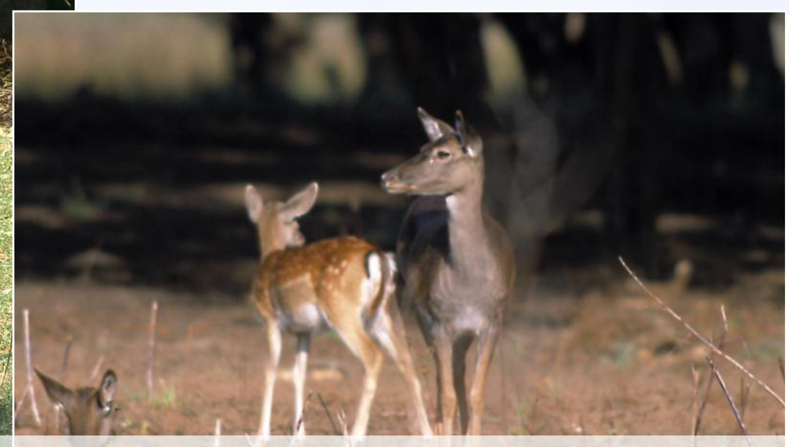
Istituto di Scienze
dell'Atmosfera
e del Clima – CNR

Simona Imperio

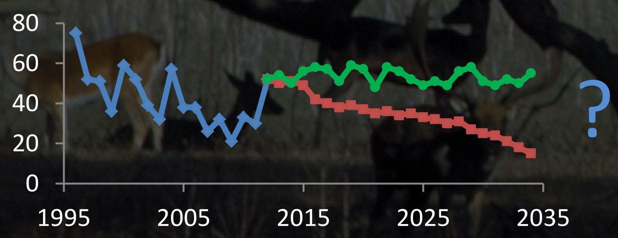


Climatic control and population dynamics: the case of Mediterranean ungulates and Alpine grouses

Population dynamics analysis

Useful to detect key factors driving population fluctuations (and key life cycle periods), in order to:

forecast future population trend



introduce detected variables in management decisions (e.g. hunting quotas)

promote conservation of sites used during the most vulnerable periods (e.g. breeding time)

Why long term time series?

Available data sets are often represented by indexes of population density

⇨ Prone to observation errors

Some mechanisms operate at lagged densities

⇨ Cycles with periods of some decades in ungulates

(up to 30-40 years: McLaren & Peterson,1994; Ogutu & Owen-Smith, 2005)

Study area:

Preserve of Castelporziano

$48\ km^2$

- In 1872 the Estate was purchased by the Italian government and assigned to the King.
- In 1946 the Estate was assigned to the President of Republic.
- In 1976 hunting was forbidden in the area.
- In 1999 Castelporziano became a Natural Reserve.

The ungulates:

Capreolus capreolus italicus

♀-♂ 18-20 kg

Mating in July-August

2 fawns in May-June

Dama dama

♀ 50 kg, ♂ 80-90 kg

Mating in September-October

1 fawn in May-June

Cervus elaphus

♀ 110 kg, ♂ 200 kg

Mating in September-October

1 fawn in May-June

Sus scrofa majori

♀ 50-70 kg, ♂ 60-90 kg

Mating in December-January

2-6 piglets in April-May

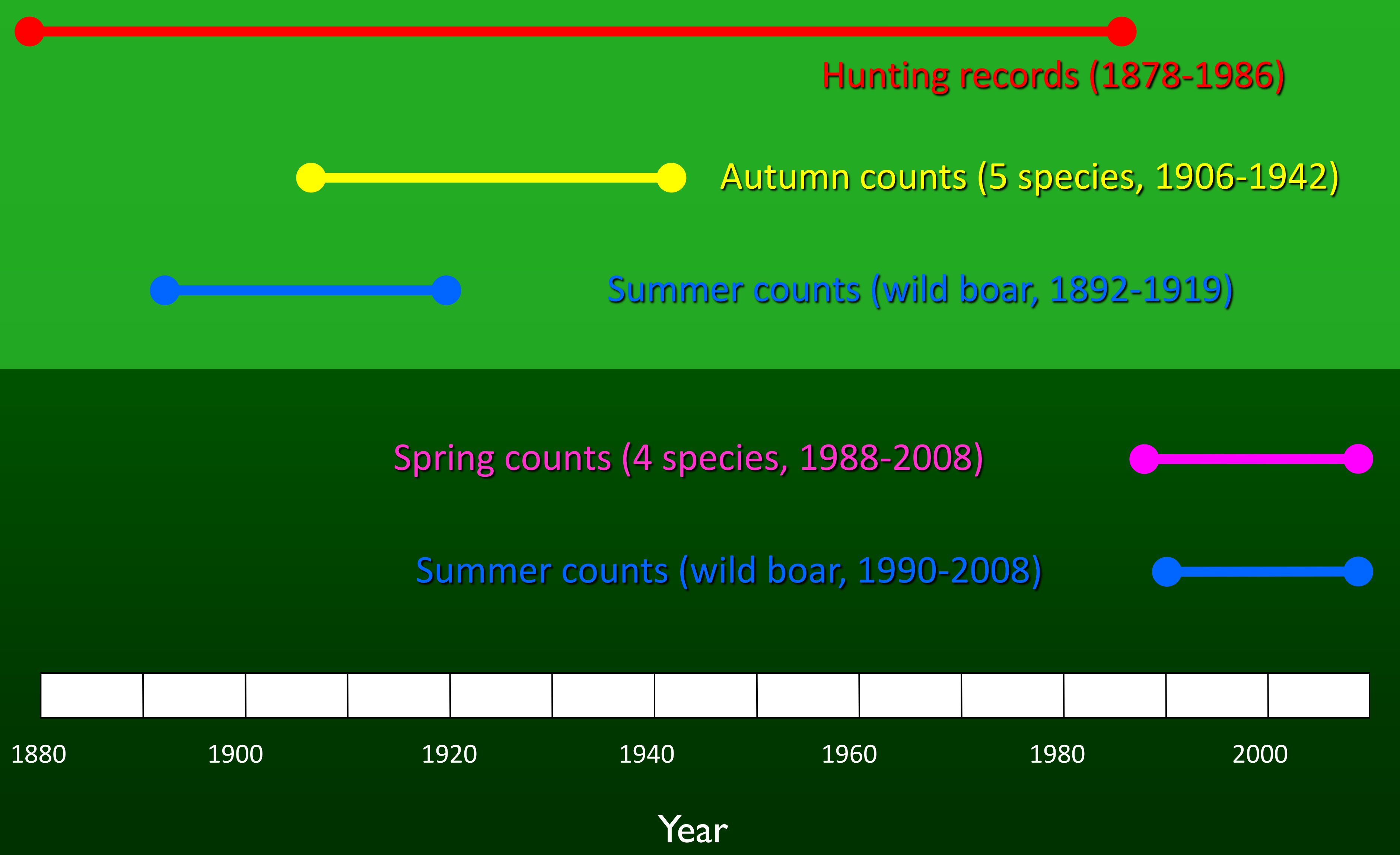
Boselaphus tragocamelus

♀ 170 kg, ♂ 240 kg

Mating in December-March (?)

2-3 kids in August-October(?)

Time series:

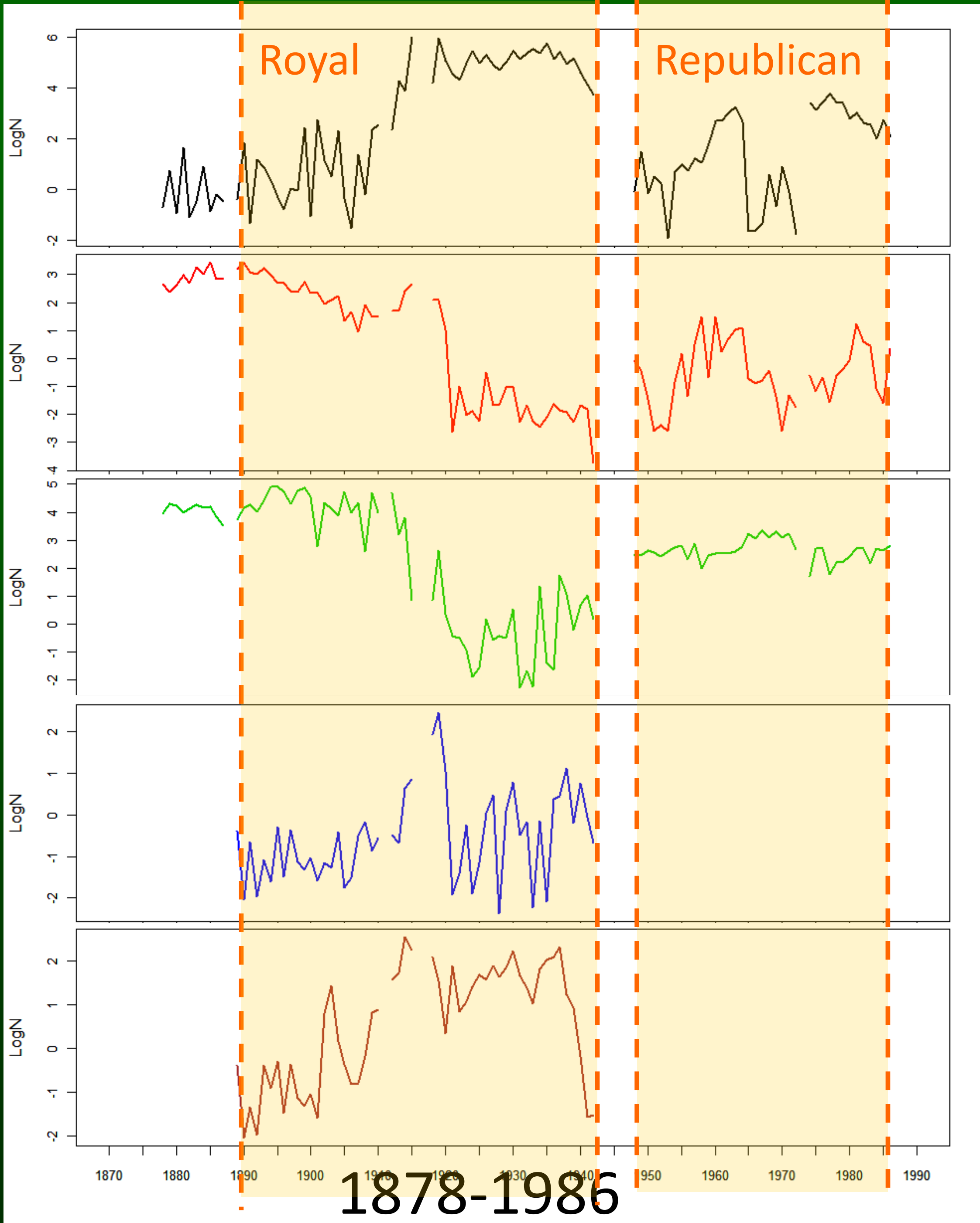

Hunting records (1878-1986)
Autumn counts (5 species, 1906-1942)
Summer counts (wild boar, 1892-1919)
Spring counts (4 species, 1988-2008)
Summer counts (wild boar, 1990-2008)
1880
1900
1920
1940
1960
1980
2000
Year

The drives:

