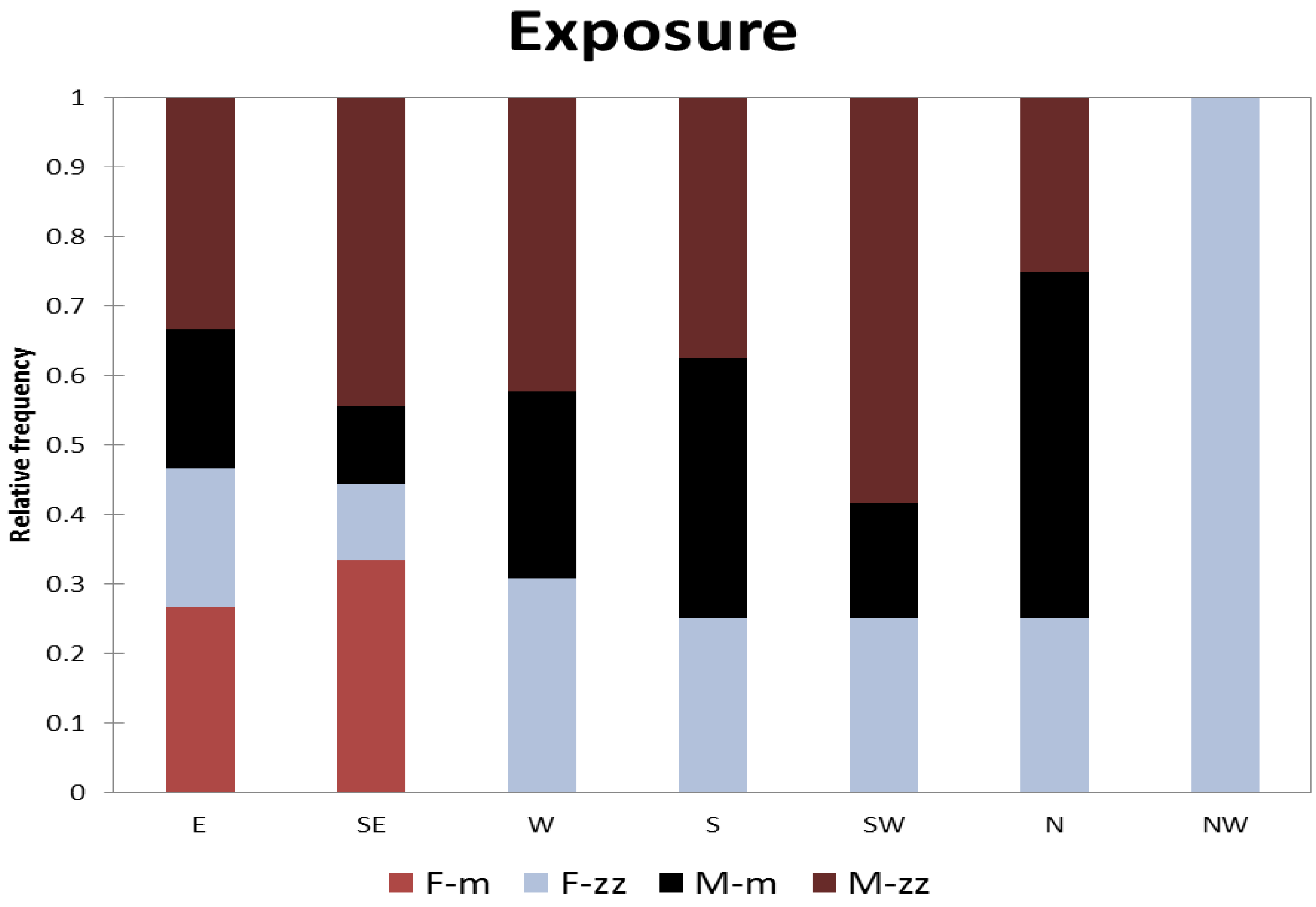
Female Morph vs.	χ^2	DF	p
Season	1.574	2	0.462
Time of day	1.151	2	0.562
Exposure	13.475	6	0.036*
Substrate	1.082	3	0.781
Habitat	1.797	3	0.616
Weather	4.172	3	0.244

Results



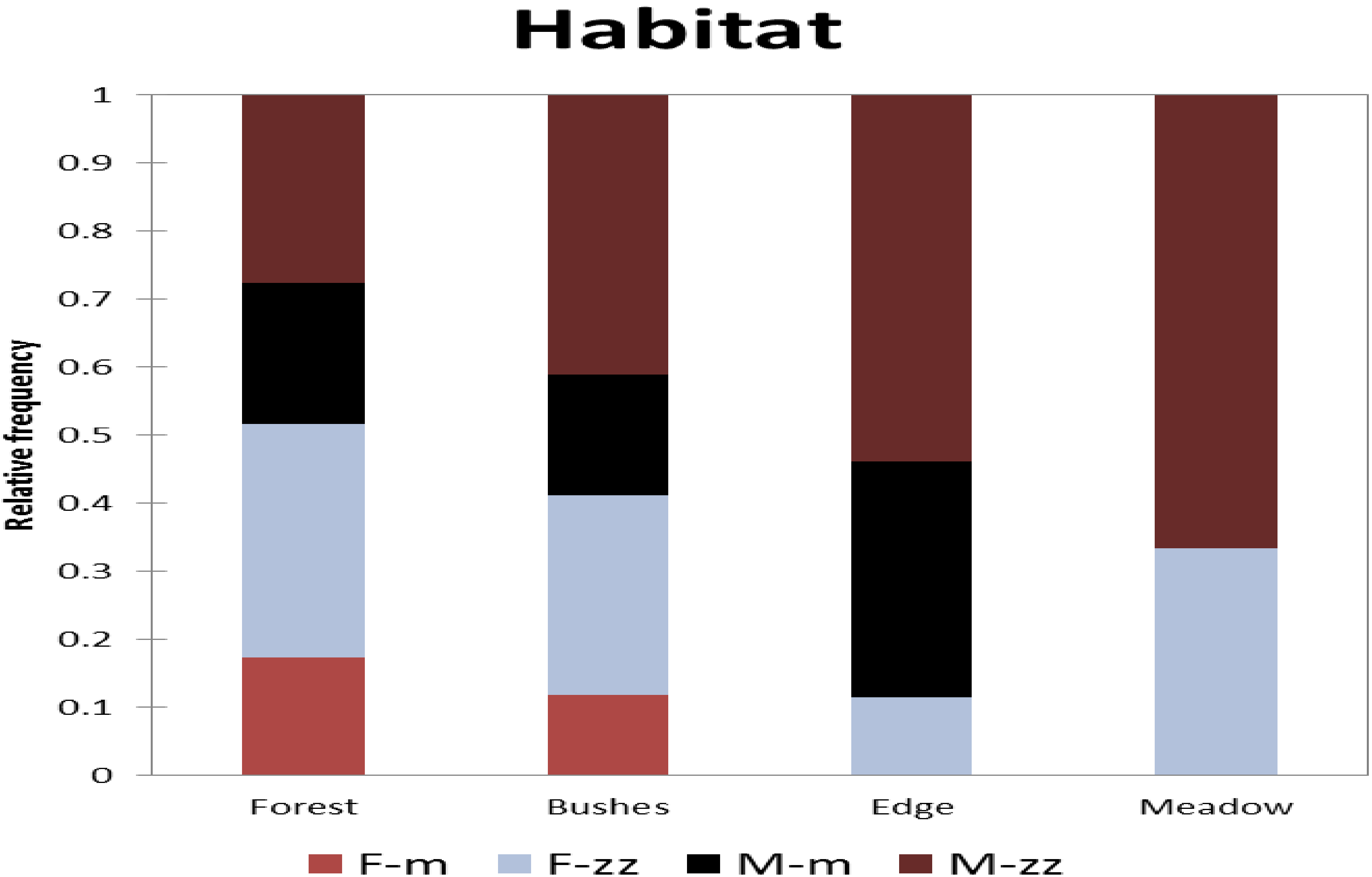
Weather Conditions
Relative frequency
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Partly cloudy
Clear
Rain
Cloudy
F-m
F-zz
M-m
M-zz