1087 hunting drives

Density estimates =

$$\frac{\text{n. killed animals}}{\text{driven area}}$$



Fallow deer

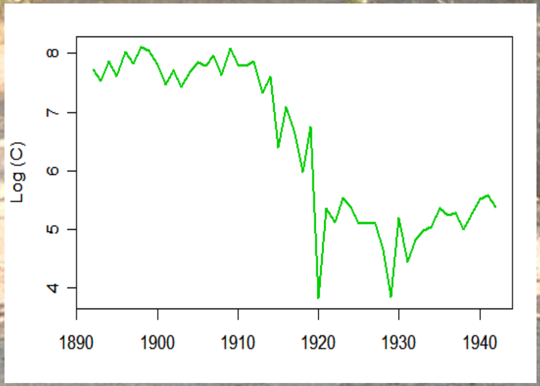
Roe deer

Wild boar

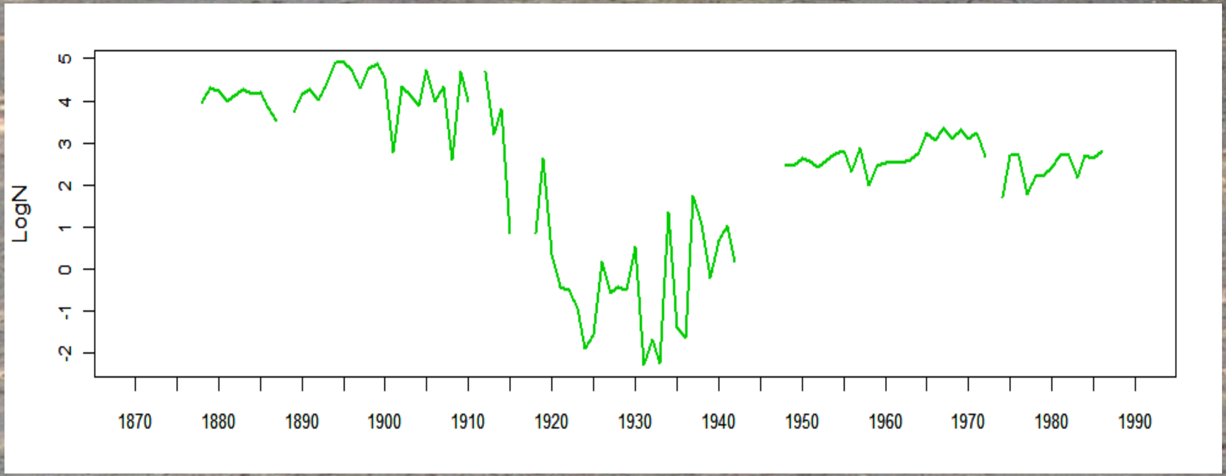
Red deer

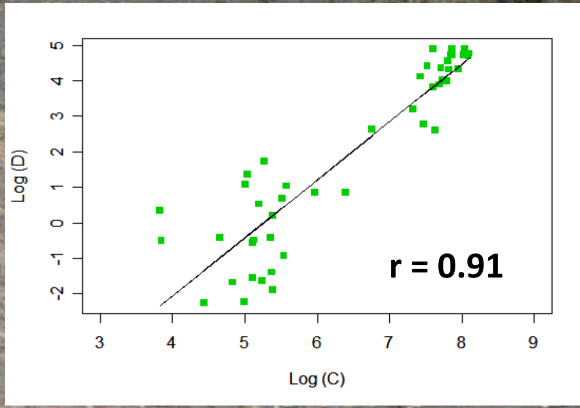
Nilgai

Counts: wild boar



Annual counts

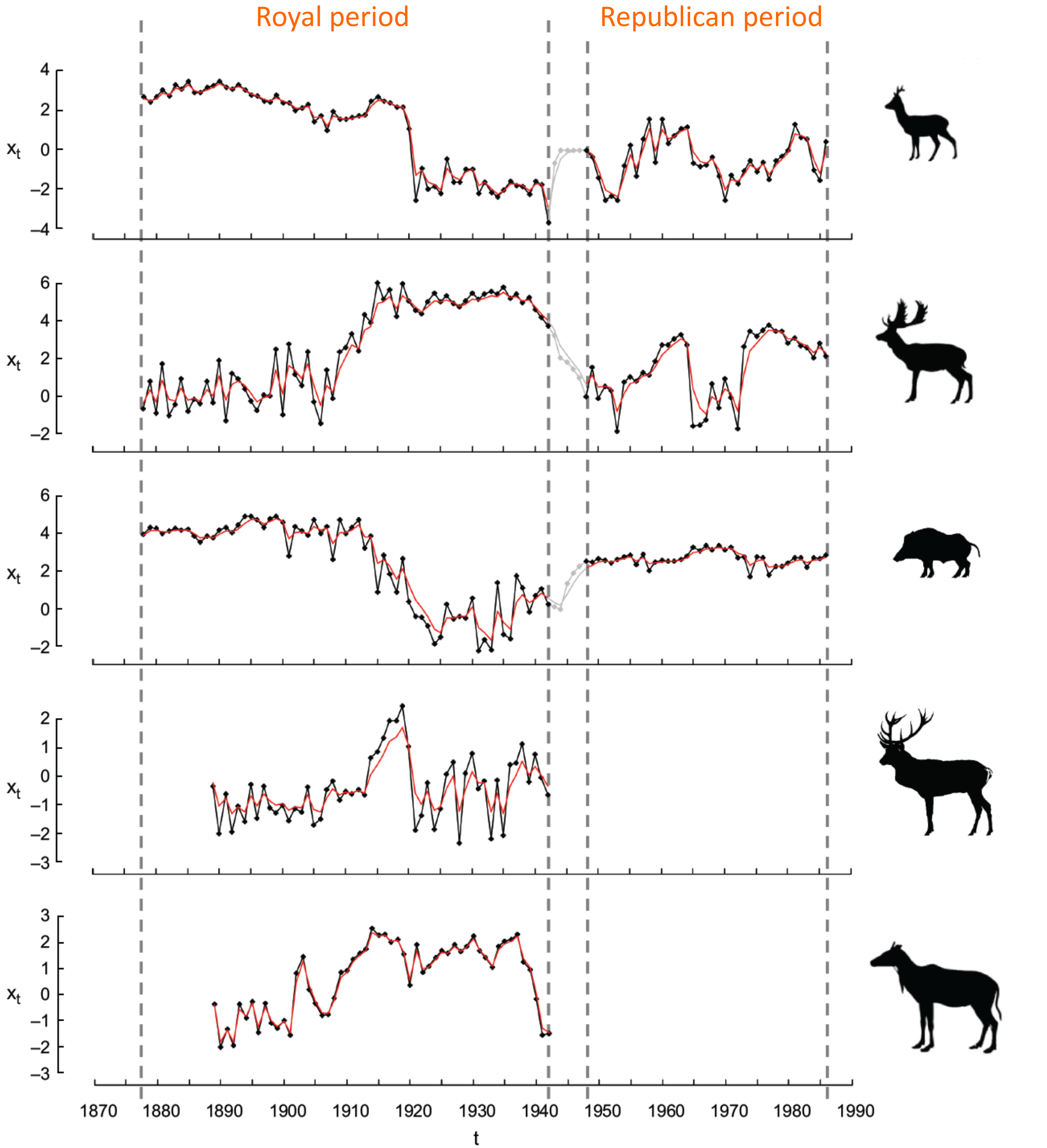




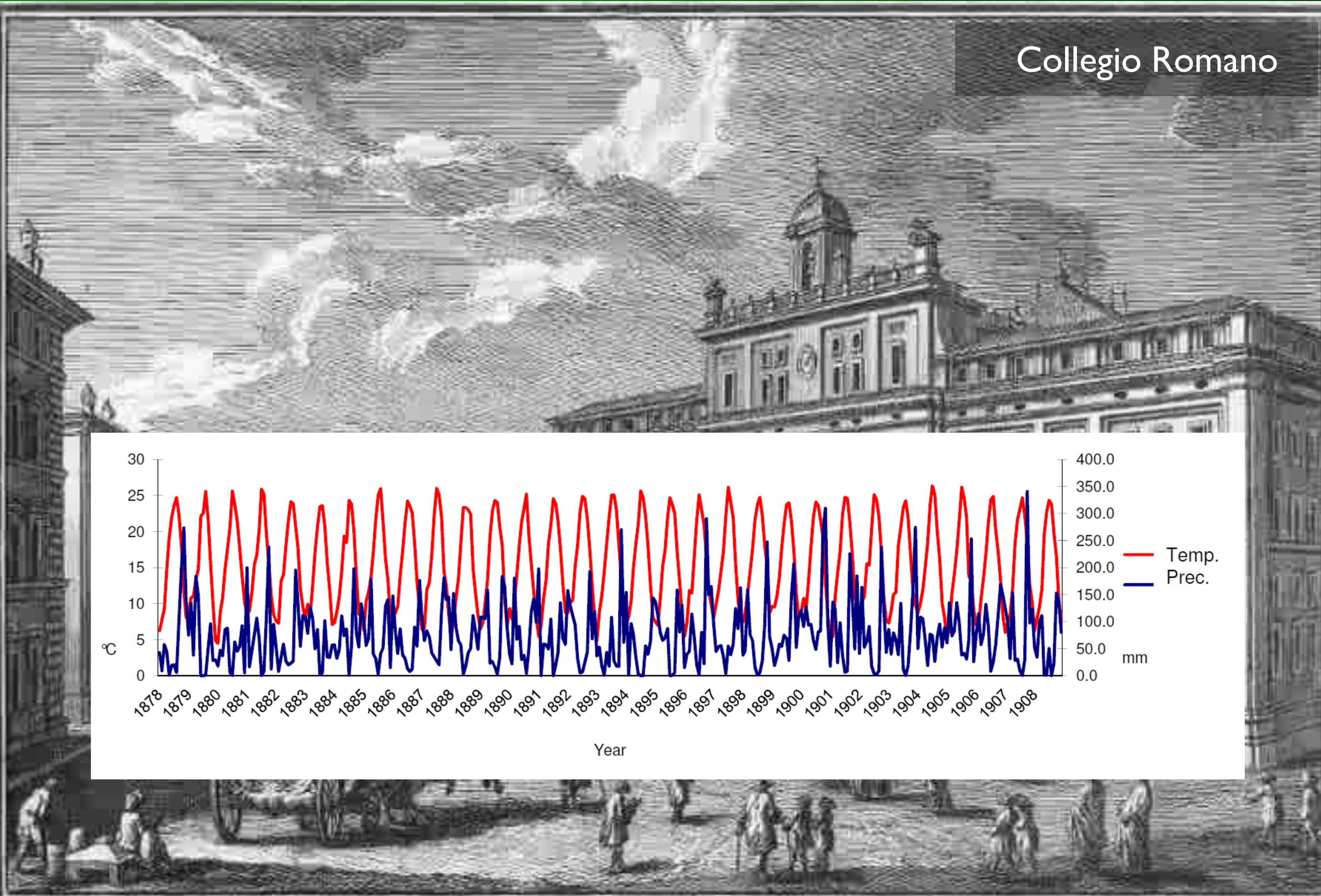
Density estimates

Kalman filter

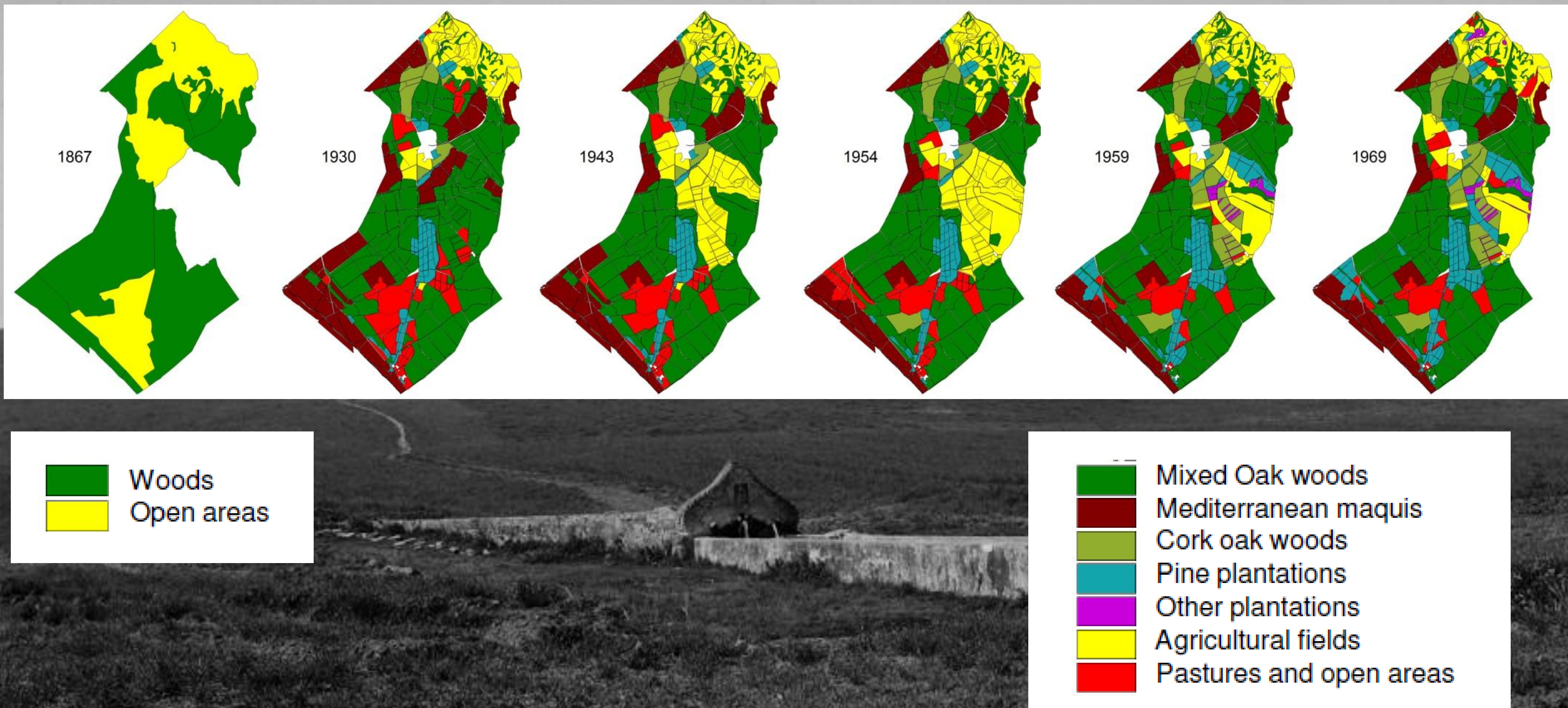
(Dennis et al. 2006)



Meteorological data



Land use


1867
1930
1943
1954
1959
1969
Woods
Open areas
Mixed Oak woods
Mediterranean maquis
Cork oak woods
Pine plantations
Other plantations
Agricultural fields
Pastures and open areas

Population models

Ricker – Lotka Volterra (LV)

$$r_{(1)} = \alpha + \beta_1 N_{(1)t-1} + \beta_2 N_{(2)t-1} + \gamma GI_{t-1} + \varepsilon$$

where $r = \ln\left(\frac{N_t}{N_{t-1}}\right)$

density dependence

interspecific interaction

climate index

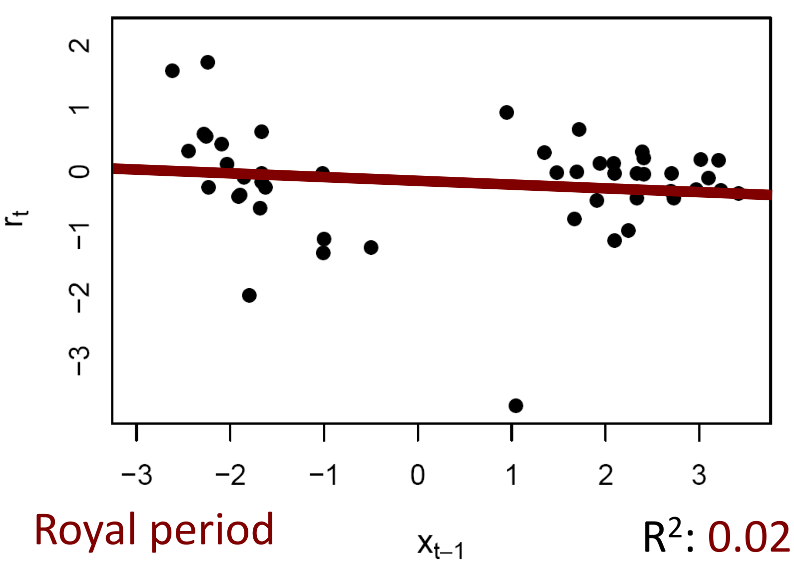
Gompertz – (GLV)

$$r_{(1)} = \alpha + \beta_1 X_{(1)t-1} + \beta_2 X_{(2)t-1} + \gamma GI_{t-1} + \varepsilon$$

where $X = \ln(N)$

Density dependence

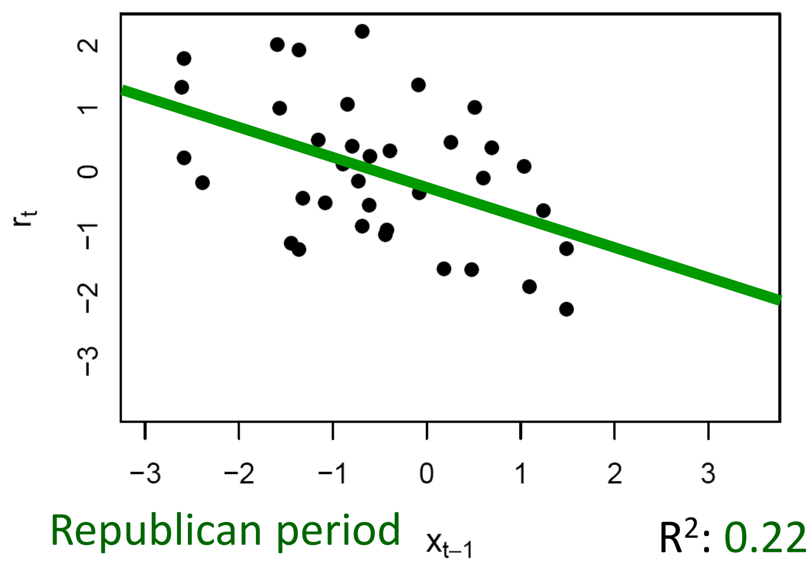
"The tendency of per capita growth rates to decrease when population size is large and increase when it is small" (Wolda and Dennis 1993)



Royal period

R^2: 0.02

randomization test p=0.19



Republican period

R^2: 0.22

randomization test p=0.0001

Stronger density dependence in Republican period than in the Royal period

No lagged density dependence

Climate forcing

Ibex in the Alps
(Jacobson et al. 2004)

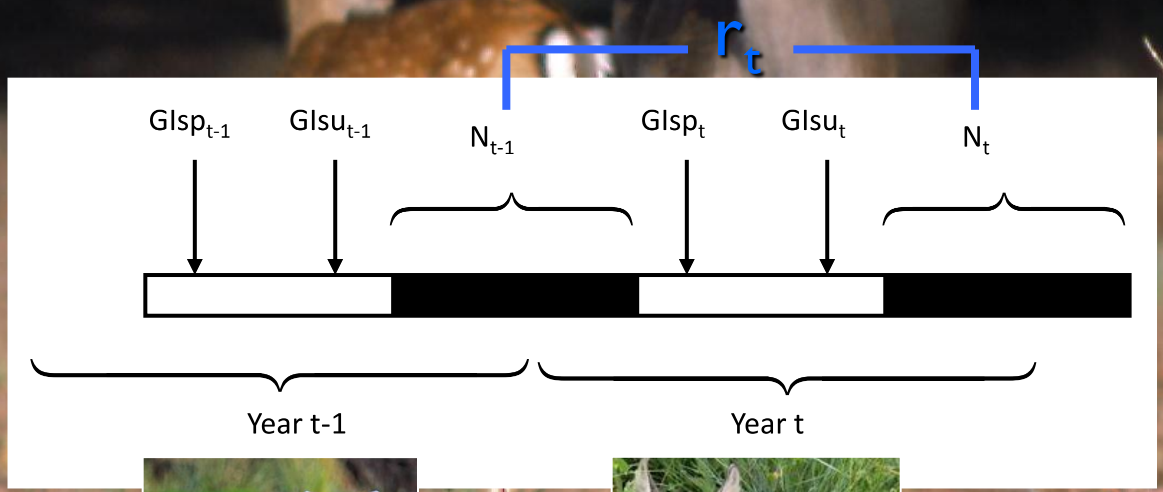
Ungulates in South Africa
(Månsson et al. 2007)

Climate: Gaussen Index

$$GI = P - 2T$$

Spring – GIsp (March-May)

Summer – GIsu (June-August)



Climate: Gaussen Index

$$GI = P - 2T$$

SPECIES	MODEL	ΔR^2
Roe deer:	$dens_{t-1}(-) + GIsp_{t-1}(+)$	0.05
Wild boar:	$dens_{t-1}(-) + GIsp_{t}(+)$	0.02
Deer:	$dens_{t-1}(-) + GImj_{t}(-)$	