Results



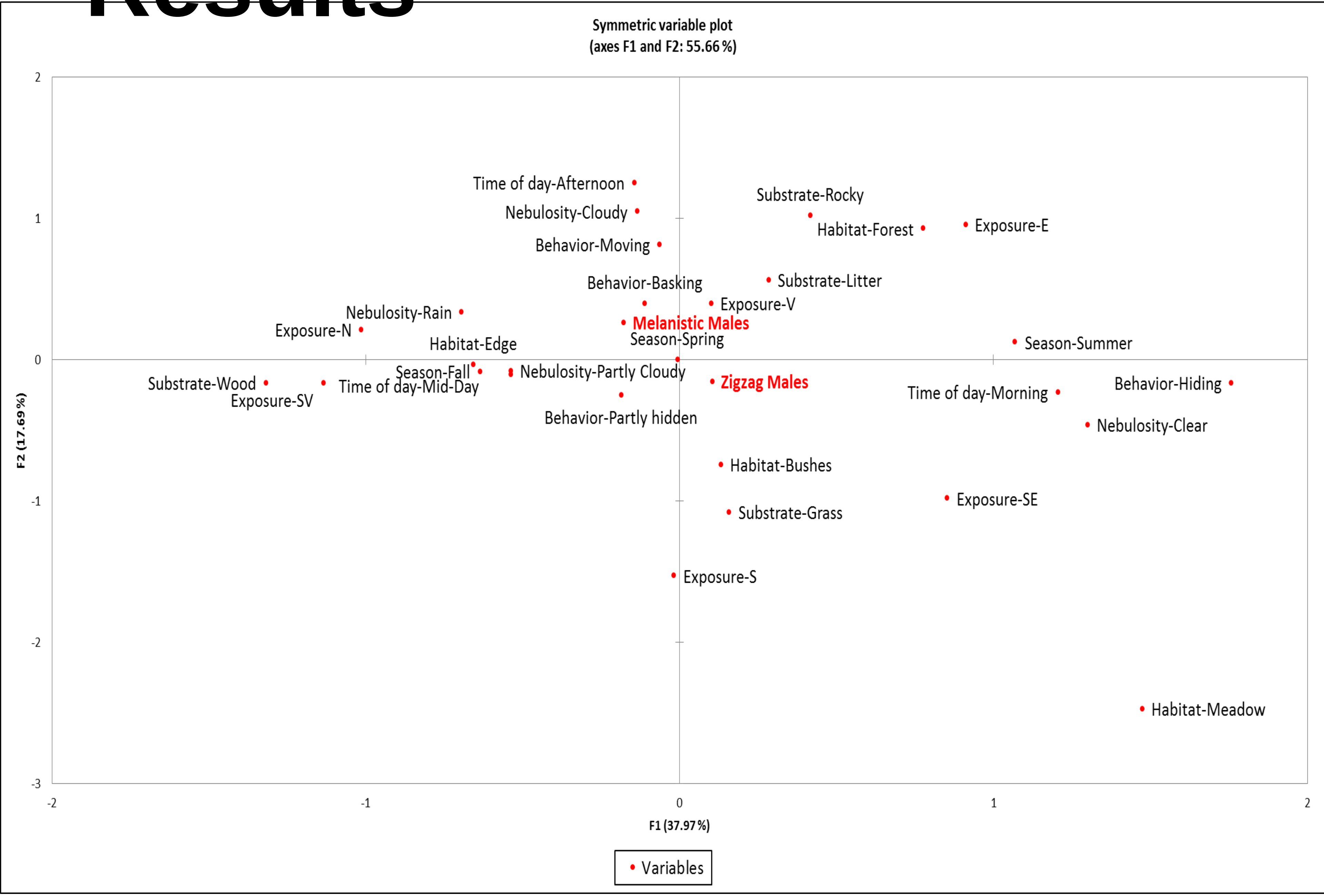
Exposure
Relative frequency
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
E
SE
W
S
SW
N
NW
F-m
F-zz
M-m
M-zz

Results



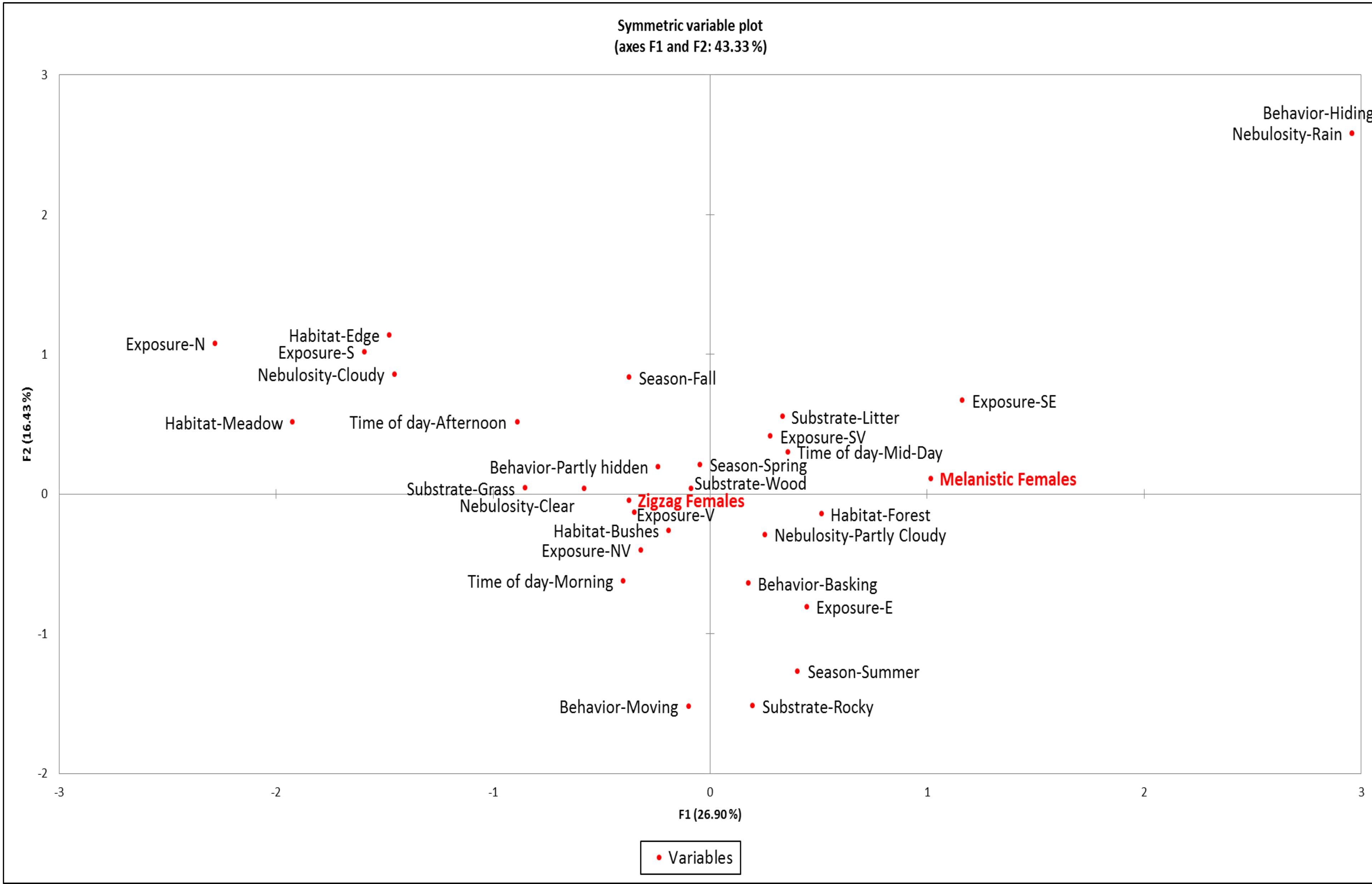
Habitat
Relative frequency
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Forest
Bushes
Edge
Meadow
F-m
F-zz
M-m
M-zz

Results



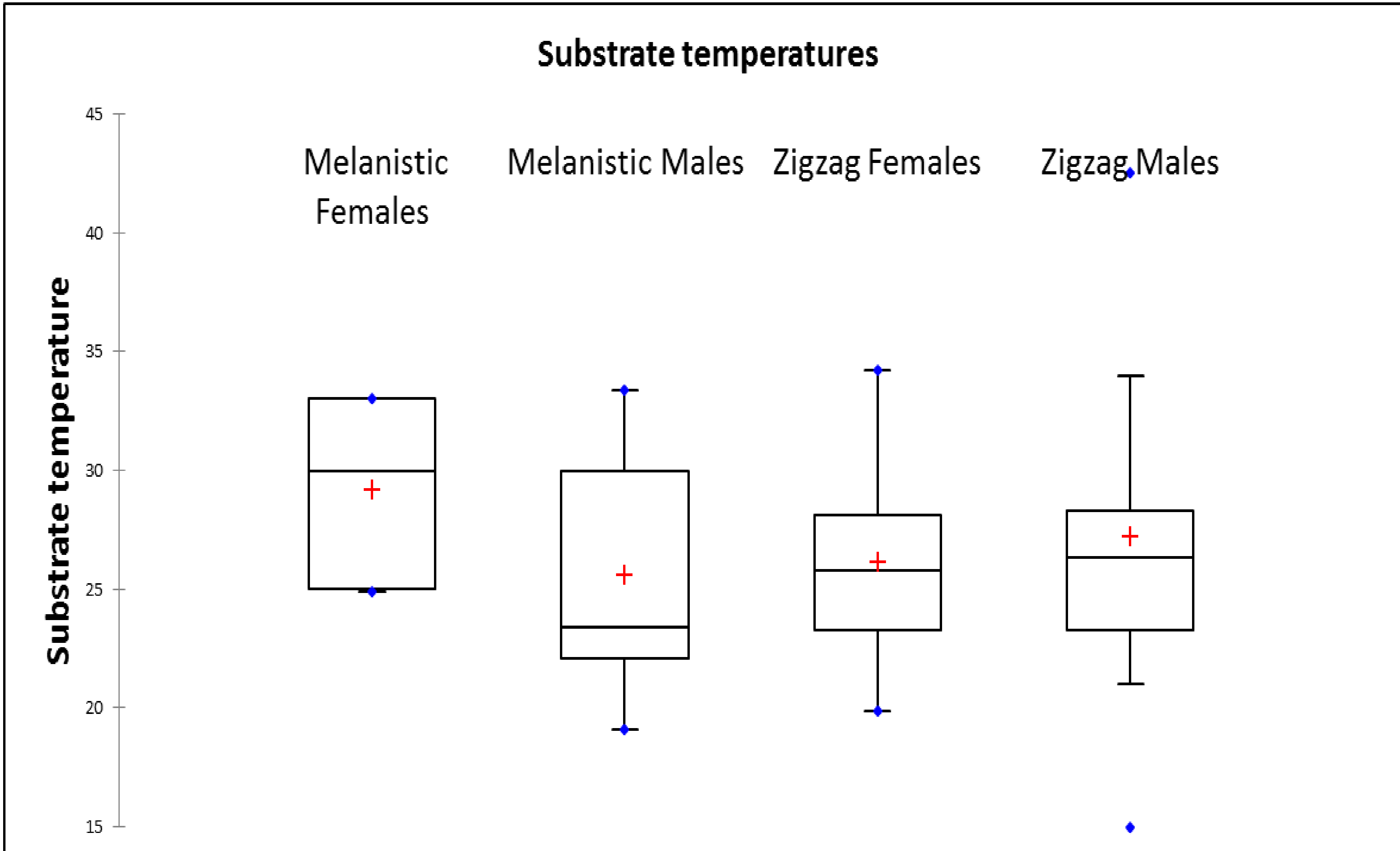
Symmetric variable plot
(axes F1 and F2: 55.66 %)
Time of day-Afternoon
Nebulosity-Cloudy
Behavior-Moving
Substrate-Rocky
Habitat-Forest
Exposure-E
Behavior-Basking
Substrate-Litter
Exposure-V
Nebulosity-Rain
Exposure-N
Melanistic Males
Season-Spring
Habitat-Edge
Season-Summer
Season-Fall
Nebulosity-Partly Cloudy
Substrate-Wood
Time of day-Mid-Day
Exposure-SV
Zigzag Males
Behavior-Hiding
Time of day-Morning
Behavior-Partly hidden
Nebulosity-Clear
Habitat-Bushes
Exposure-SE
Substrate-Grass
Exposure-S
Habitat-Meadow
F2 (17.69 %)
F1 (37.97 %)
2
1
0
-1
-2
-3
-2
-1
0
1
2
Variables

Results



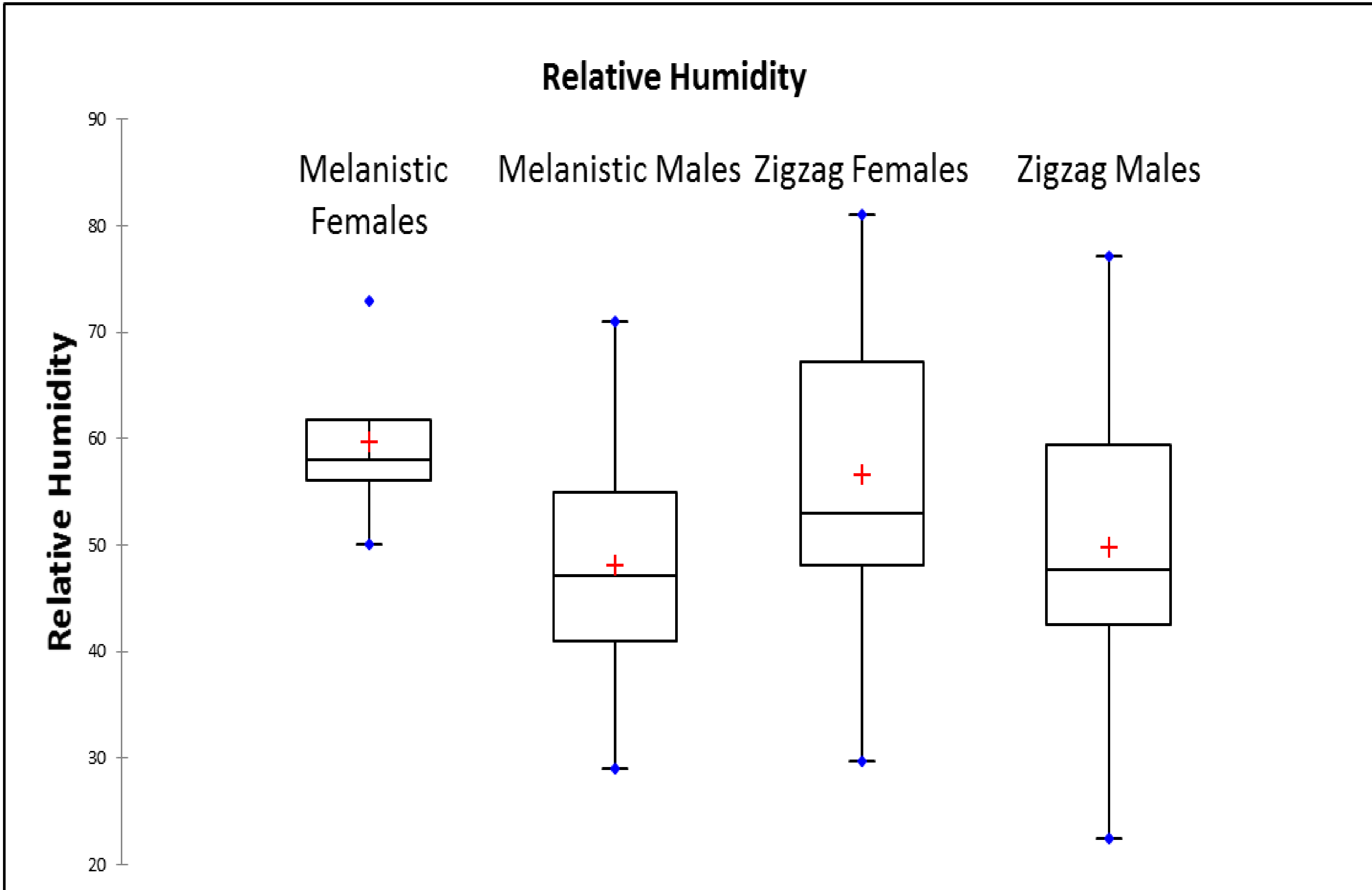
Symmetric variable plot
(axes F1 and F2: 43.33 %)
Behavior-Hiding
Nebulosity-Rain
Exposure-N
Habitat-Edge
Exposure-S
Nebulosity-Cloudy
Season-Fall
Exposure-SE
Habitat-Meadow
Time of day-Afternoon
Substrate-Litter
Exposure-SV
Time of day-Mid-Day
Behavior-Partly hidden
Season-Spring
Melanistic Females
Substrate-Grass
Substrate-Wood
Zigzag Females
Nebulosity-Clear
Exposure-V
Habitat-Forest
Habitat-Bushes
Nebulosity-Partly Cloudy
Exposure-NV
Time of day-Morning
Behavior-Basking
Exposure-E
Season-Summer
Behavior-Moving
Substrate-Rocky
F2 (16.43 %)
F1 (26.90 %)
3
2
1
0
-1
-2
-3
Variables

Results



Substrate temperatures
Substrate temperature
45
40
35
30
25
20
15
Melanistic Females
Melanistic Males
Zigzag Females
Zigzag Males

Results



Relative Humidity
Relative Humidity
90
80
70
60
50
40
30
20
Melanistic Females
Melanistic Males
Zigzag Females
Zigzag Males

Conclusions

- Our study shows weak support for the differential habitat use hypothesis, with only one habitat characteristic (microhabitat exposure) being significantly associated with morph, but only for females.

- However, observational data does suggest that activity patterns do differ, with only melanistic vipers being active during rainy periods, although no differences were observed between basking site temperatures.

- Despite utilizing the same microhabitats, spatial segregation during the mating season may lead to assortative mating, and thus play an important role in the maintenance of colour polymorphism, and potentially in ecological speciation.


Thank you for listening!

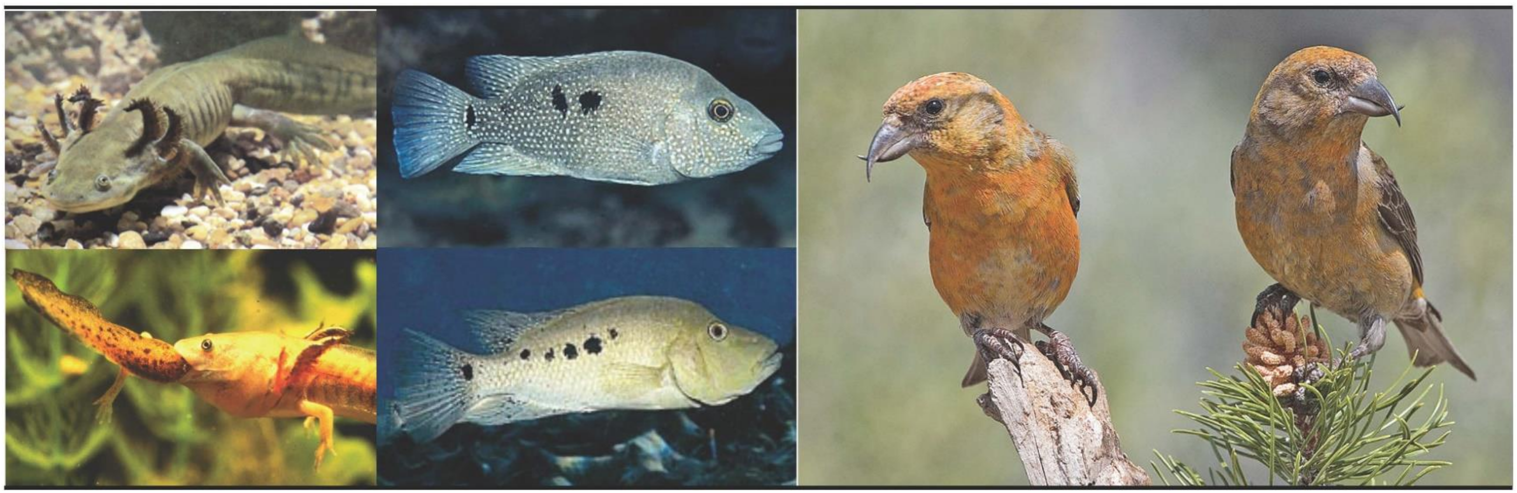
Does the type of competition matter in disruptive selection?