Multiple models

Species	Royal period		Republican period	
Fallow deer	$R^2=0.51$	x_{t-1}(fallow d) + x_{t-1}(wild b) + x_{t-1}(nilgai) + PP	$R^2=0.44$	x_{t-1}(fallow d) + $GIsp_{t-1}$ + $GIsu_{t-1}$ + NW
Roe deer	$R^2=0.52$	x_{t-1}(roe d) + x_{t-1}(nilgai) + x_{t-1}(fallow d) + $GIsp_{t-1}$ + NW + PP	$R^2=0.22$	x_{t-1}(roe d) + HE
Wild boar	$R^2=0.52$	x_{t-1}(wild b) + x_{t-1}(roe d.) + x_{t-1}(red d) + HE + NW	$R^2=0.55$	x_{t-1}(wild b) + $GIsp_t$ + NW
Red deer	$R^2=0.46$	x_{t-1}(red d) + x_{t-1}(nilgai)		
Nilgai	$R^2=0.45$	x_{t-1}(nilgai) + HE + NW		

Positive effect
Negative effect

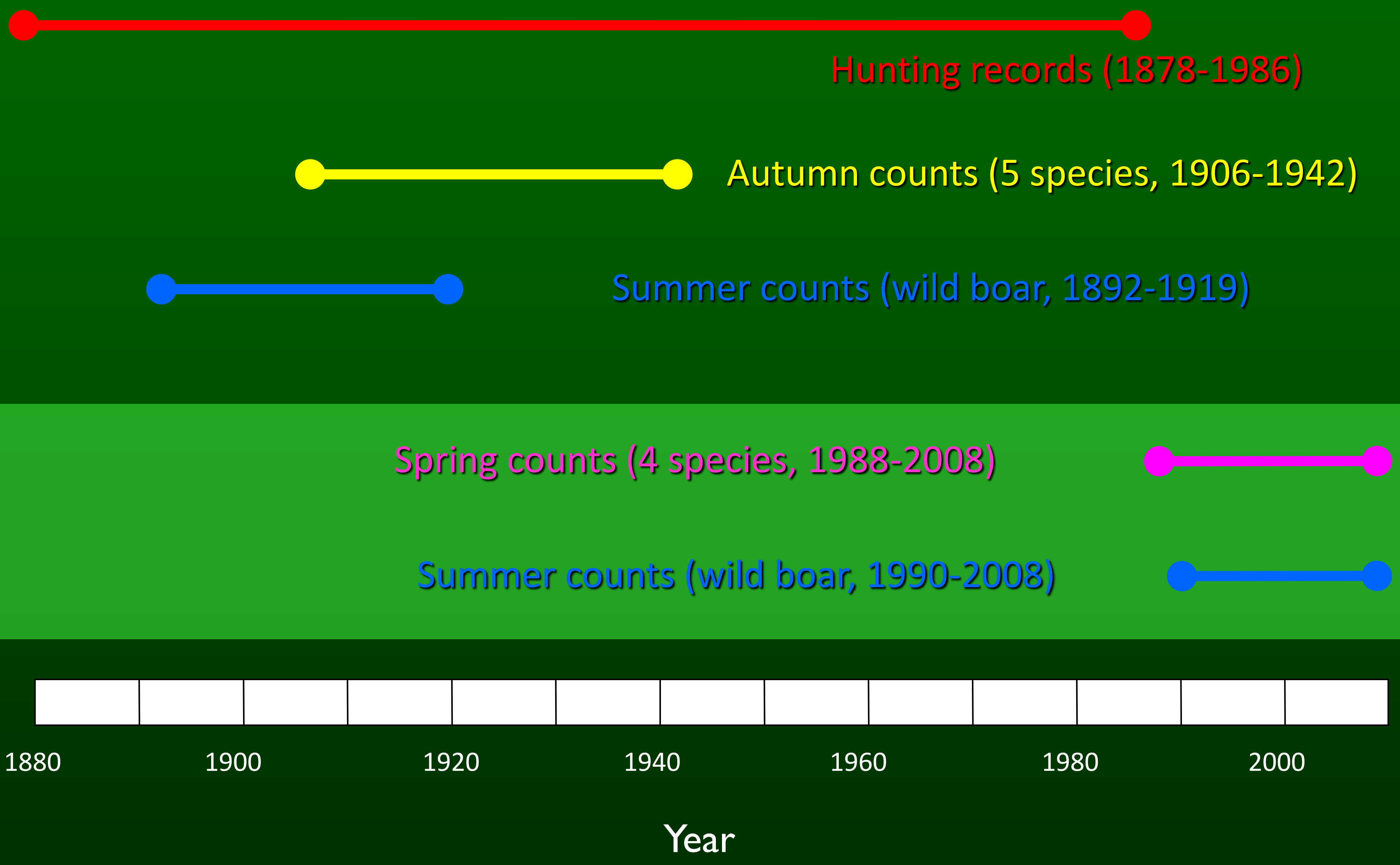
x = ln(density)
HE = hunting effort

NW = Natural woods
PP = Pine plantations

Conclusions – historical data

- ✓ Density dependence is present in all the species, but it is stronger during the second period (< # species).
- ✓ Competition and facilitation affect foraging behaviour, but their effect on population dynamics was never demonstrated before.
- ✓ Spring-summer drought have some negative effect on fecundity of deer and on piglets survival.
- ✓ Heavy rainfall in May-June reduce fawns survival.
- ✓ At present, climate appears to play a minor role with respect to density dependence on the dynamics of Mediterranean ungulates.
- ✓ Drawbacks: no population structure; no data on food availability independent from climate (e.g. masting).

Time series: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1900
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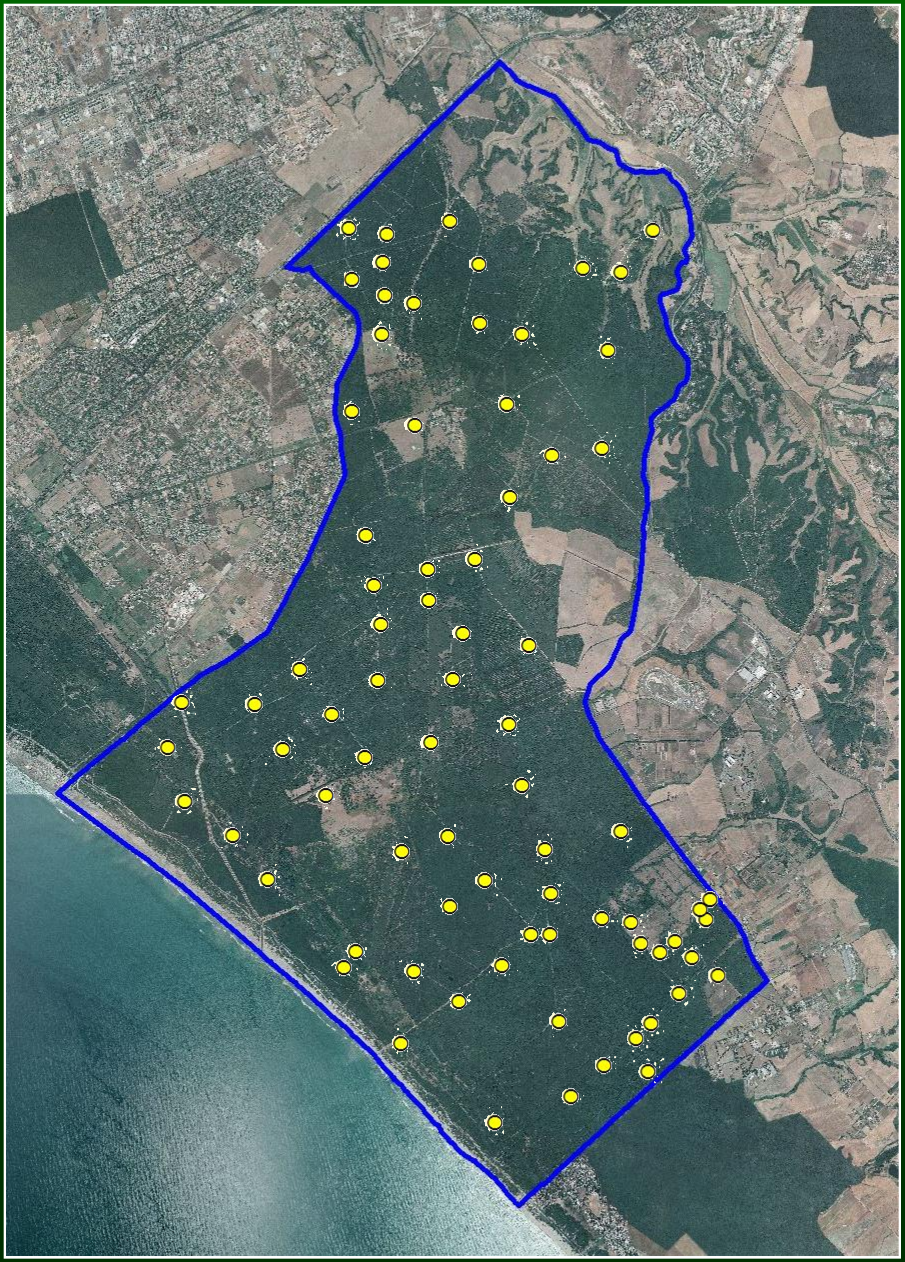
1940
1960
1980
2000
Year

Count data

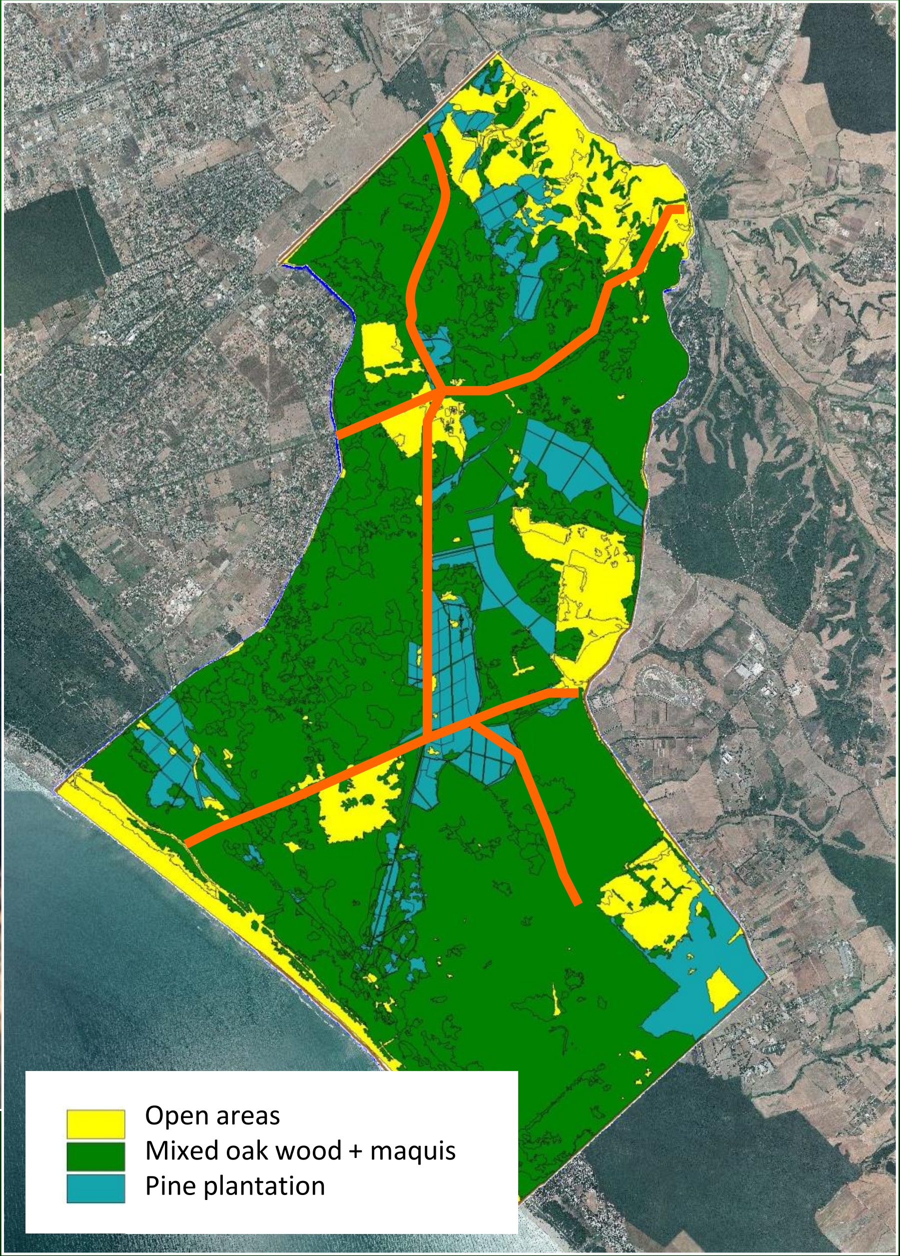
Spring counts (1988-2008)

- ✓ 28-45 vantage points (mean 35,6±1,9)
- ✓ 4-5 replicates



Count data

Detectability of animals can be affected by different factors



N-mixture models for replicated counts

(Royle A., 2004)

- The number of counted animals at site *i* at time *t* (n_{it}) is a binomial random variable:

$$n_{it} \sim \text{Binomial}\ (N_i, p)$$

where N_i = number of available individuals at site *i*

and p = detection probability

- N_i is a random effect with a certain distribution *f*, e.g. Poisson distribution with mean λ :

$$f\,(N\,;\,\lambda)$$

N-mixture models for replicated counts

(Royle A., 2004)

- λ is affected by covariates (x_{ij}, j = 1, 2, … r measured at site i):

$$\log(\lambda_i) = \beta_0 + \sum_{j=1}^{r} x_{ij}\beta_j$$

- also p can be affected by covariates:

$$\operatorname{logit}(p_{ij}) = \alpha_0 + \sum_{j=1}^{r} x_{ij}\alpha_j$$

- likelihood function:

$$L(p,\lambda \mid \{n_{it}\}) = \prod_{i=1}^{R} \left\{ \sum_{N_i = \max_t n_{it}}^{\infty} \left(\prod_{t=1}^{T} \mathrm{Bin}(n_{it}; N_i, p) \right) f(N_i; \lambda) \right\}$$

Abundance estimates

Model

Density % wood

Detect. % open areas + main roads + time

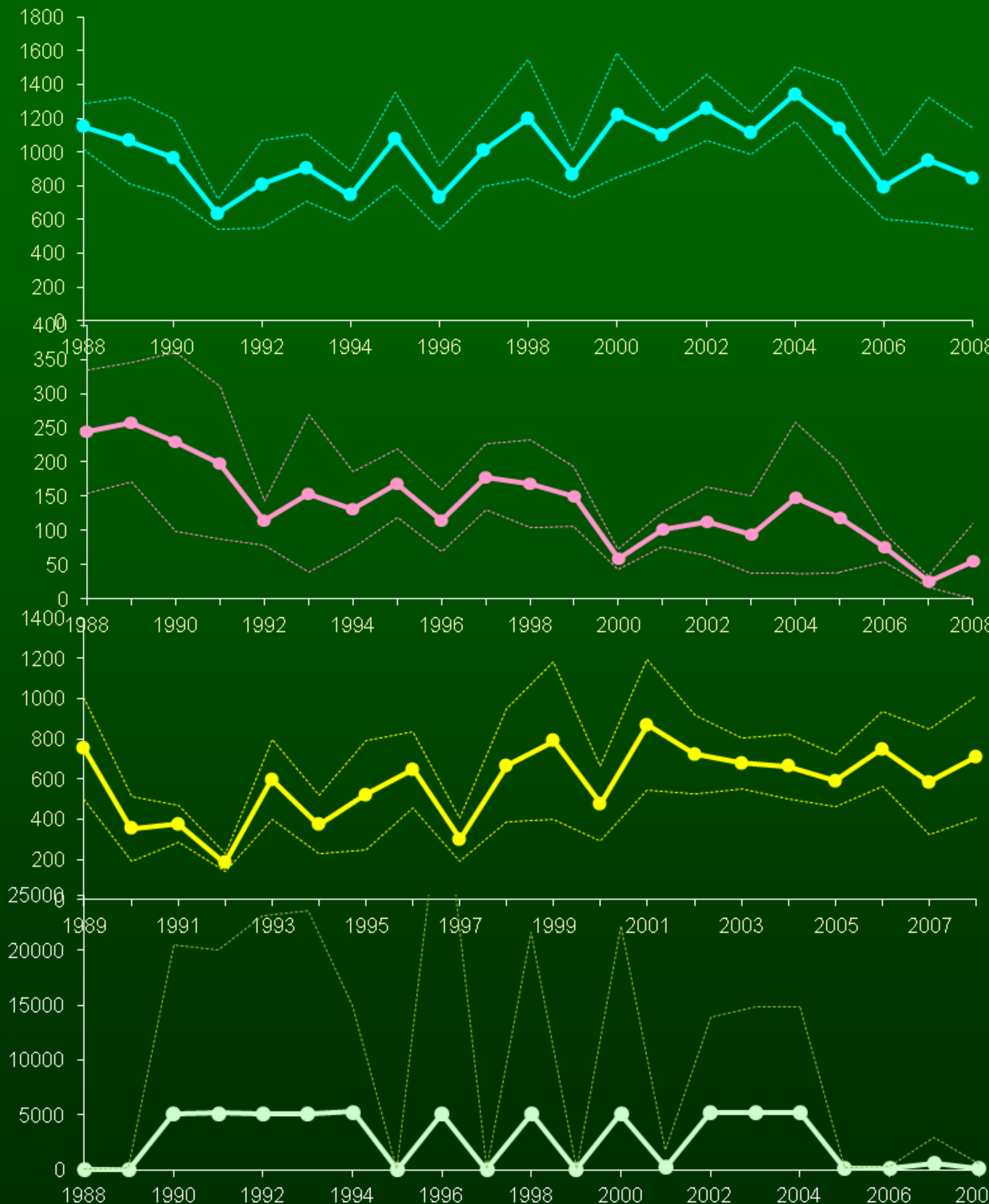
Density % open areas

Detect. –

Density –

Detect. % open areas + time

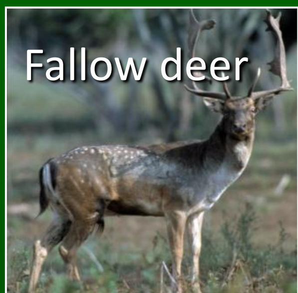
X

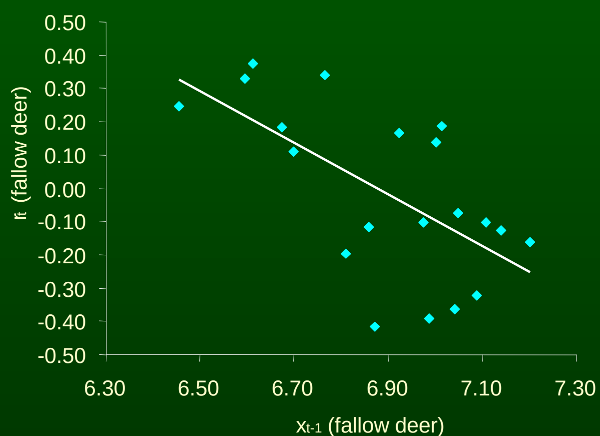


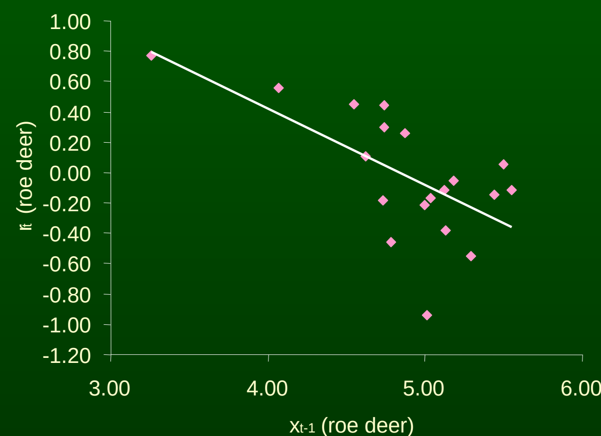
Positive effect

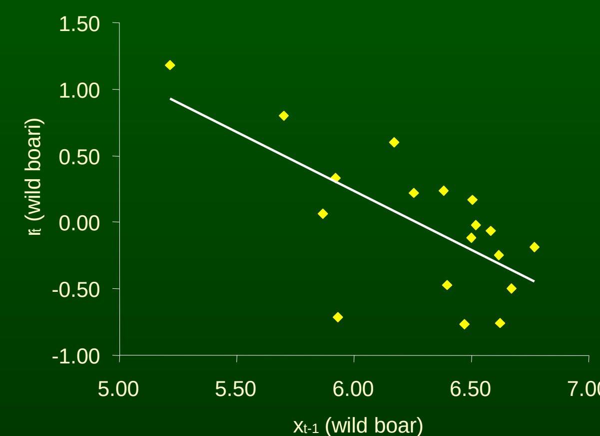
Negative effect

Growth rate:





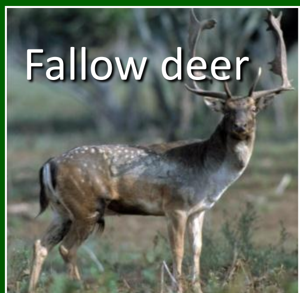


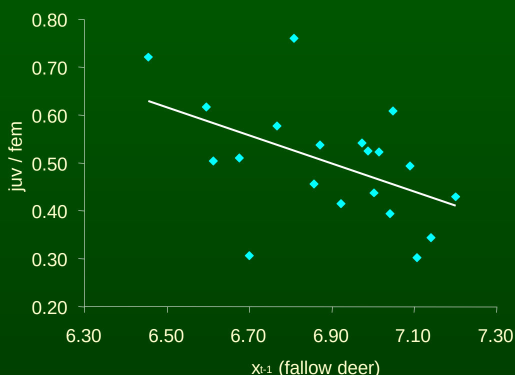


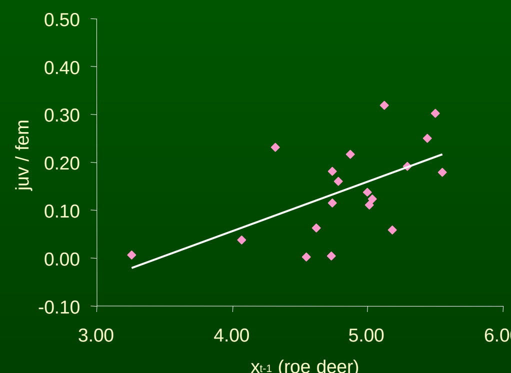
✓ Density dependence

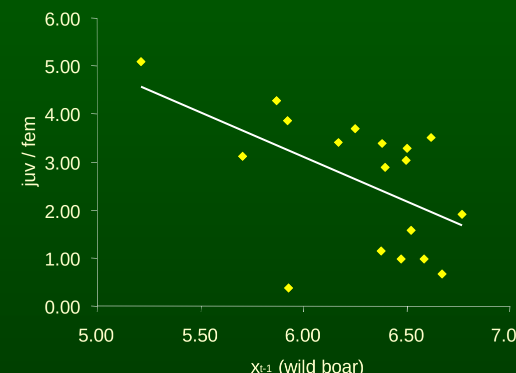
✓ No harvest rate, inter-specific interaction, climate effect and masting

Recruitment (juv/fem):



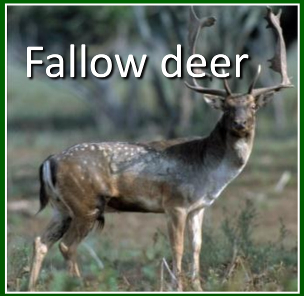


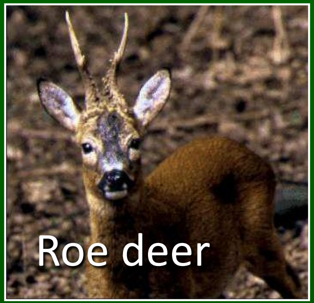




✓ Density dependence (roe deer – Allee effect?)

Recruitment (juv/fem):

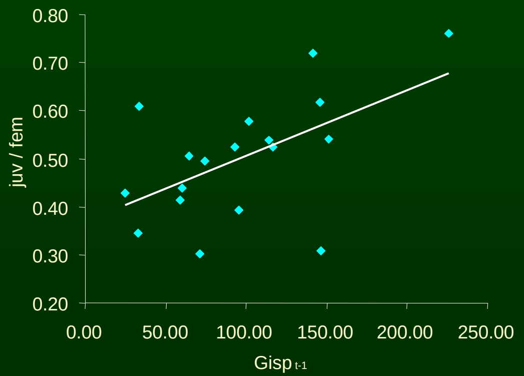


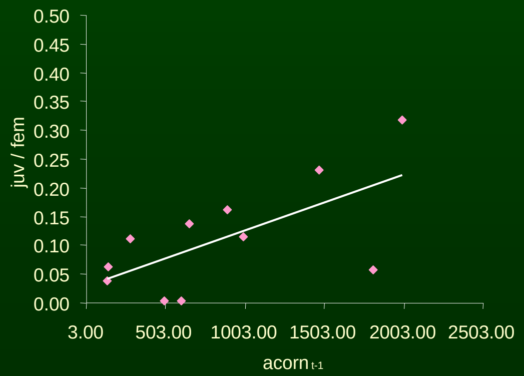


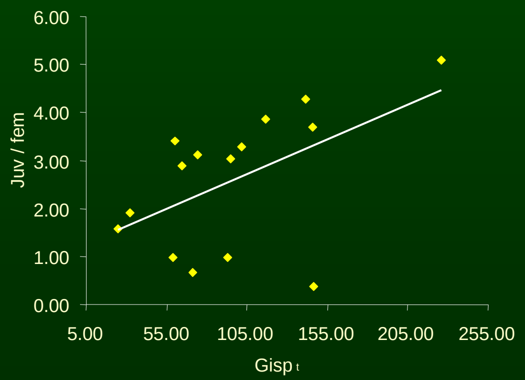
✓ Gisp$_{t-1}$

✓ Masting

✓ Gisp$_{t}$







Conclusions – recent data

- ✓ Analyses of recent data confirm the ones of historical data (Republican period): growth rate is mainly function of density dependence, for all the species.
- ✓ Roe deer: a possible “Allee effect” threats the survival of the population.
- ✓ Some environmental variables affect recruitment (spring drought, masting) but not growth rate.

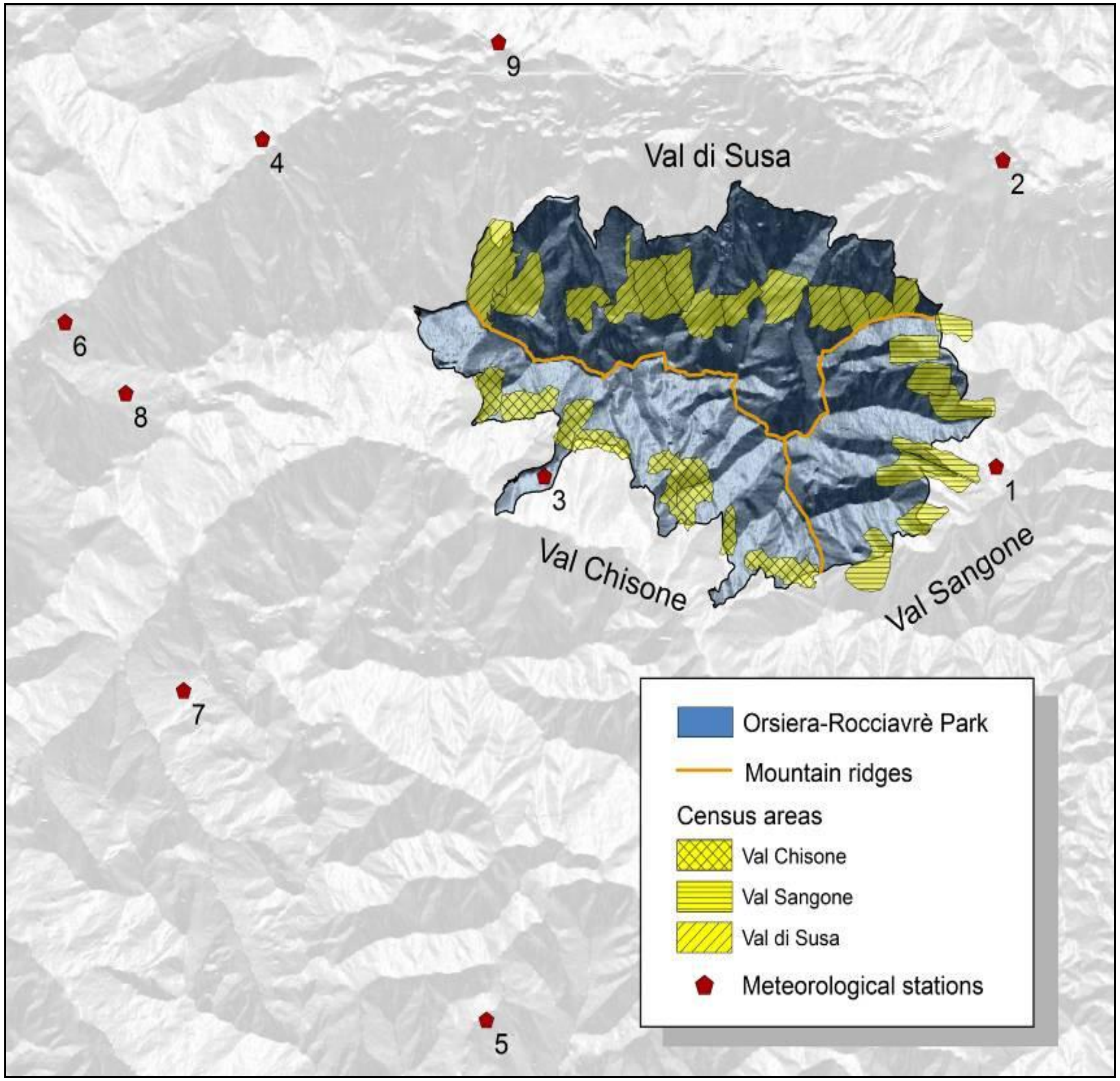
Alpine Grouses: special adaptations to mountain climate

feathers with a
secondary vexillum

feathered toes and
corneous scales

well-developed
caeca

snow burrows



Black grouse (*Tetrao tetrix*)

1991-2009

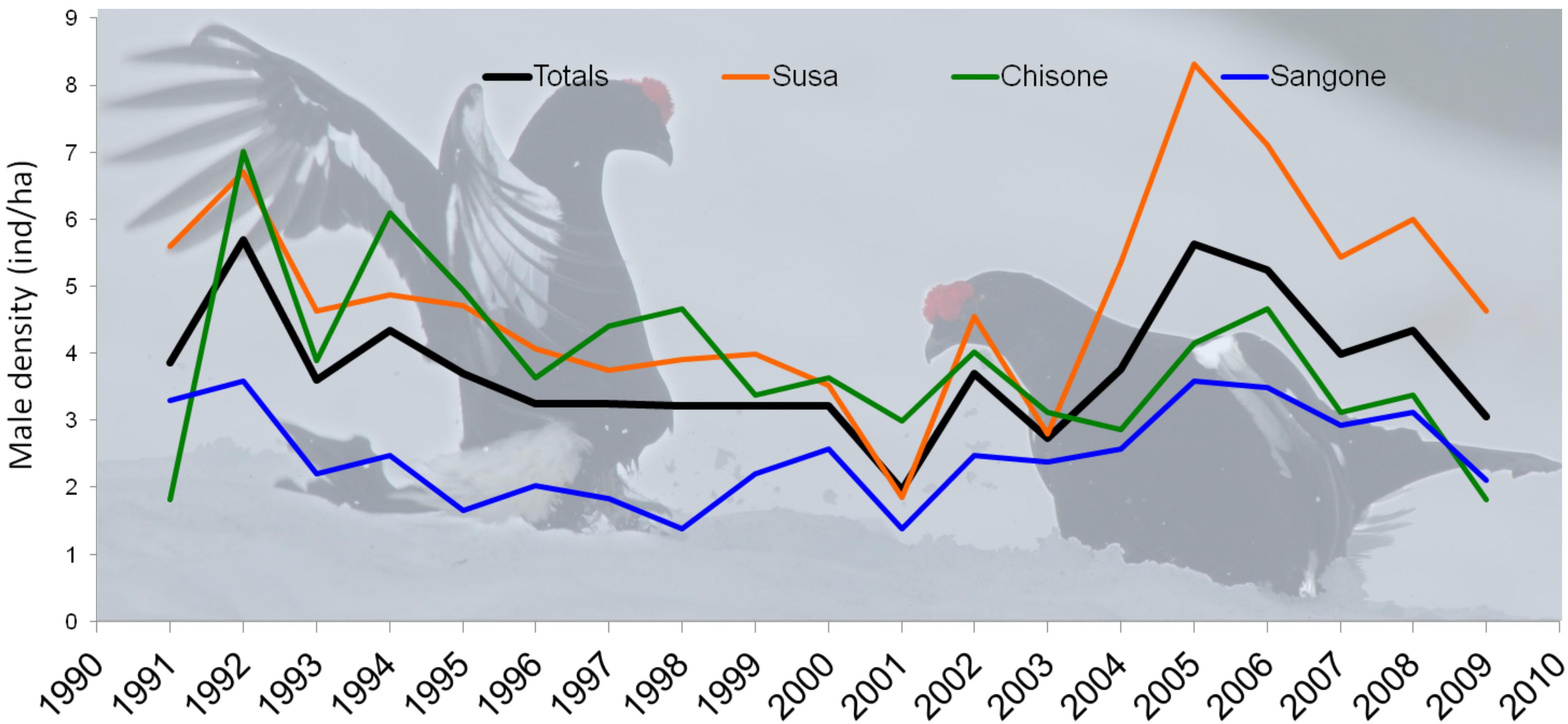
Number of leks
Number of males per lek
Number of single males