Alexandru STRUGARIU & Ryan A. MARTIN

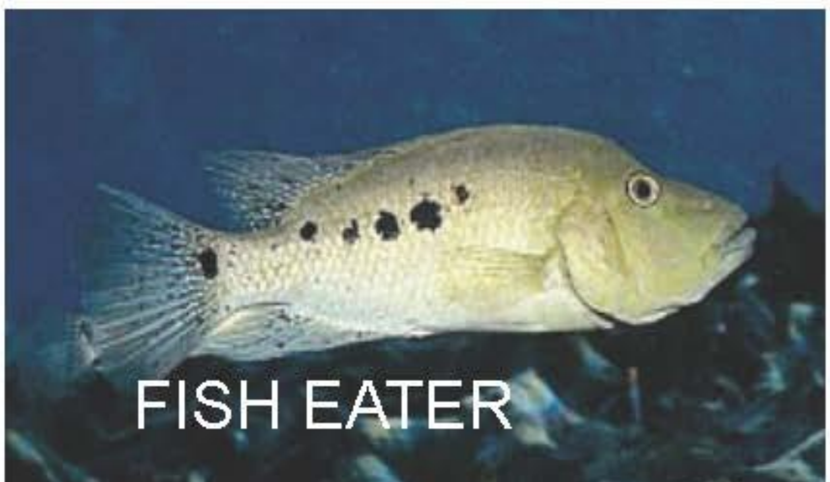
Funding by
FULBRIGHT ROMANIA

Resource polymorphism

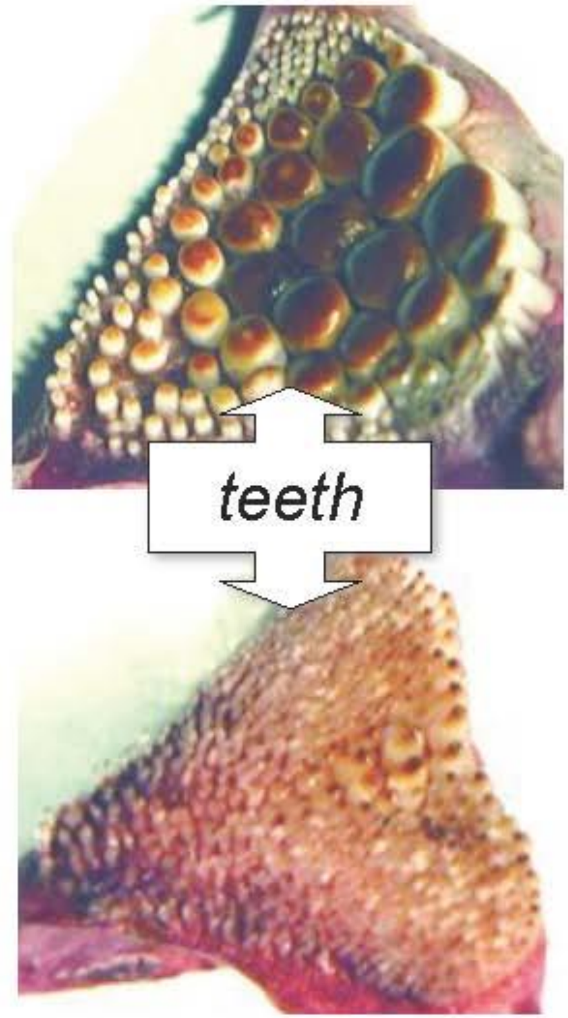
Co-occurring, morphological or behavioral morphs utilizing separate resource or habitat "niches"



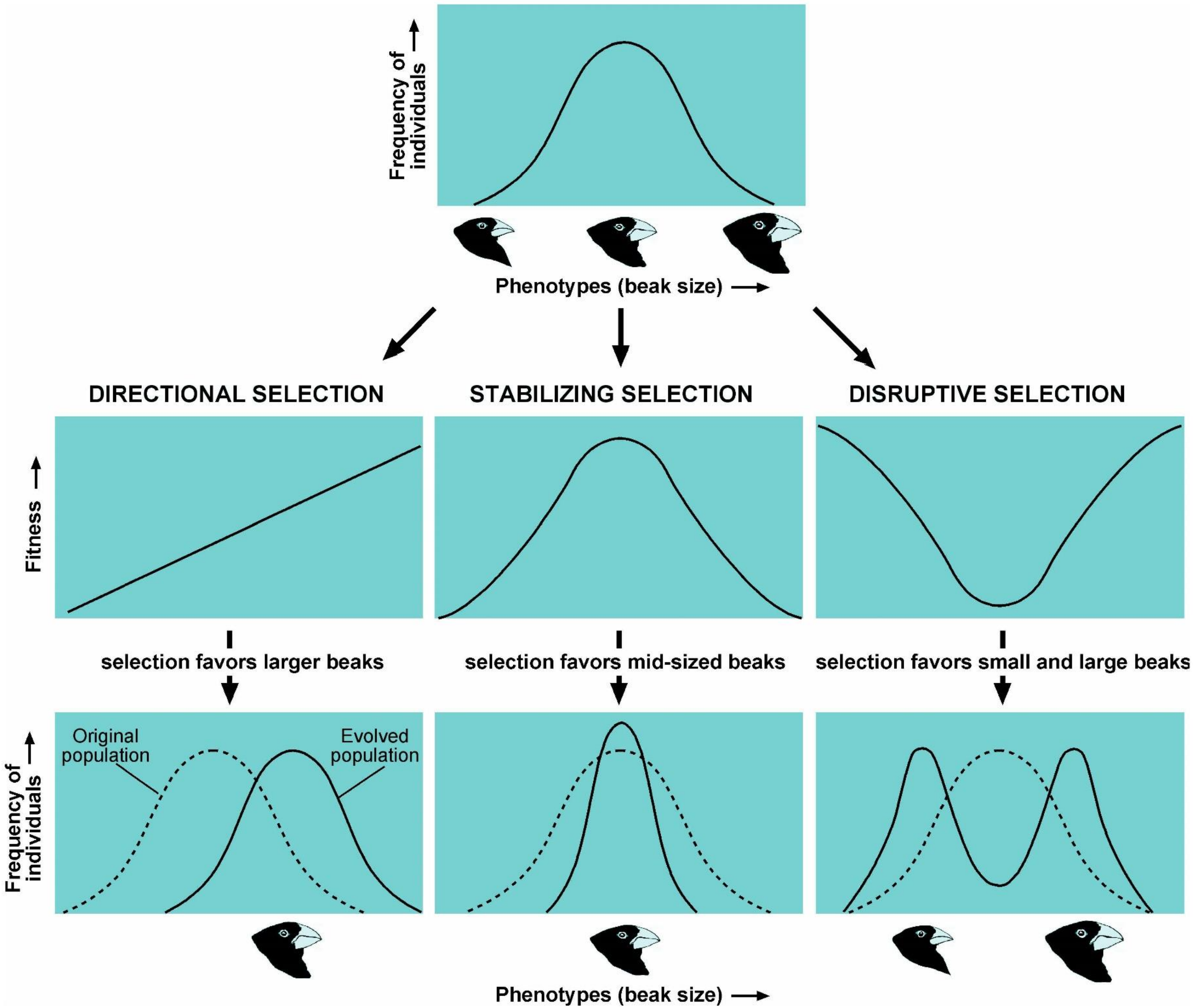
Resource polymorphism



Photos: Juan Miguel Artigas Azas

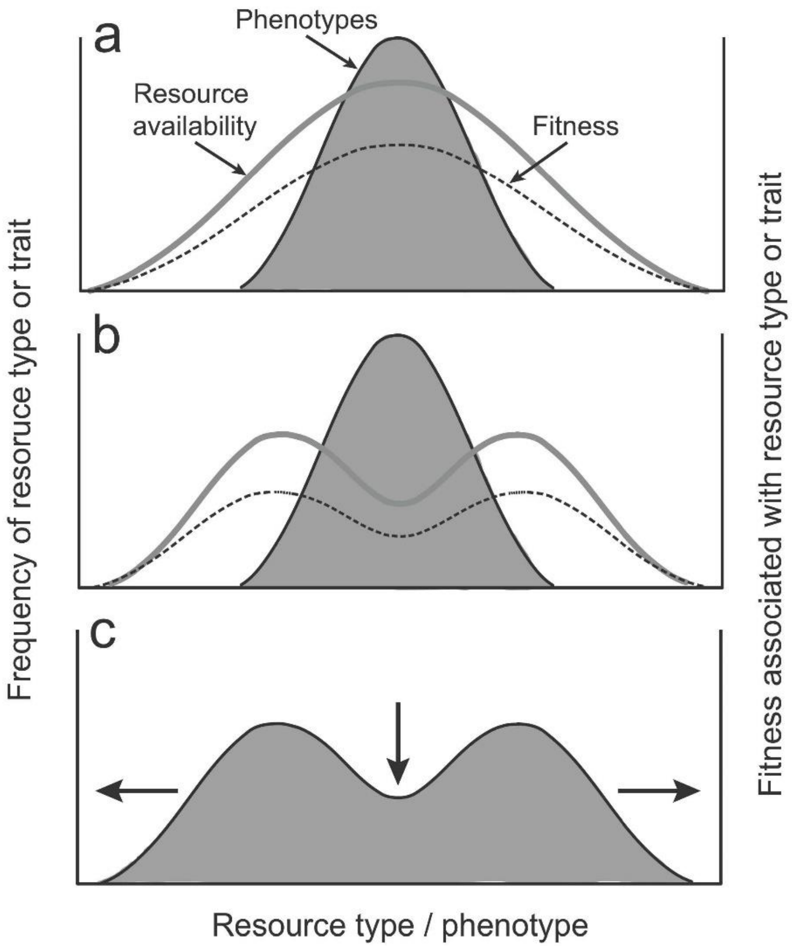


Photos: Darrin Hulsey



modified from Pfennig & Kingsolver 2009

When can competition cause disruptive selection?



- phenotypic variation = variation in resource use
- similar phenotypes compete more intensely
- competition is density & frequency dependent
- resulting in stable disruptive selection

So…

- Through negative frequency dependent interactions, intraspecific resource competition is one of the key drivers of disruptive selection.

However,

- Intraspecific competition for resources can take different forms, being either indirect (exploitative competition) or direct (interference competition).
- While most general models of disruptive selection assume competition is exploitative, empirical data are lacking.

Therefore,

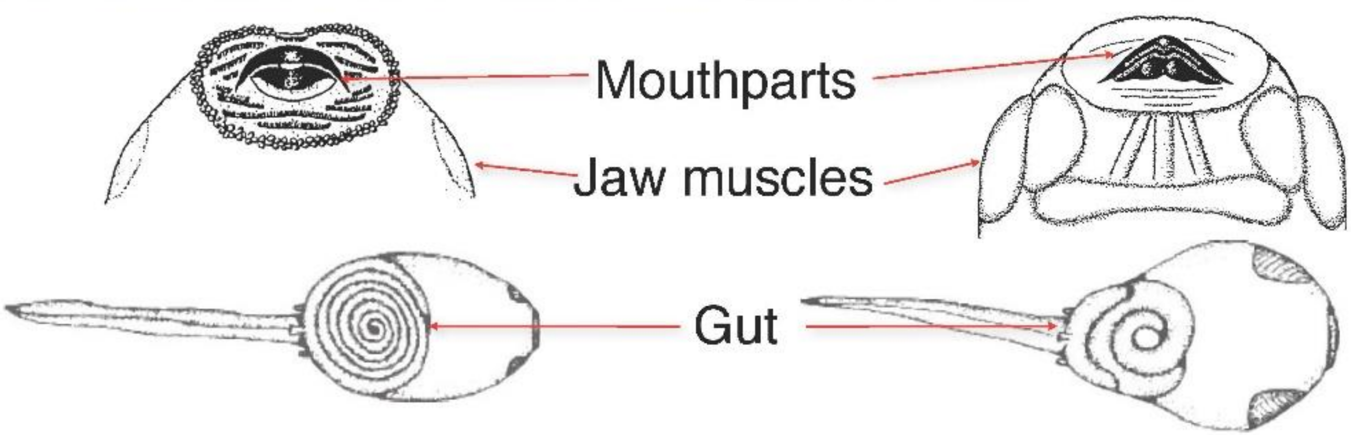
- We experimentally investigated whether the type of competition is relevant in disruptive selection using the Mexican spadefoot toad as a study system.