9 meteorological stations (Arpa Piemonte)

$y_t = \log(N_t / N_{t-1})$	Susa	Chisone	Sangone
Totals	0.93 (<0.0001)	0.73 (0.001)	0.78 (<0.0001)
Susa		0.47 (0.05)	0.69 (0.001)
Chisone			0.41 (0.09)

Significative coerence in population fluctuations

Probable control by a common factor



density dependence **+** meteo-climatic variables

Empirical stochastic models with density dependence and two meteo-climatic variables

$$y_t = a + bN_{t-1} + cC_1 + dC_2 + \sigma W_t \equiv Y_t + \sigma W_t$$

$$y_t = \log(N_t / N_{t-1})$$

Model ID	Variables	*p*	R^2	AICc	Outliers	Excess
Tot2 (N)	N, T_{int} - June $_{t-1}$ (1) T_{int} - Dec $_{t-1}$ (2)	< 0.001	0.82	-61.8	0.11	0.33
Tot4 (X)	logN, P - June $_{t-1}$ (1) T_{int} - Dec $_{t-1}$ (2)	< 0.001	0.80	-59.6	0.06	0.42

a, b, c and *d* are parameters to be estimated,

C_1 and C_2 are the selected climatic variables,

W_t is a random gaussian, zero-mean, temporally uncorrelated random variable.

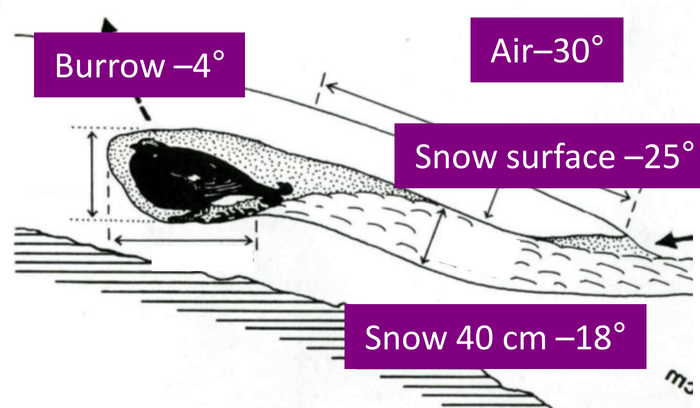
Density dependence	Negative effect of rainfalls in June	Positive effect of temperature range in December

Lindström et al., 1997

+

Summers et al., 2004
Ludwig et al., 2010

+



Klaus et al. 1990

Model ID	Variables	*p*	R^2	AICc	Outliers	Excess
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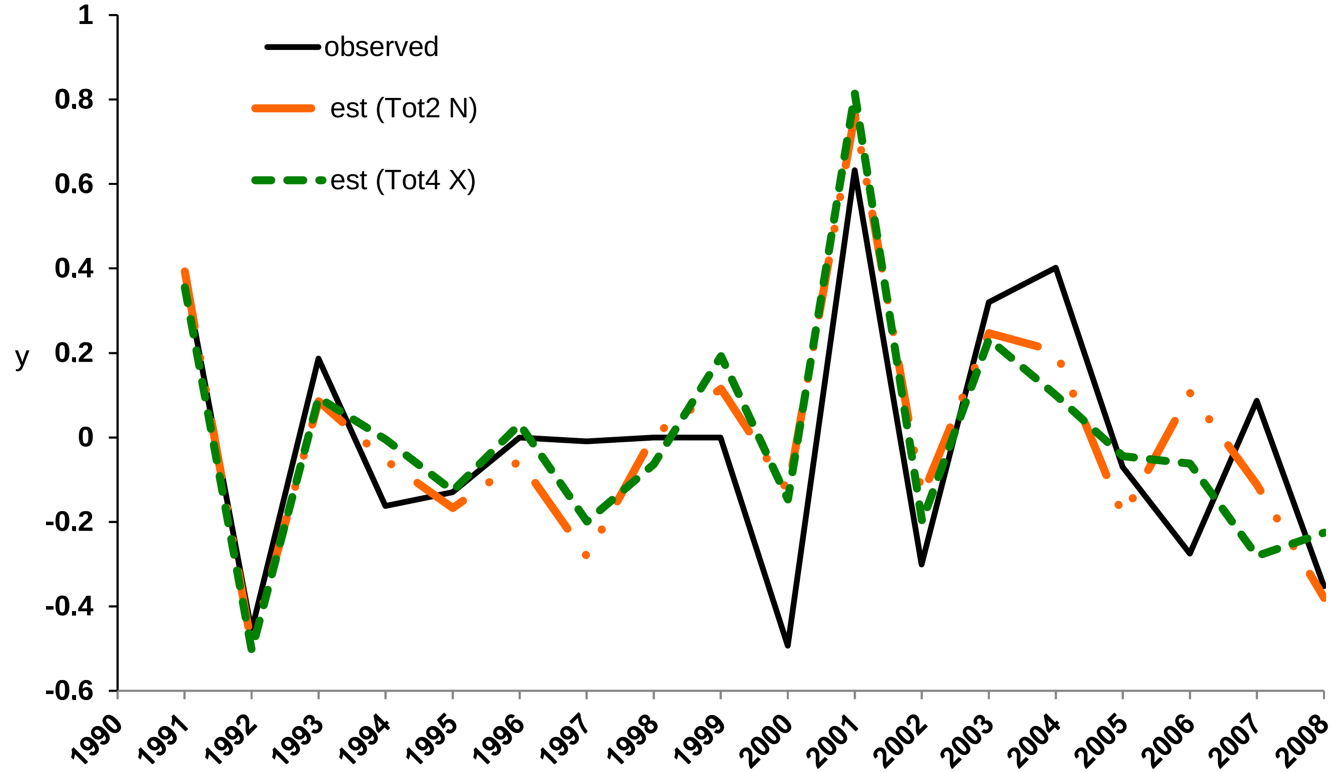
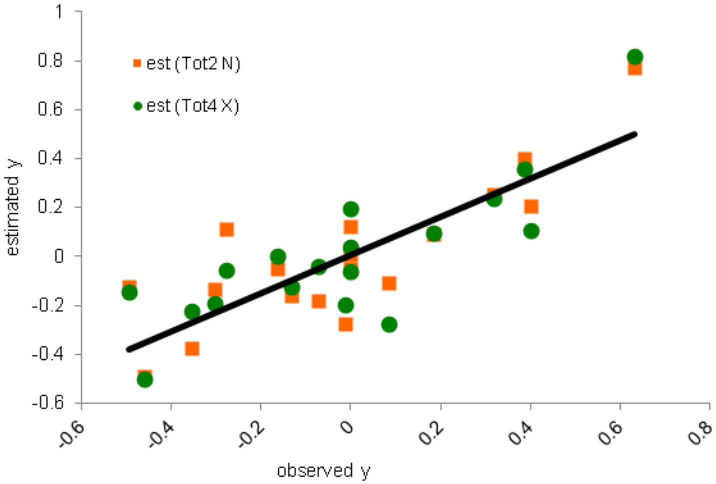
Tot4 (X)	logN , P - June $_{t-1}$ (1) T_{int} - Dec $_{t-1}$ (2)	< 0.001	0.80	-59.6	0.06	0.42

Validation:

Leave one out cross validation
(Michaelsen,1987)

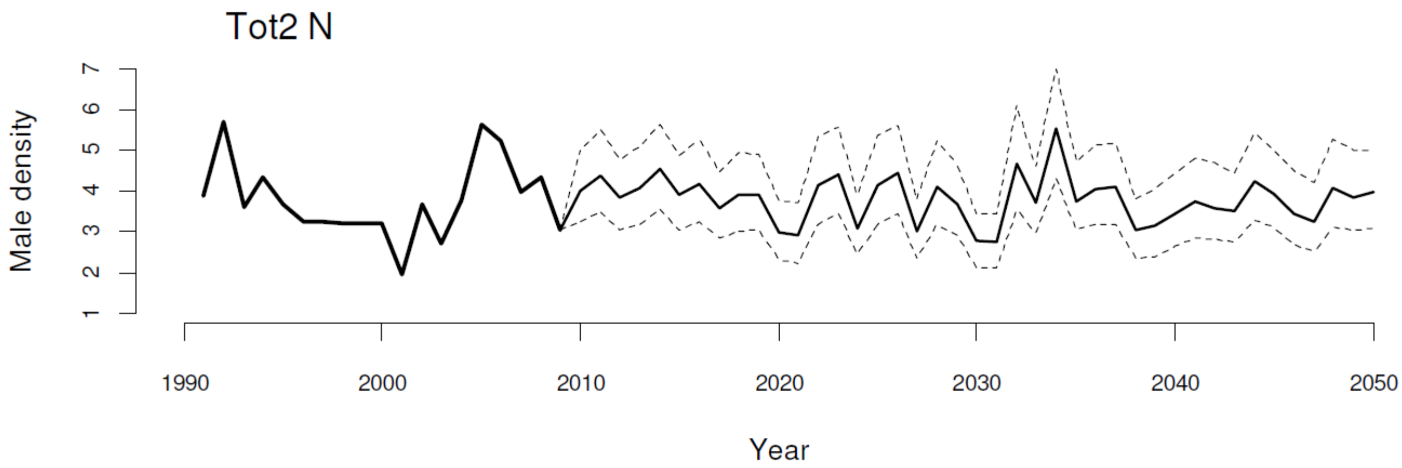


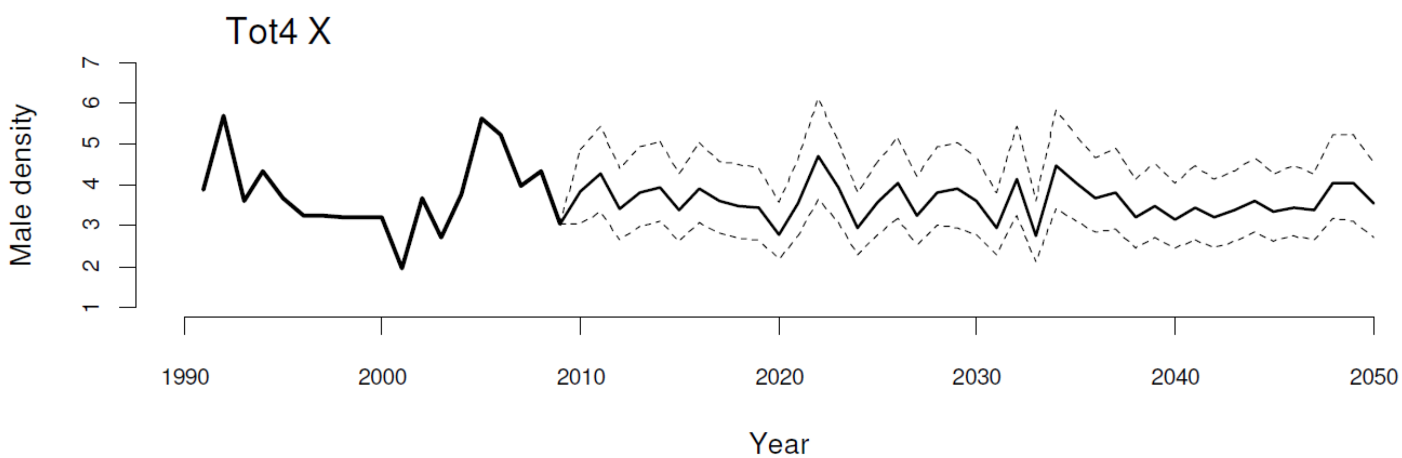


Expvar=82% CE=0.67 (Tot2N)

Expvar=80% CE=0.65 (Tot4X)

Black grouse: population projections (PROTHEUS model - A1B scenario)



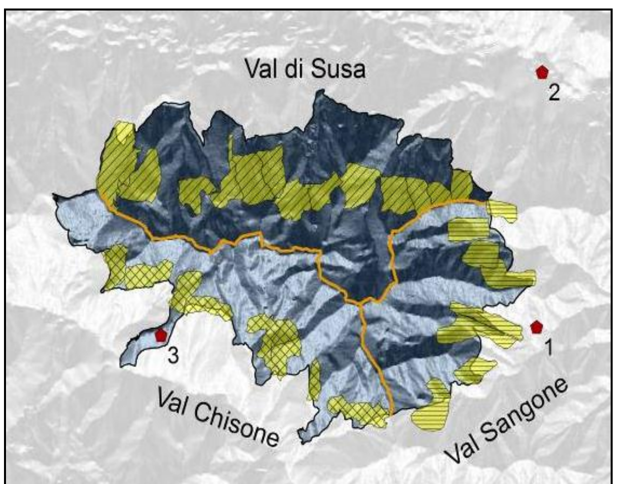


Caveats: - snow cover is not included in the populations models
- indirect effects of climate change (e.g. modifications in vegetation cover)