Study system: Mexican spadefoot toads (*Spea multiplica*) tadpoles

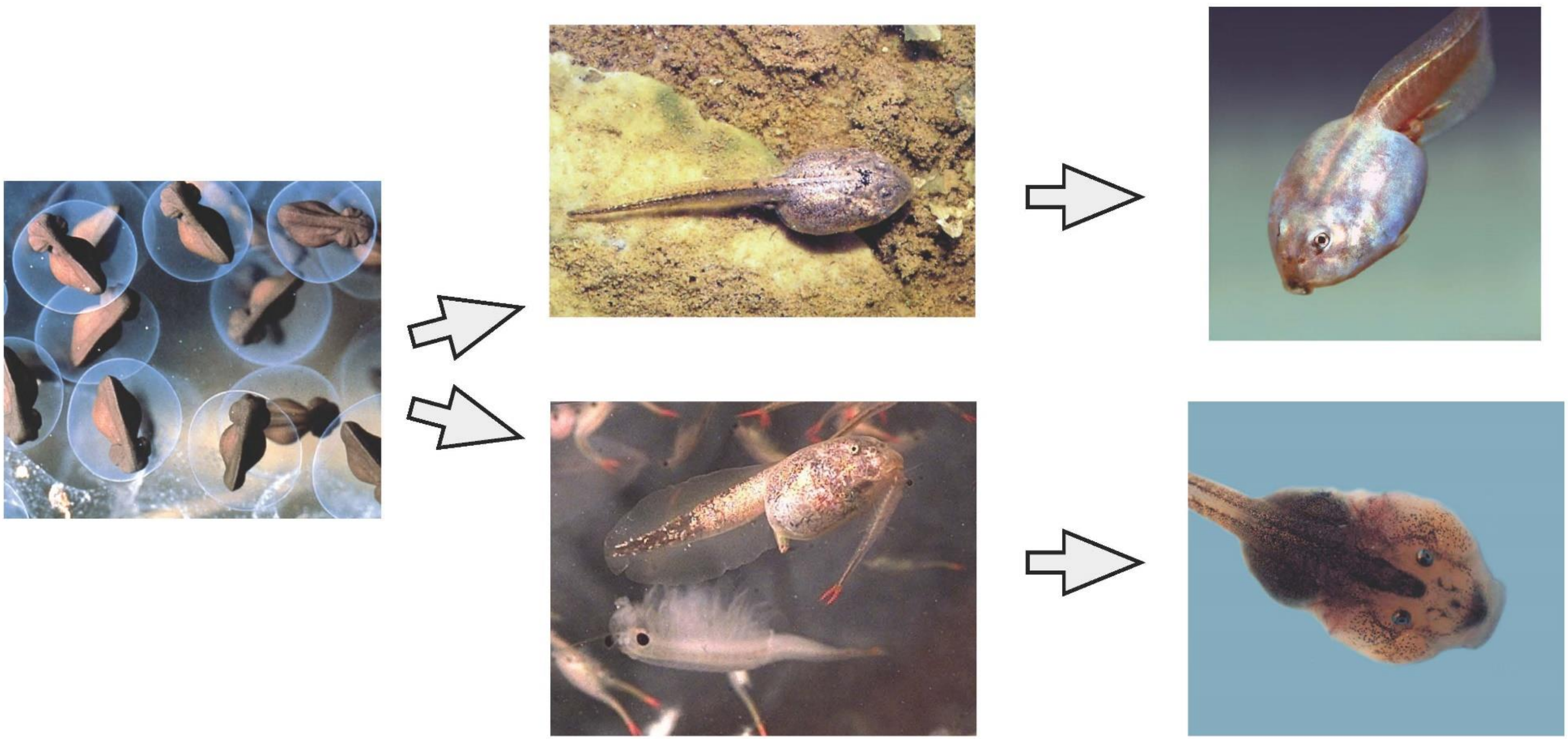
Each morph is an ecological specialist

Omnivore morph

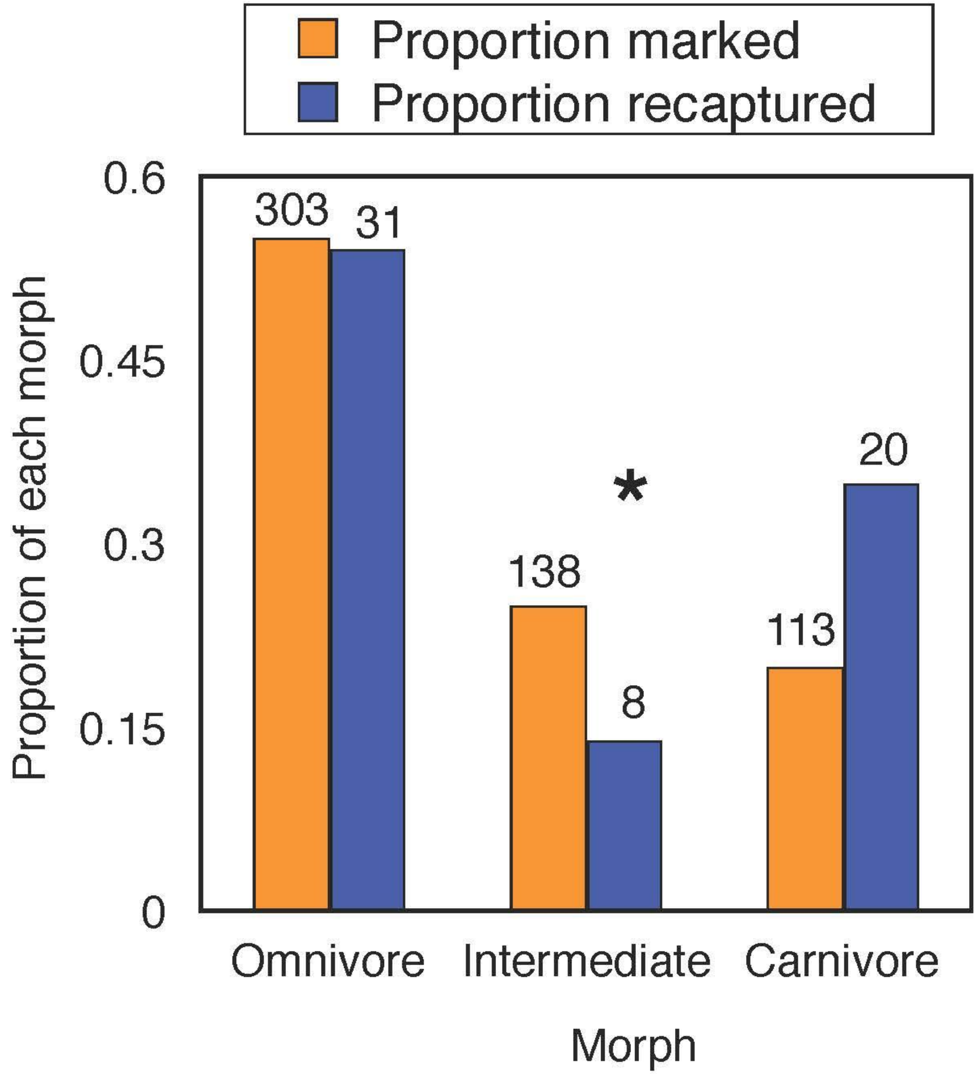
Carnivore morph



Morph determination is environmentally triggered



And is favored by disruptive selection



Martin & Pfennig 2009. *Am Nat*

Sampling area: southern AZ and NM

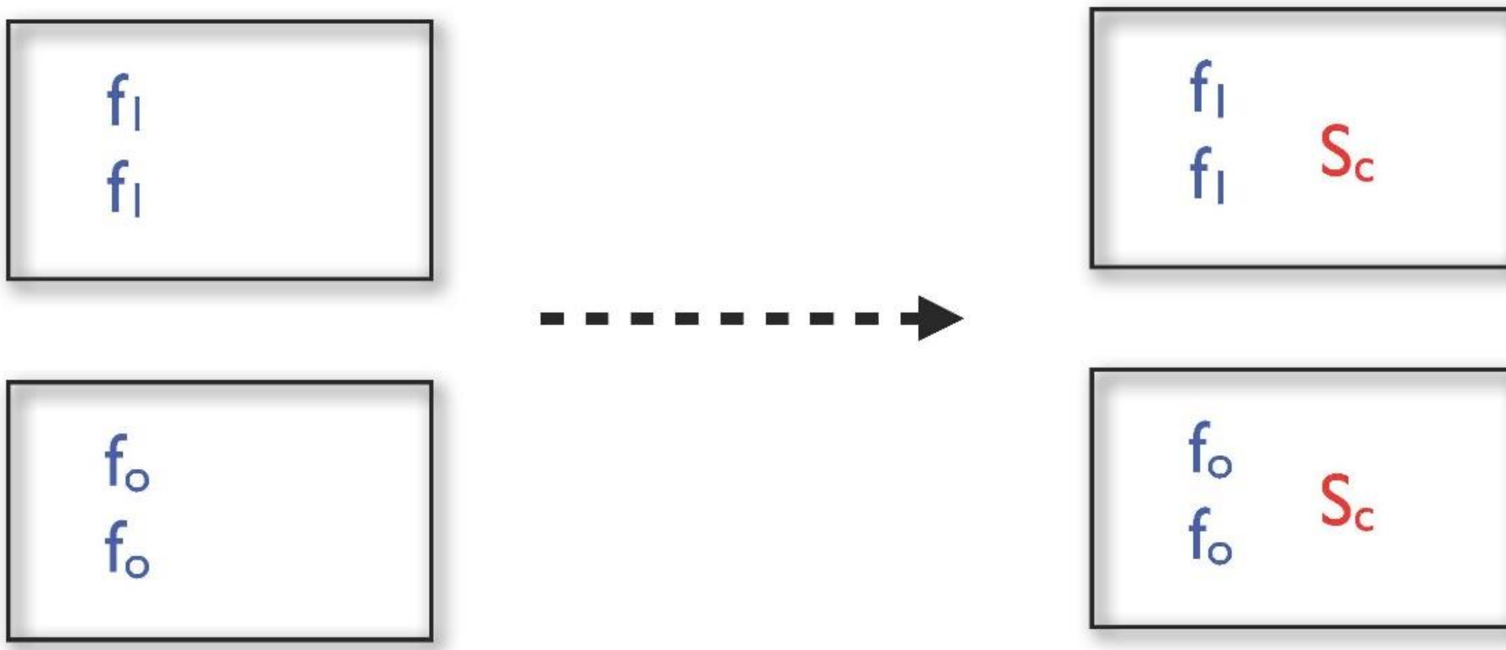
South-Western Research Station, Portal, AZ

Three experiments to assess effects of interference competition

i. Carnivores may preferentially consume intermediate morphs

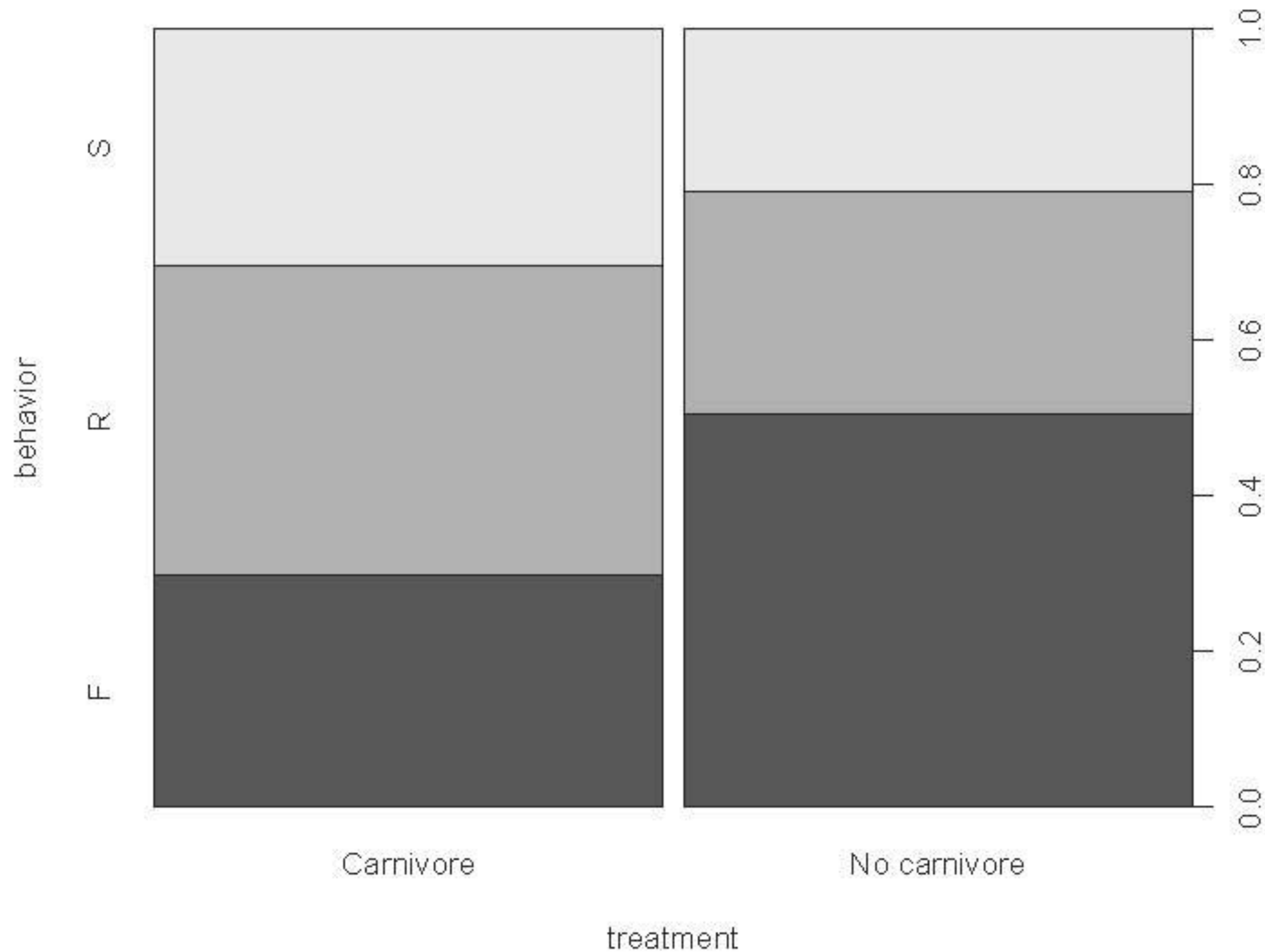
drumroll……..
8 Omnivores consumed
12 Intermediates consumed