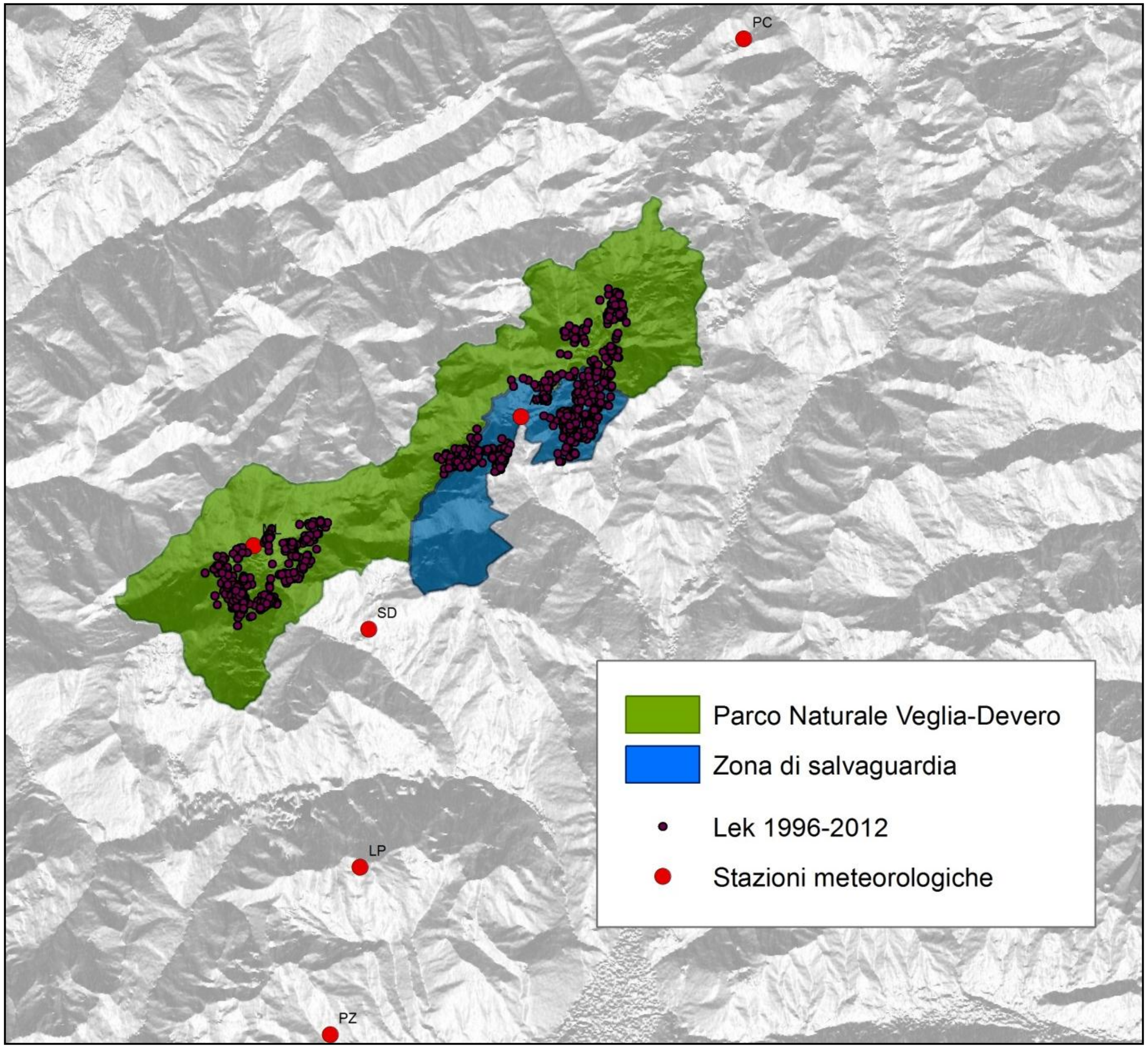
Black grouse:
population projections

(Ec-Earth model
RCP 2.6, 4.5, 8.5 scenarios)

20% decrease



Model ID	1991-2009	2031-2050 (RCP 2.6)		2031-2050 (RCP 4.5)		2031-2050 (RCP 8.5)	
Tot1 - N	**3.77**±0.95	**3.65**±0.87	(2.76-4.80)	**3.71**±0.99	(2.79-4.84)	**3.61**±0.90	(2.69-4.75)
Tot1 - X		**3.69**±0.81	(2.79-4.87)	**3.75**±0.98	(2.83-4.97)	**3.66**±0.89	(2.76-4.84)
Tot2 - N		**3.46**±0.59	(2.67-4.42)	**3.45**±1.08	(2.66-4.42)	**3.38**±1.14	(2.62-4.34)
Tot2 - X		**3.46**±0.55	(2.67-4.46)	**3.58**±1.04	(2.79-4.63)	**3.47**±1.10	(2.68-4.49)
Tot3 - N		**3.60**±0.50	(2.75-4.67)	**3.43**±0.90	(2.62-4.47)	**3.44**±0.78	(2.61-4.49)
Tot3 - X		**3.30**±0.54	(2.54-4.28)	**3.40**±1.03	(2.63-4.38)	**3.17**±1.03	(2.45-4.08)
Tot4 - N		**3.47**±0.49	(2.68-4.47)	**3.32**±0.94	(2.55-4.27)	**3.27**±0.79	(2.54-4.20)
Tot4 - X		**3.47**±0.44	(2.70-4.45)	**3.40**±0.86	(2.65-4.38)	**3.33**±0.73	(2.58-4.27)
Su1 - N	**4.83**±1.52	**4.57**±1.38	(2.92-6.96)	**4.68**±1.59	(3.01-7.11)	**4.63**±1.47	(3.00-7.05)
Su1 - X		**4.67**±1.27	(3.12-6.98)	**4.83**±1.55	(3.23-7.22)	**4.67**±1.39	(3.14-6.97)
Su2 - N		**4.34**±0.89	(2.79-6.49)	**4.40**±1.70	(2.80-6.63)	**4.37**±1.71	(2.86-6.54)
Su2 - X		**4.41**±0.83	(2.95-6.59)	**4.68**±1.69	(3.15-6.95)	**4.57**±1.61	(3.03-6.87)
Su3 - N		**4.51**±0.73	(2.95-6.76)	**4.22**±1.34	(2.70-6.32)	**4.21**±1.15	(2.70-6.32)
Su3 - X		**4.47**±0.65	(3.07-6.58)	**4.30**±1.24	(2.95-6.33)	**4.31**±1.12	(2.94-6.26)
Su4 - N		**4.35**±0.71	(2.85-6.52)	**4.08**±1.43	(2.63-6.15)	**4.06**±1.15	(2.67-6.12)
Su4 - X		**3.48**±0.45	(2.70-4.48)	**3.42**±0.88	(2.66-4.39)	**3.32**±0.72	(2.58-4.27)
Ch1 - N	**3.87**±1.28	**3.65**±1.02	(2.45-5.33)	**2.95**±0.76	(1.93-4.42)	**3.59**±1.11	(2.40-5.30)
Ch1 - X		**3.78**±0.89	(2.71-5.26)	**3.25**±0.80	(2.33-4.51)	**3.75**±1.00	(2.69-5.24)
Ch2 - N		**3.23**±0.87	(1.99-5.07)	**2.34**±0.65	(1.34-3.88)	**3.09**±0.85	(1.91-4.88)
Ch2 - X		**3.57**±0.71	(2.46-5.17)	**3.08**±0.54	(2.13-4.50)	**3.50**±0.69	(2.41-5.10)
Ch3 - N		**3.63**±0.85	(2.43-5.35)	**3.22**±1.07	(2.13-4.82)	**3.56**±1.05	(2.38-5.29)
Ch3 - X		**3.71**±0.69	(2.66-5.14)	**3.47**±1.08	(2.50-4.84)	**3.72**±0.89	(2.66-5.18)
Ch4 - N		**3.24**±0.86	(2.08-4.95)	**2.79**±0.77	(1.72-4.33)	**3.07**±0.77	(1.99-4.71)
Ch4 - X		**3.55**±0.69	(2.49-5.06)	**3.28**±0.68	(2.30-4.66)	**3.47**±0.63	(2.42-4.94)
Sa1 - N	**2.49**±0.70	**2.13**±0.34	(1.50-3.03)	**1.99**±0.34	(1.37-2.85)	**2.00**±0.50	(1.39-2.86)
Sa1 - X		**2.14**±0.32	(1.53-2.97)	**2.01**±0.29	(1.45-2.78)	**2.04**±0.44	(1.46-2.81)
Sa2 - N		**2.40**±0.50	(1.60-3.51)	**2.44**±0.64	(1.64-3.55)	**2.44**±0.58	(1.64-3.54)
Sa2 - X		**2.40**±0.47	(1.65-3.50)	**2.49**±0.63	(1.72-3.65)	**2.46**±0.58	(1.68-3.55)
Sa3 - N		**2.25**±0.36	(1.61-3.10)	**2.27**±0.63	(1.62-3.12)	**2.19**±0.68	(1.57-3.02)
Sa3 - X		**2.24**±0.34	(1.66-3.03)	**2.30**±0.59	(1.69-3.12)	**2.23**±0.64	(1.65-3.04)
Sa4 - N		**2.19**±0.33	(1.54-3.10)	**2.11**±0.49	(1.47-2.97)	**2.06**±0.49	(1.44-2.90)
Sa4 - X		**2.19**±1.56	(1.58-3.03)	**2.15**±0.46	(1.56-2.98)	**2.08**±0.45	(1.50-2.86)

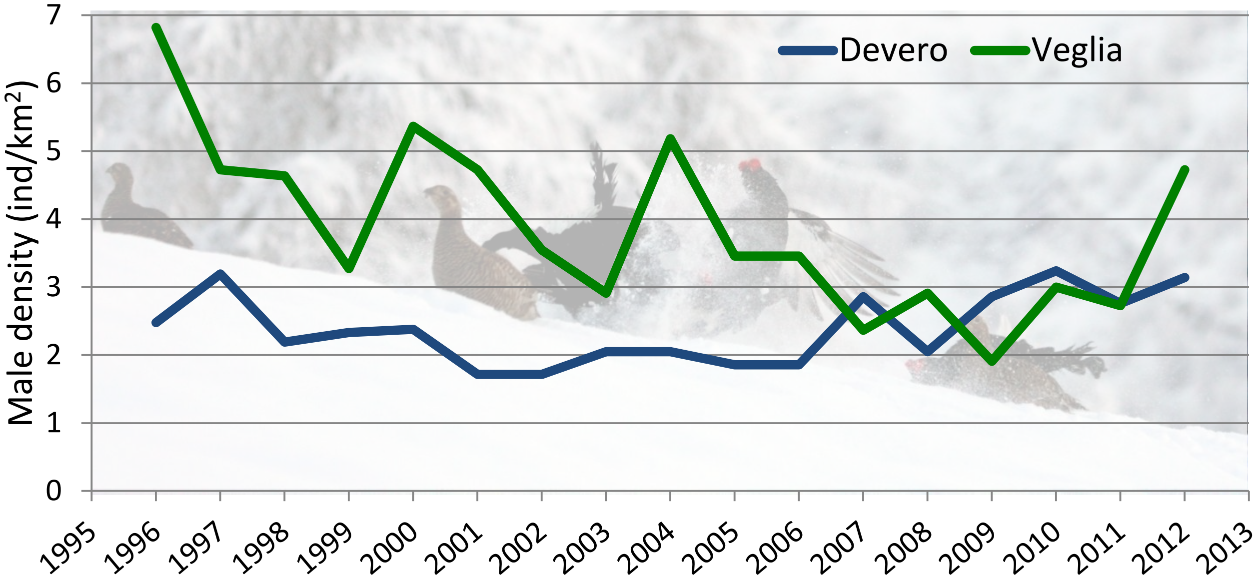


Black grouse (*Tetrao tetrix*)

1996-2012

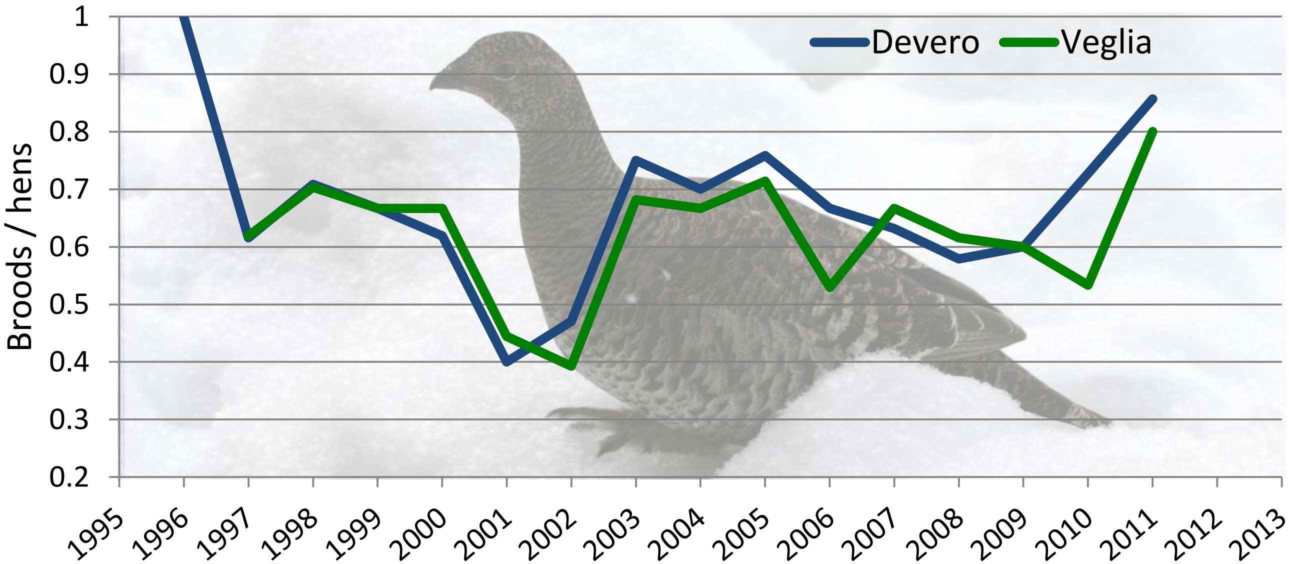
Number of males (spring)
Breeding success (summer)
Parasite load

6 meteorological stations (Arpa Piemonte)

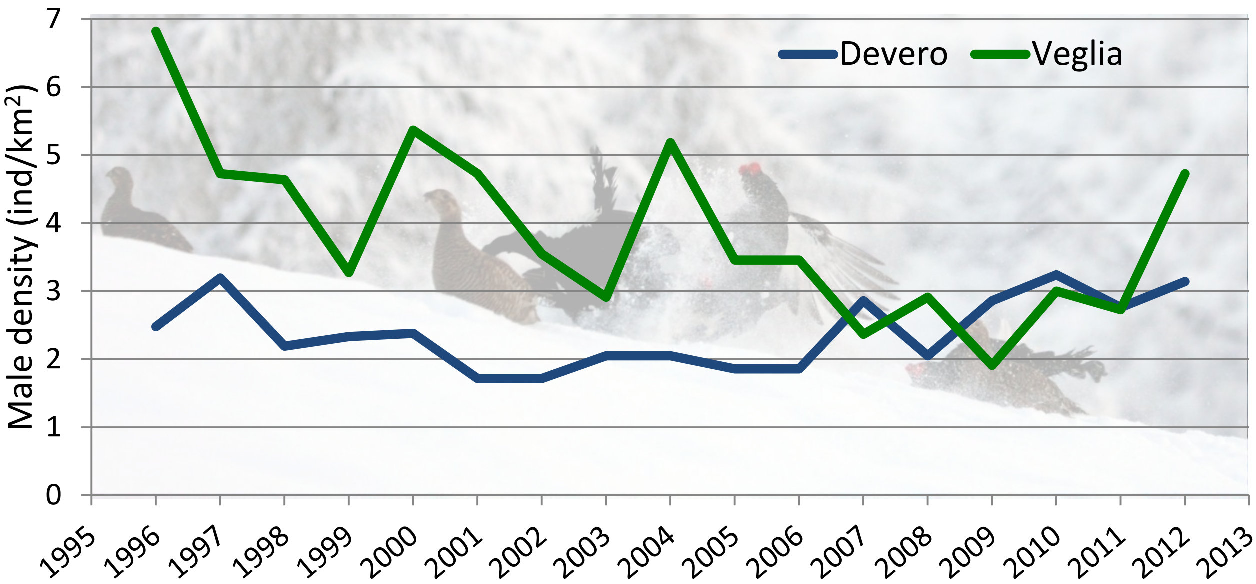


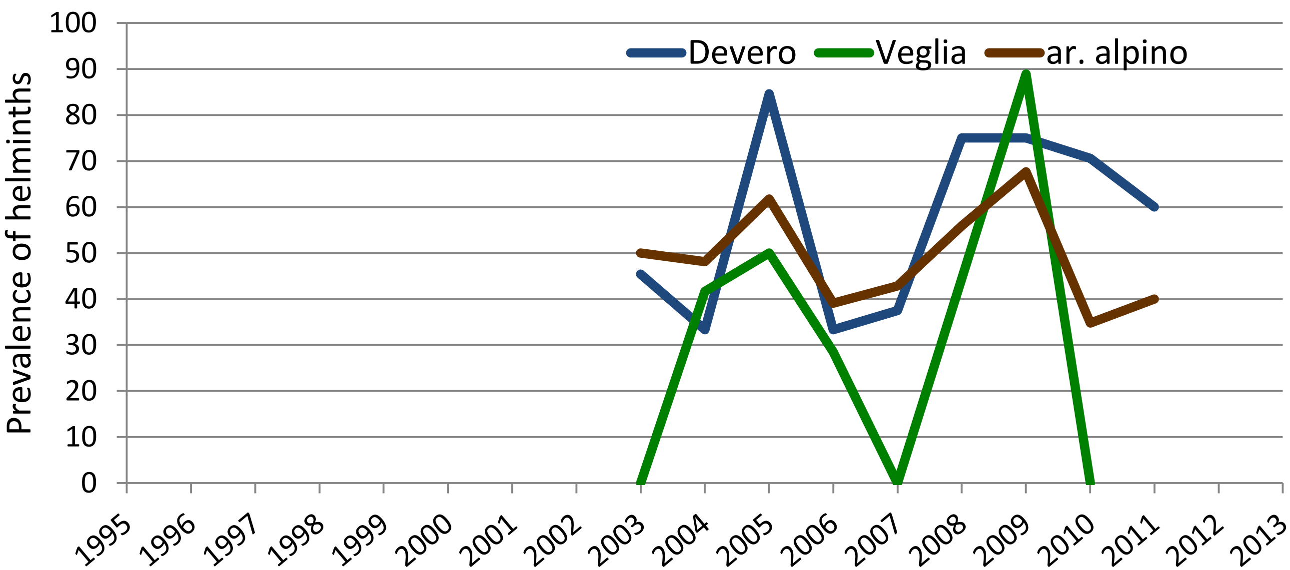
No correlation between the two areas (p=0.42)

(mountain ridge > 2.300 m)

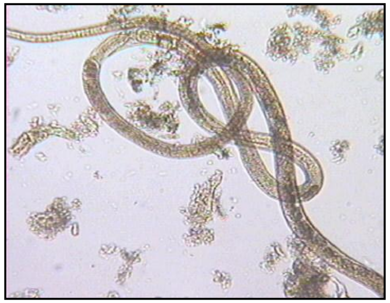


Highly significant correlation between the two areas (p=0.0003)

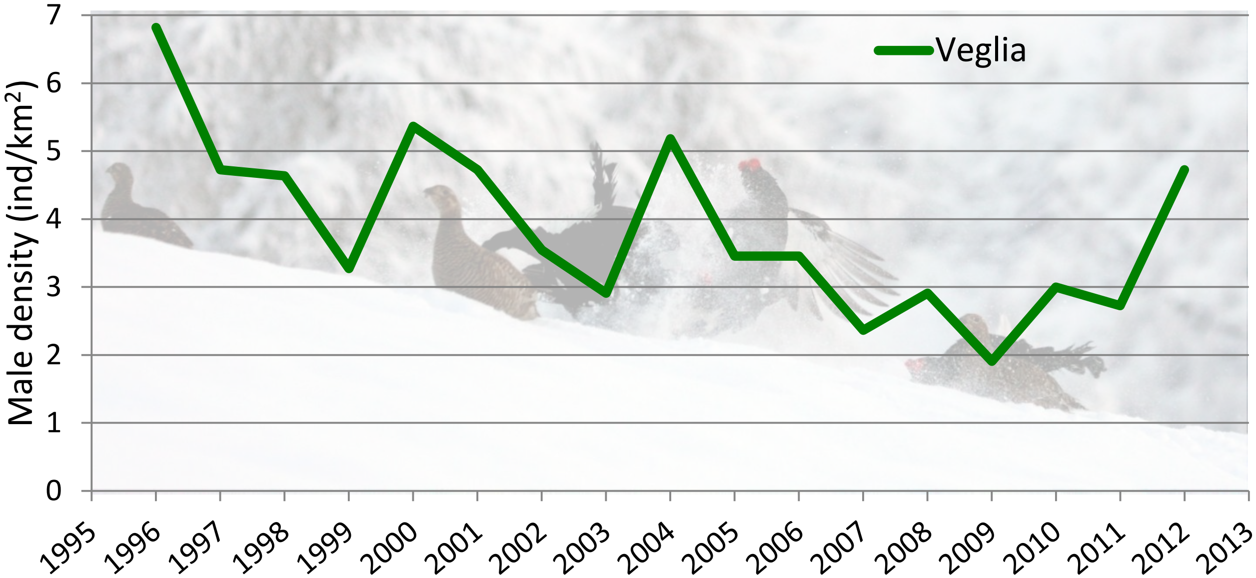


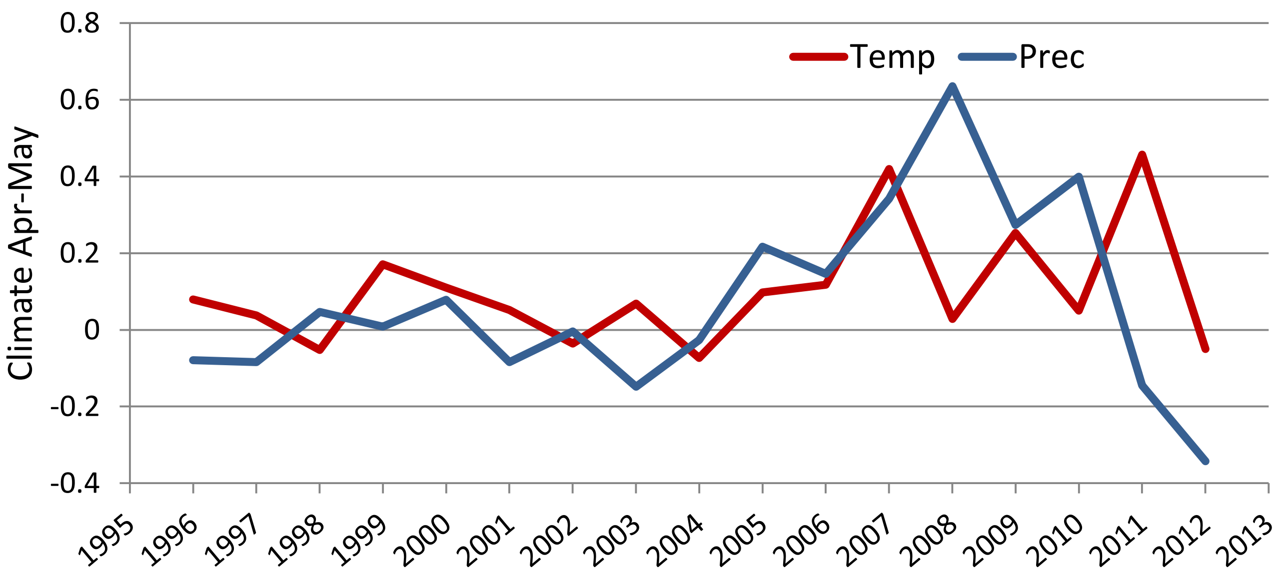


Ascaridia sp.



Capillaria sp.





Selected model
(detrended data):

density dipendence –

+

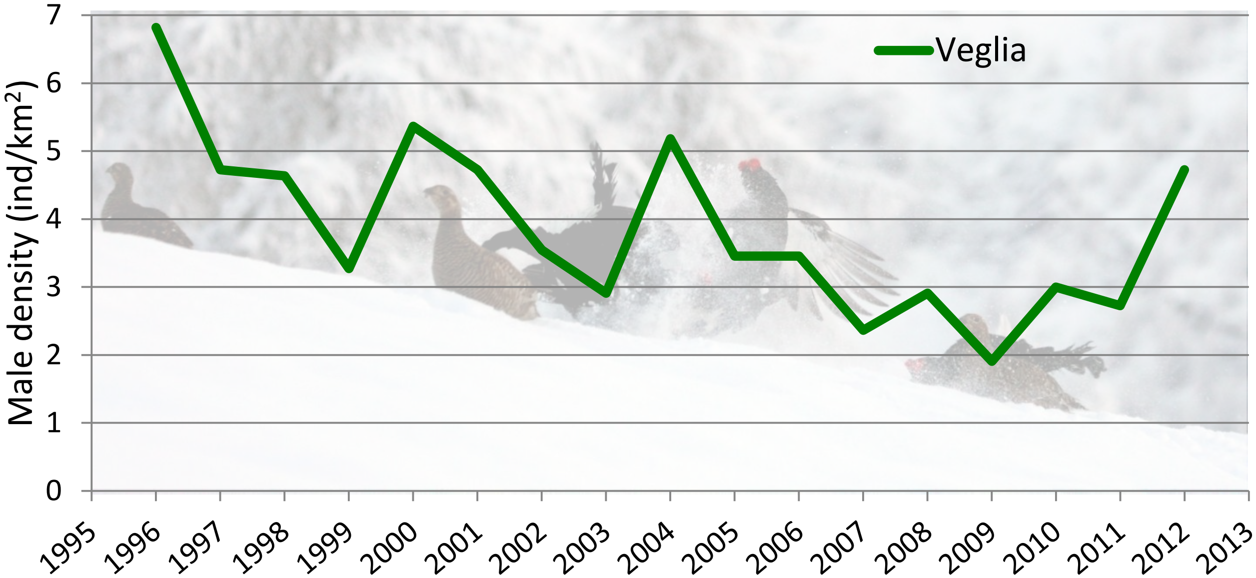
P (April-May)$_{t-1}$ –

+

T_{max} (April-May)$_{t-1}$ +

$p<0.0001$ $R^2=0.81$

Prevalence and intensity of helminth parasites!



Selected model

(detrended data):

density dipendence –

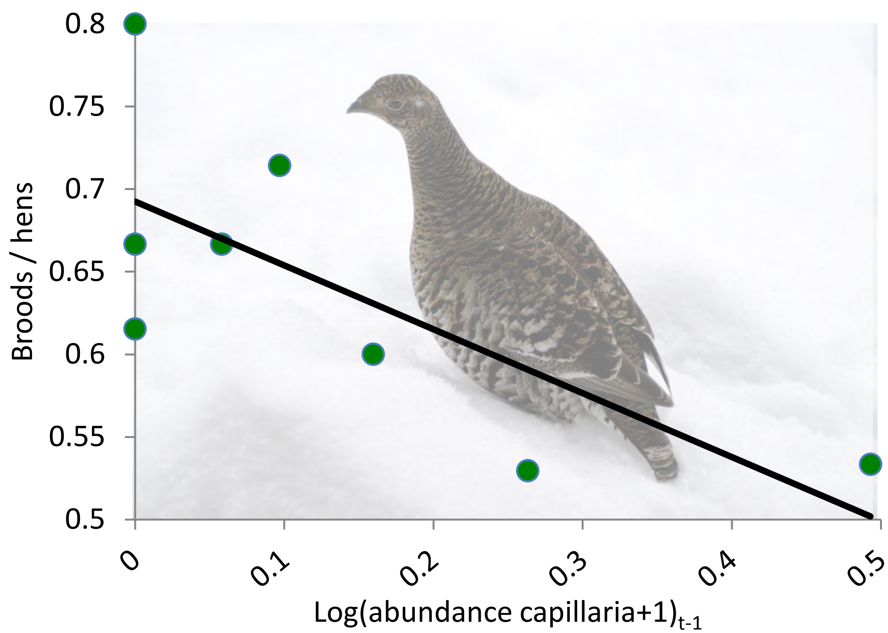
\+

P (April-May)$_{t-1}$ –

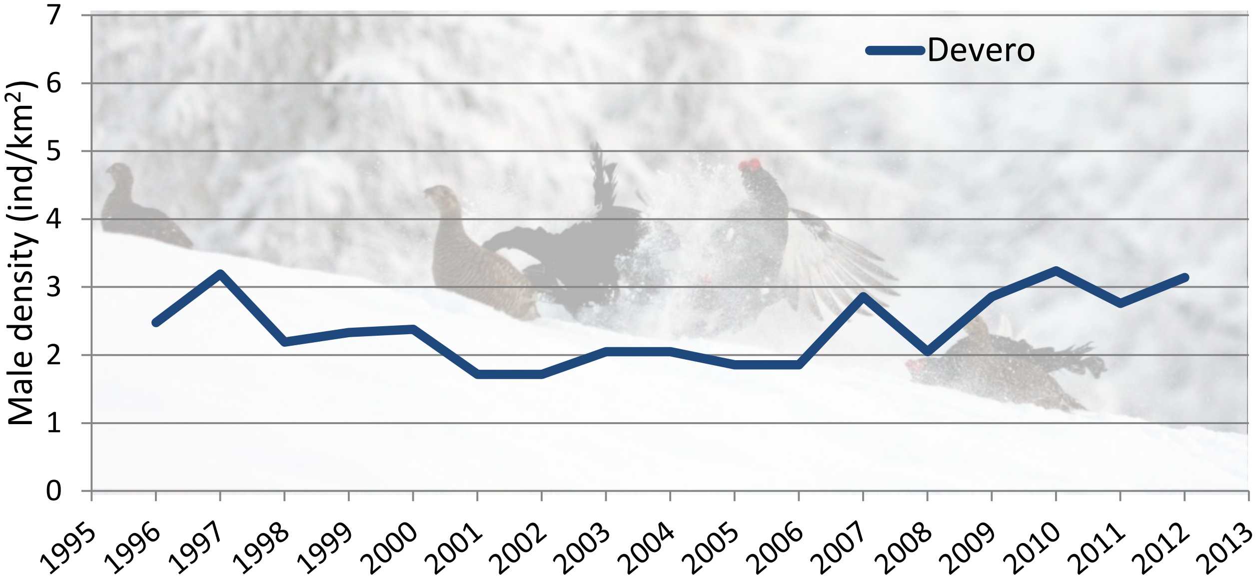
\+

T_{max} (April-May)$_{t-1}$ +

$p<0.0001$ $R^2=0.81$



Prevalence and intensity of helminth parasites!



Selected model:

density dependence –

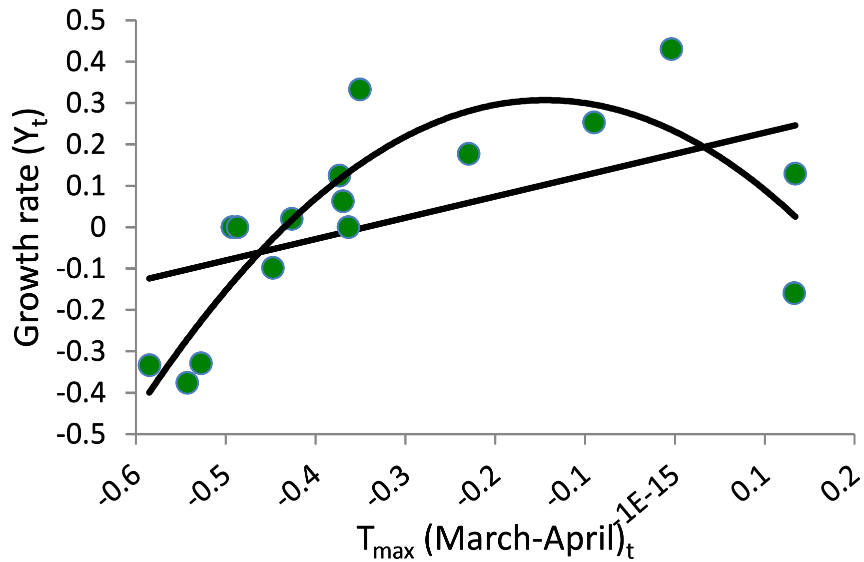
+

P (Dec-Feb)$_{t-1}$ +

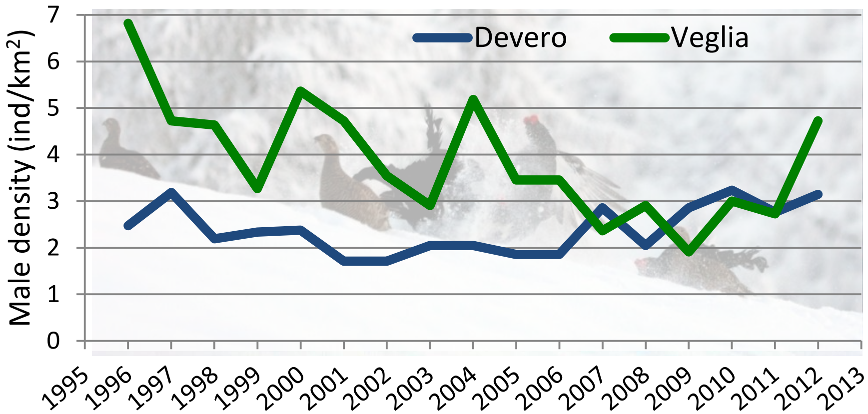
+

T_{max} (March-April)$_t$ +

$p<0.001$ $R2=0.74$



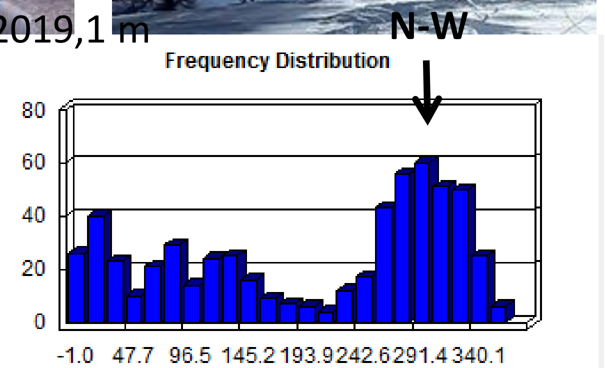
Why the two areas are so different?