ii. Carnivores may modify the foraging behavior of other tadpoles

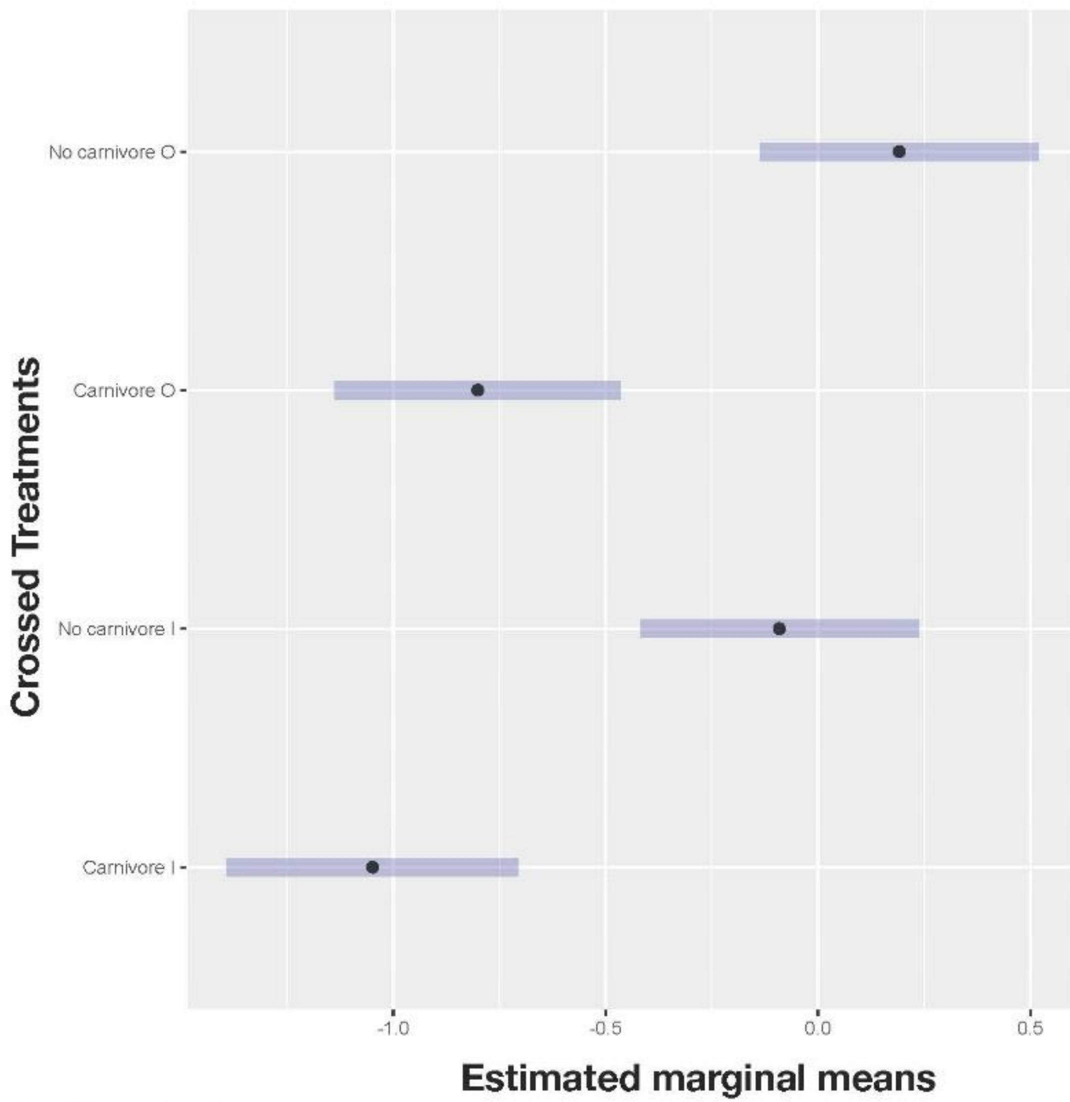


1. five minute acclimation
2. five minutes of scan recording for **swimming, feeding, resting**
3. carnivore introduction
4. five minute acclimation
5. five minutes of scan recording of behavior