Spring observations in Devero:

Mean altitude: 2019,1 m

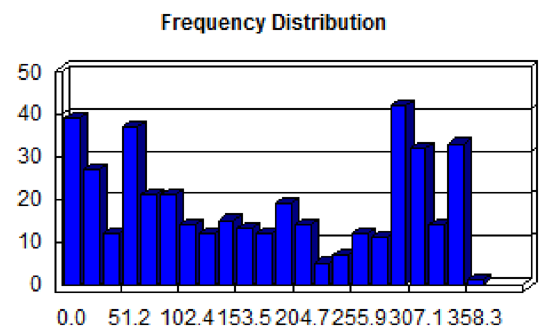
Aspect:

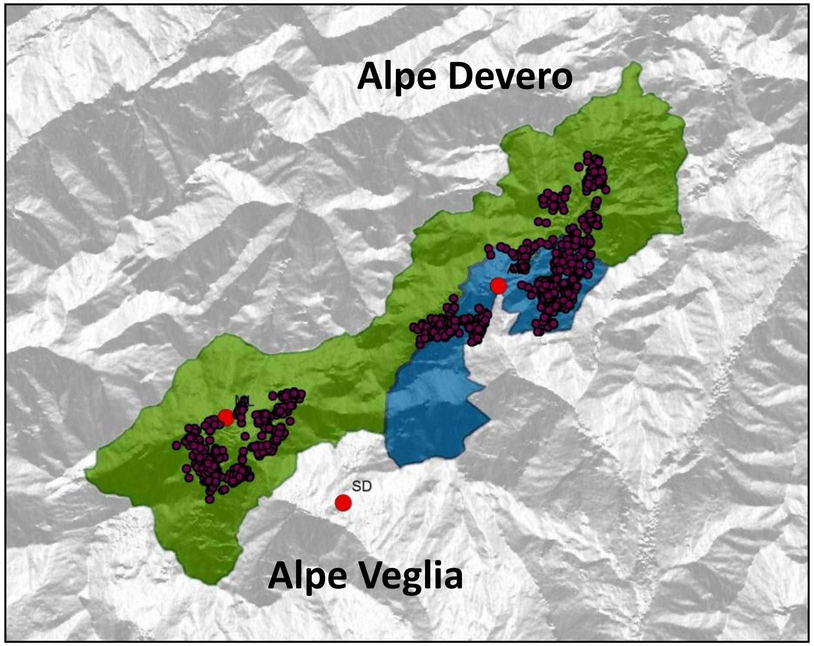


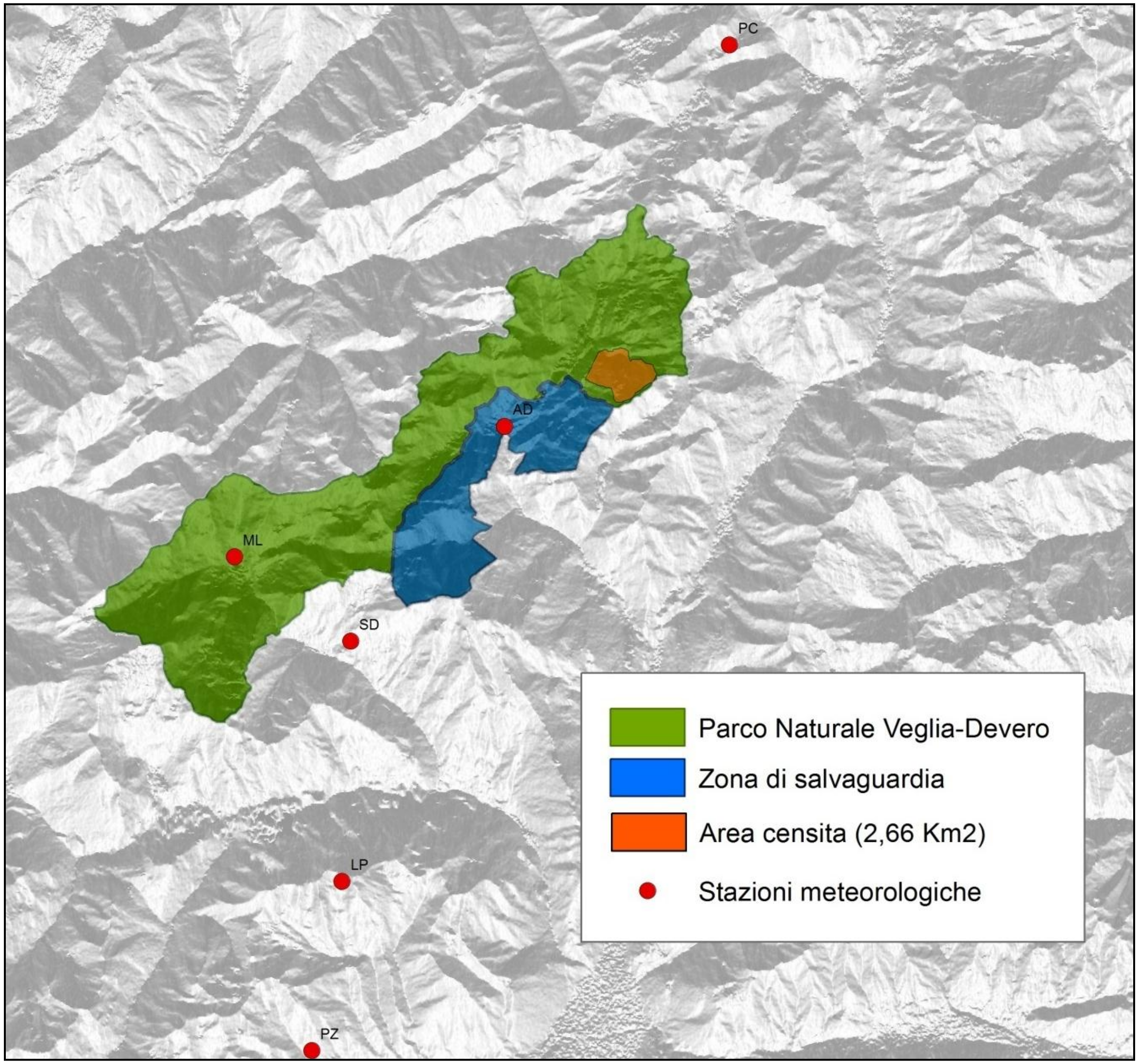
Spring observations in Veglia:

Mean altitude: 1950,4 m

Aspect:





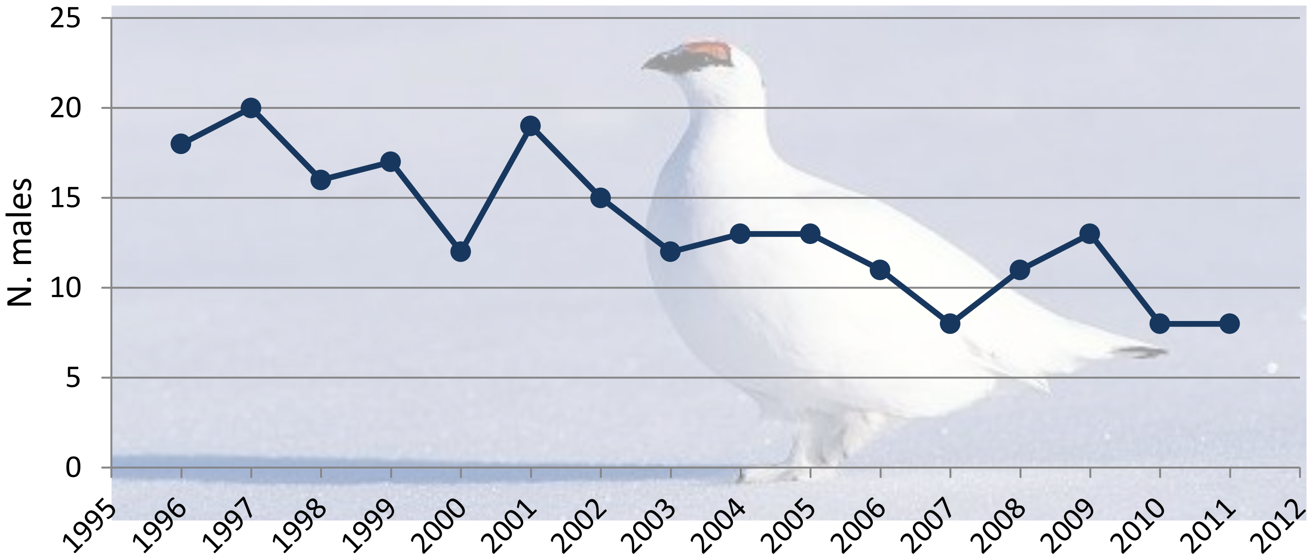


Rock ptarmigan
(*Lagopus mutus helveticus*)

1996-2011

Number of males

6 meteorological stations (Arpa Piemonte)



Selected model
(detrended data):

density dipendence –

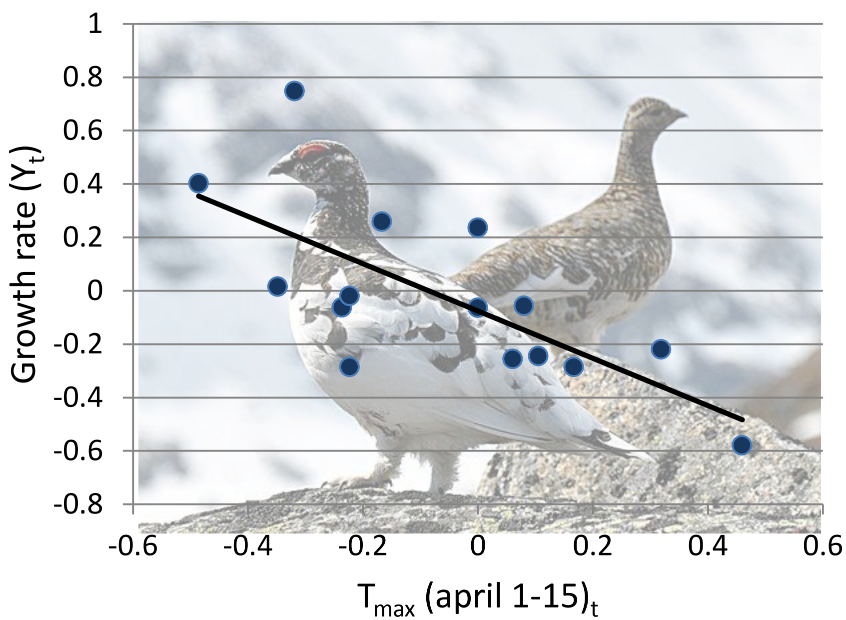
+

P (Feb 1-15)$_t$ +

+

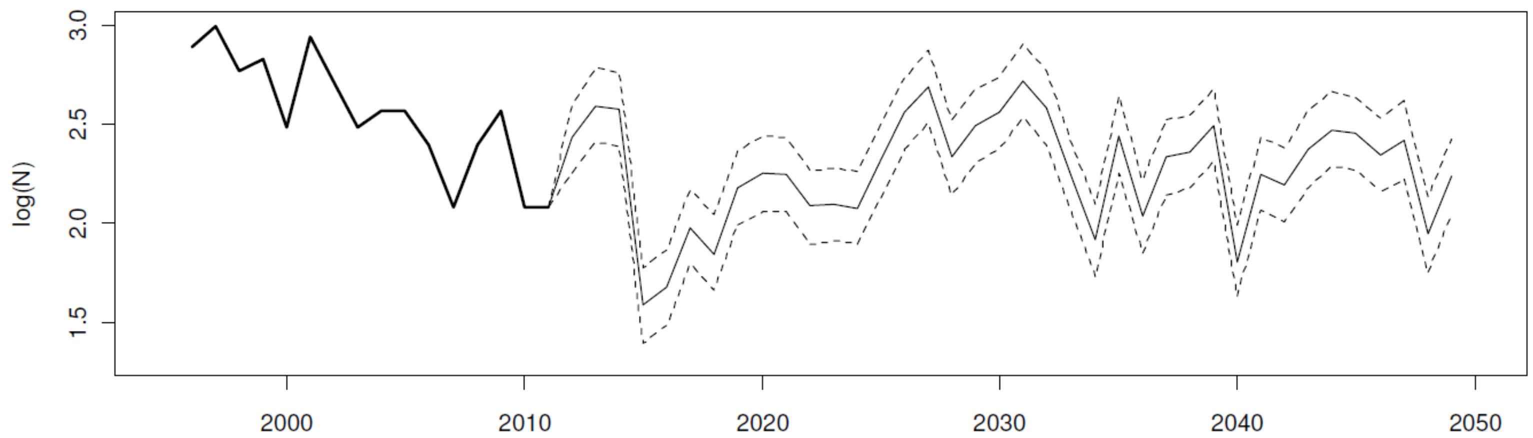
T_{mean} (Apr 15-30)$_t$ –

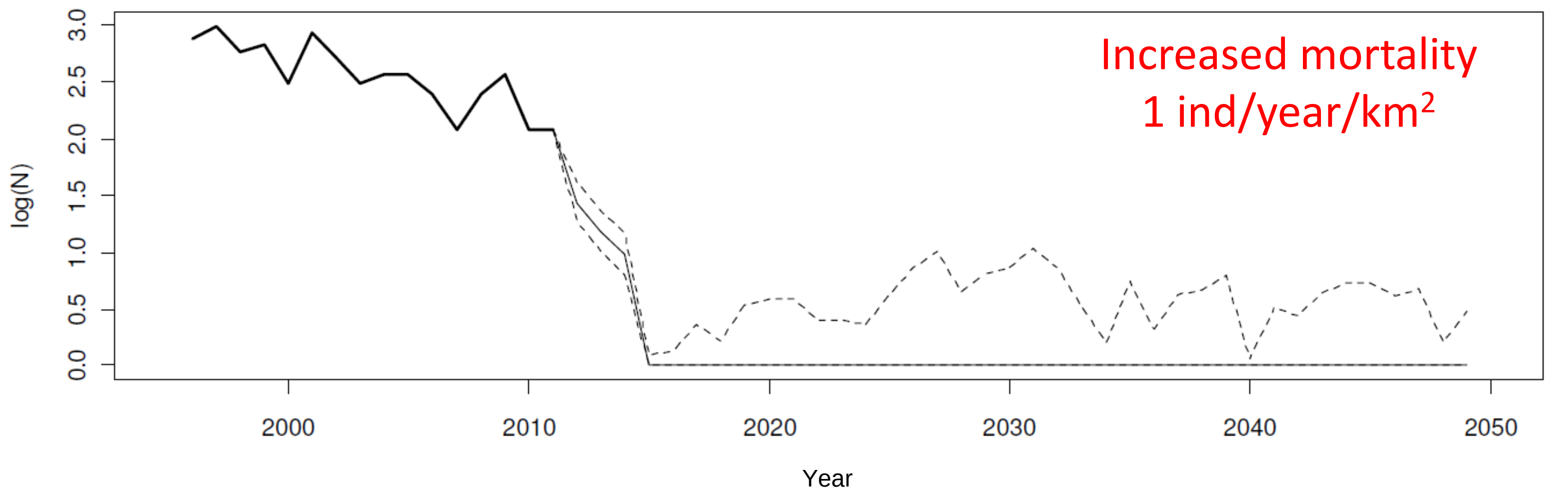
$p<0.0001$ $R^2=0.91$



Mismatch between snowmelt and moult?

Rock ptarmigan: population projections (PROTHEUS - A1B scenario)





Thank you for your attention

and thanks to:

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Regione and ARPA Piemonte
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