Carnivores modified foraging behavior



Foraging



No Carnivore / Omnivore focal tads

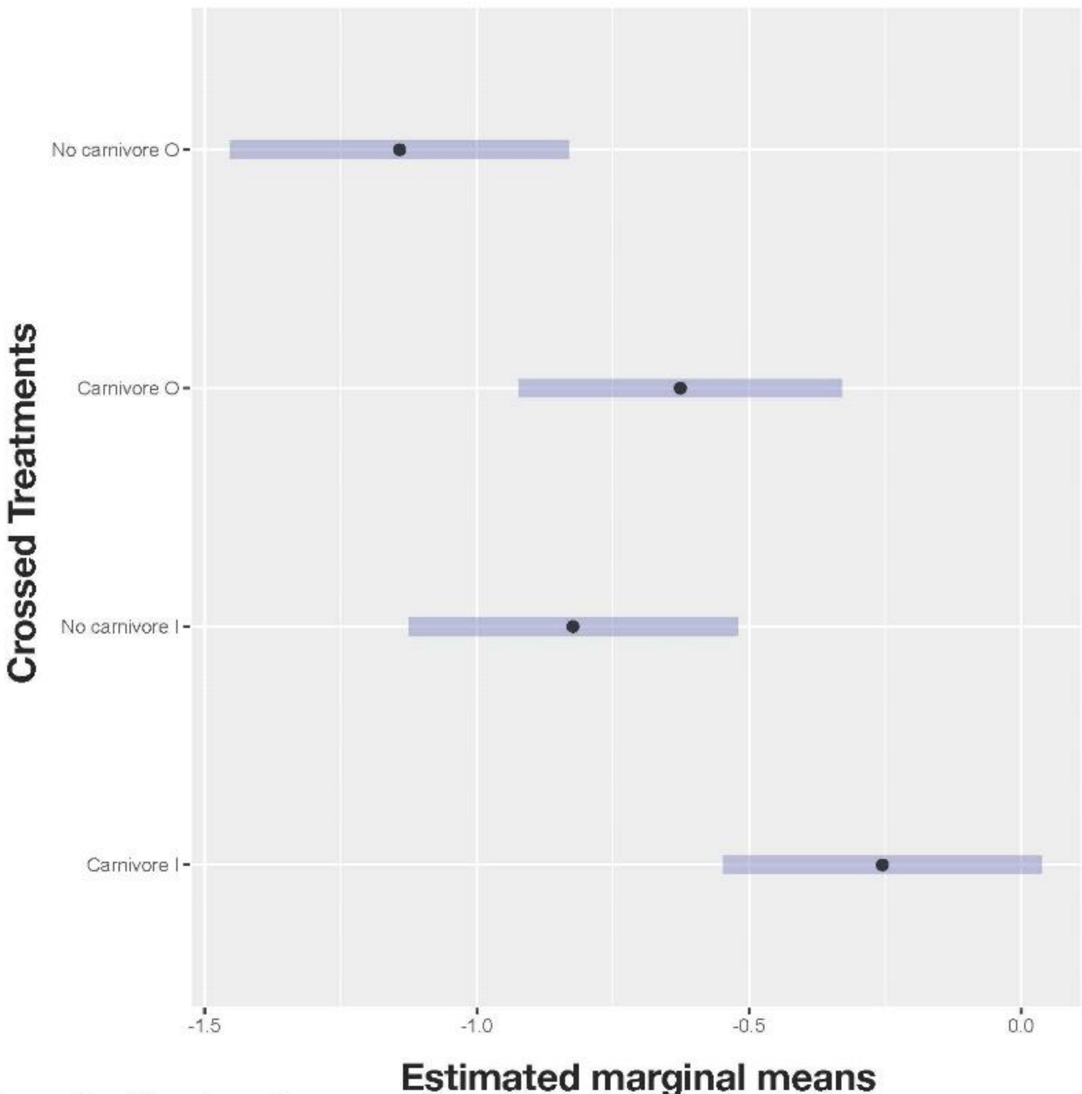
Carnivore / Omnivore focal tads

No Carnivore / Intermediate focal tads

Carnivore / Intermediate focal tads

Significant effects of treatment and morph

Resting



No Carnivore / Omnivore focal tads

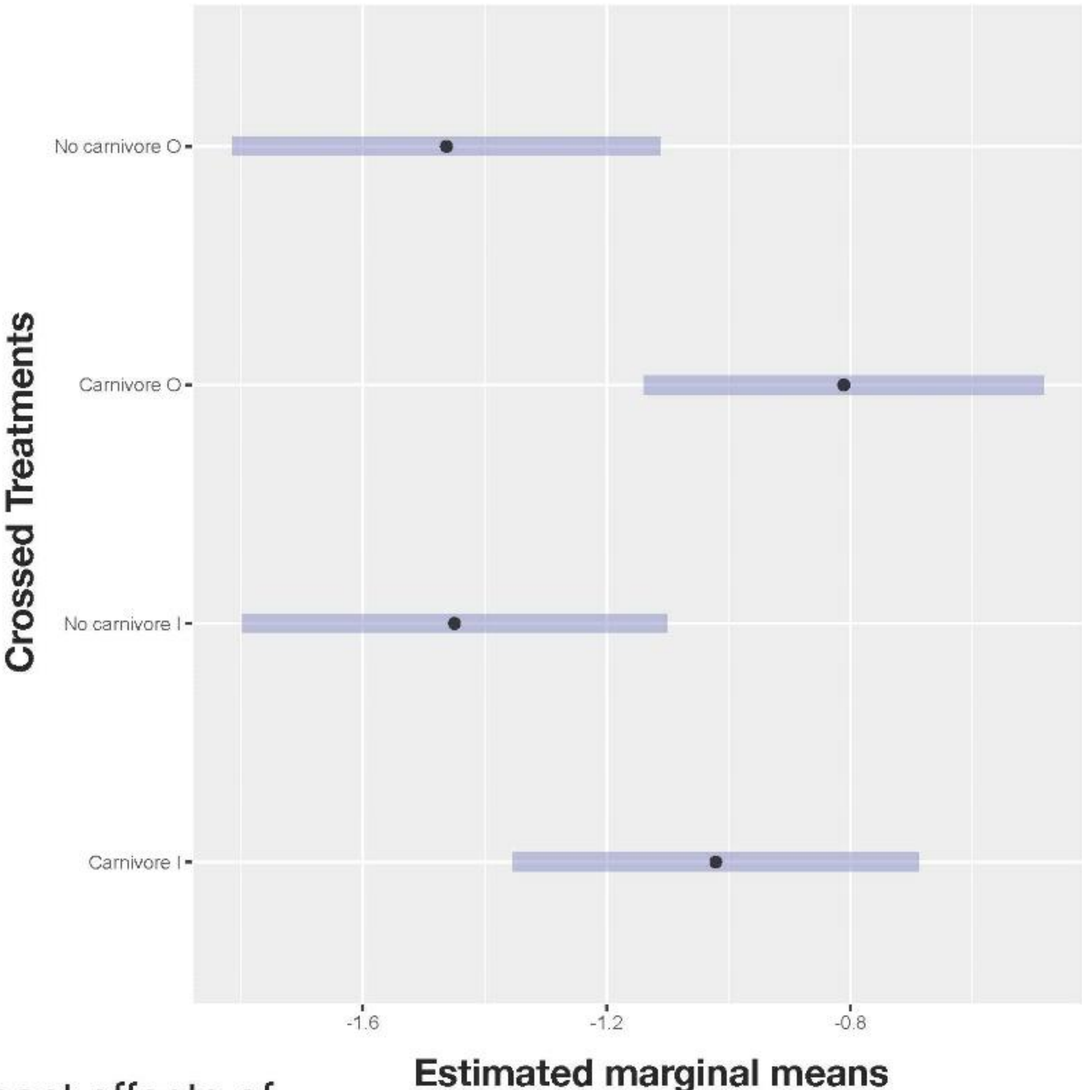
Carnivore / Omnivore focal tads

No Carnivore / Intermediate focal tads

Carnivore / Intermediate focal tads

Significant effects of treatment and morph

Swimming



No Carnivore / Omnivore focal tads

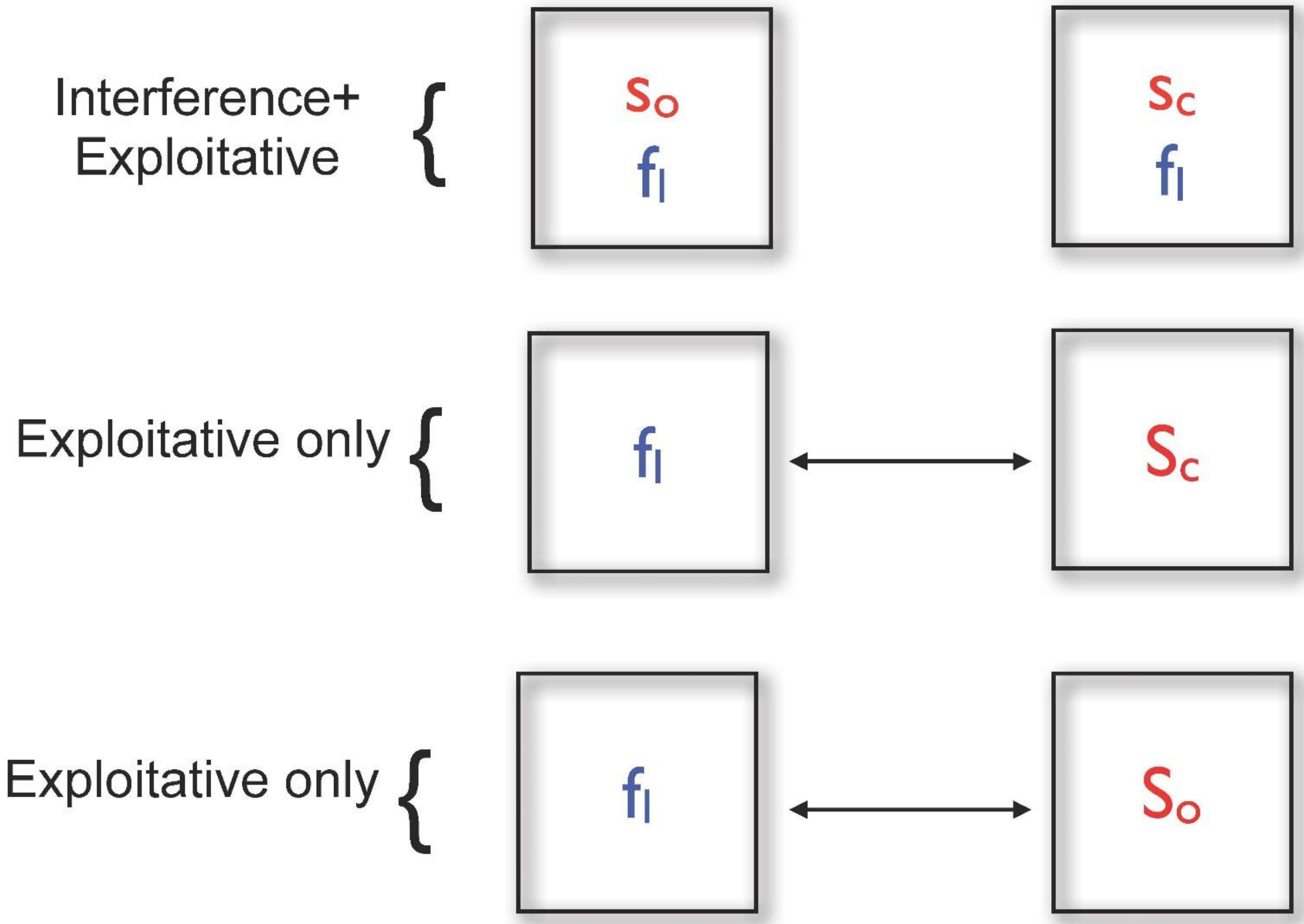
Carnivore / Omnivore focal tads

No Carnivore / Intermediate focal tads

Carnivore / Intermediate focal tads

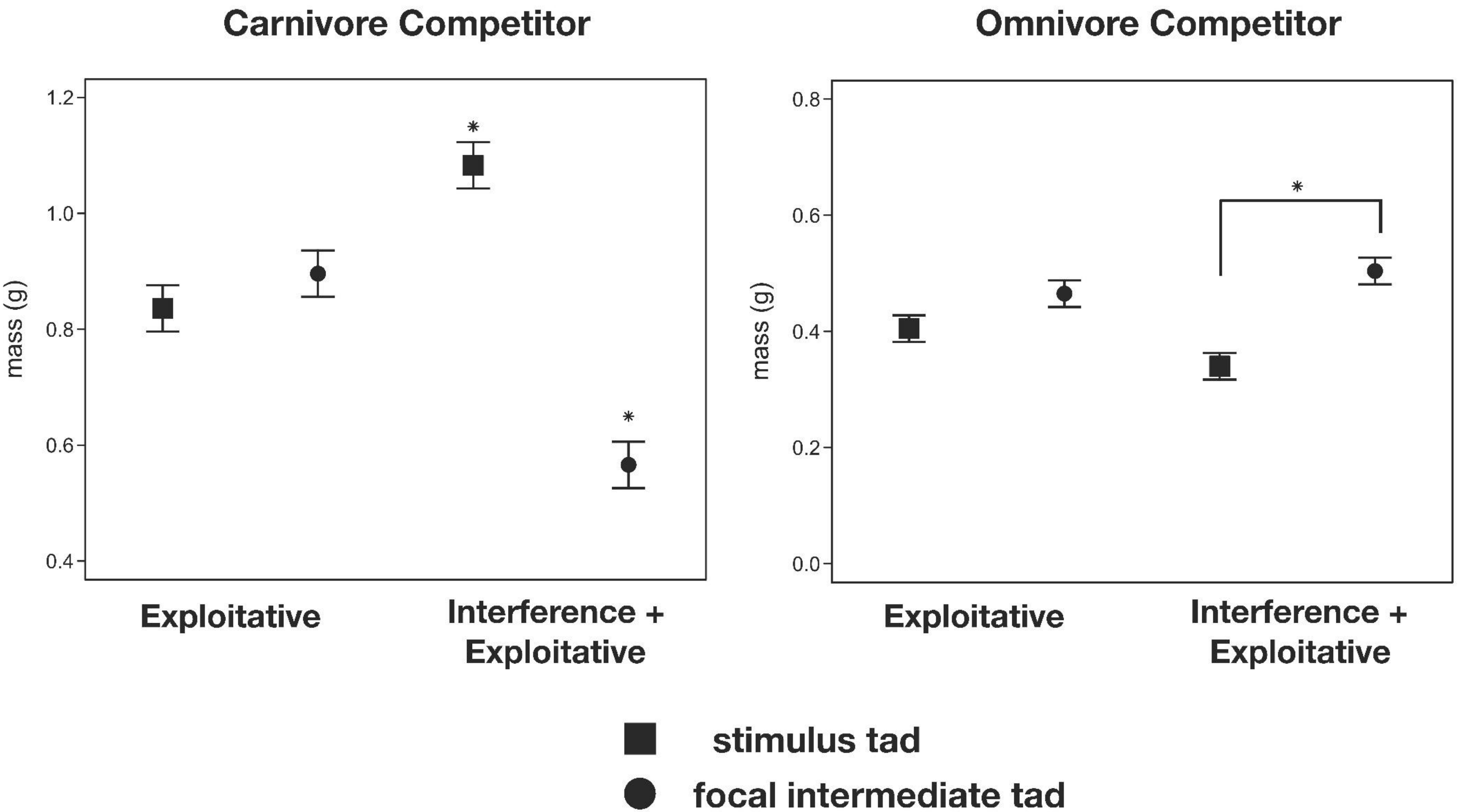
Significant effects of treatment only

iii. Experimentally disentangle effects of interference from exploitative competition



n = 96

Interference and exploitative competition differ
Morphs differ in their competitive effects



Vă mulțumesc pentru atenție!