Grazing by goats on islands affects the populations of an endemic Mediterranean lizard

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Abstract

Grazing of goats on Mediterranean islets is a common practice. Its consequences on plant communities are well documented, although not on vertebrates. We aim to shed light on the effect of livestock farming on lizards by investigating five populations of the insular lizard, *Podarcis gaigeae*, differing in the duration and intensity of grazing. Data on grazing regime, invertebrate abundance, tick prevalence, infestation levels, gull nests and lizard densities were collected during a period of 6 consecutive years. Grazing had a negative impact on insect populations, thus decreasing food availability for lizards. Tick prevalence and infestation levels were higher in places of continuous grazing. Goat activity disturbed gulls, which avoid nesting, so depriving the islets of marine subsidies. As a consequence of all these factors, lizard densities were higher in ungrazed and lower in grazed biotopes. Grazing effects were more severe on islets communities than on the main island populations. Our data imply that management action should be taken to conserve the highly diverse islet populations.

Introduction

Habitat deterioration, due to anthropogenic activities, is one of the most important factors in the extinction of animal species (Primack, 1998). Even activities with low environmental cost can alter habitat and cause significant negative effects (Amo, López & Martín, 2006). Grazing is a major factor, which has led to large-scale ecosystem devastation after the 'industrialization' of livestock farming during the last 150 years (Fleischner, 2002).

The impact of livestock grazing on vegetation is well documented (Fleischner, 1994). Vegetation structure complexity is of pivotal importance for the welfare of animal communities, and lizards are no exception (D'Cruze & Kumar, 2011). Grazing-induced changes in vegetation cause numerous problems to lizards by altering microhabitats and razing refuges (Pettigrew & Bull, 2011), causing shifts in the thermal quality of habitats (Vitt *et al.*, 1998) and decreasing terrestrial arthropod communities (Woodcock *et al.*, 2005). The final outcome is expressed as lower lizard population densities (Bock, Smith & Bock, 1990).

Further to this, grazing has another, indirect, effect on lizards. Livestock carry many ectoparasites, notably mites and ticks (Liebisch, 1997). Many species of hard ticks (Ixodidae) parasitize reptiles, especially lizards (Casher *et al.*, 2002). Although infestation by ticks is probably not a direct cause of mortality (Schall, Prendeville & Hanley, 2000), ticks have been reported to affect lizards in many ways such as they may induce secondary infections and diseases by transmitting blood parasites (Bull & Burzacott, 1993), remove blood and induce anaemia (Chilton & Bull, 1993), reduce reproductive performance (Vaclav, Prokop & Fekia, 2007) and cause behavioural changes (Main & Bull, 2000). Such changes may have deleterious effects on the survival of insular populations, which are more susceptible to extinction than their mainland peers (Foufopoulos, Marm & Ives, 2011).

An interesting case of grazing is the use of islets as pastures for free-roaming goats, which is common throughout the Mediterranean Sea (Bergmeier & Dimopoulos, 2003). Stockbreeders release goats, providing no food or water. Goats feed on the islets' vegetation, isolated in these natural folds until shepherds collect them. Grazing causes perturbation to the fragile islet ecosystems. Vegetation decreases and consequently invertebrate communities, the main lizard prey, are most probably affected as well (e.g. Rambo & Faeth, 1999).

Although food availability is restricted in the islands, and especially in Mediterranean islets (Castilla, Vanhooydonck & Catenazzi, 2008), an additional nutrient input supports some islet communities: marine subsidies. Sea birds are responsible for the energy inflow from sea to terrestrial ecosystems through guano, fish scraps and their decomposing carcasses (Anderson & Polis, 1999). This 'manna from heaven' fuels local plant, arthropod and eventually, lizard communities (Barrett *et al.*, 2005).

Grazing-induced effects on lizards have already been assessed on the mainland. In this study, we examined patterns in the density of lizard populations in an insular system, the Skyros Archipelago (Aegean Sea, Greece), which is home to the endemic Skyros wall lizard, *Podarcis gaigeae*. The satellite islets host lizard populations that deviate in many traits from their main island peers. For instance, the Mesa Diavates islet population differs in body size and behaviour (Pafilis *et al.*, 2009*a*), colour morphs (Runemark *et al.*, 2010) and reproductive performance (Pafilis *et al.*, 2011). The phenotypic diversity of such population is of particular ecological and conservation value.

Focusing on five biotopes under different grazing regimes, we had two main objectives: (1) to assess the main effects of grazing (decrease of arthropod availability as consequence of vegetation decline, tick infestation and elimination of gull colonies), and (2) to compare estimates of population densities between grazed and ungrazed biotopes. We predicted that grazing would boost tick prevalence and cause the departure of gull populations, thus triggering a chain reaction: the soil is deprived of nutrients (Kolb, Jerling & Hambäck, 2010); plant communities decrease with a subsequent fall in primary productivity (Bergmeier & Dimopoulos, 2003); herbivorous invertebrates are reduced while detritivore and scavenger invertebrates lack food (gull carcasses and their food remains). As a result, local food webs risk collapse and lizards, the top predators on islets, have to deal with this exacerbated food scarcity (Pafilis *et al.*, 2009*a*).

Materials and methods

Study system

The Skyros Archipelago (N 38°51′, E 24°33′) comprises the main island of Skyros and 21 surrounding islets of varying sizes, the majority of which harbour the endemic Skyros wall lizard. *P. gaigeae* is a small-bodied lacertid lizard [snout to vent length (SVL) around 60 mm, body mass 6.58 ± 1.3 g] that lives in most habitats and feeds on terrestrial arthropods, mainly insects (Valakos *et al.*, 2008). Because of the restricted extent of its range, International Union for Conservation of Nature included *P. gaigeae* in the list of vulnerable species (Lymberakis, 2009).

Skyros has a long history of overgrazing. Animal husbandry is one of the island's oldest activities, and is still flourishing. Pindar (522–443 BC) himself praised the abundance of milk that Skyros goats produced (Race, 1997). The Skyrians even coined a silver didrachm (a coin worth two drachmas) depicting two goats feeding on a fig leaf (middle of the 5th century BC). Large flocks of sheep and goat are free to graze on Skyros that harbours a total of 38 500 animals. The breeding of livestock contributes an impressive 30% to the local income, representing the backbone of the Skyros economy (source: Skyros Municipality). Islets did not escape of this widely practiced activity; depending on size, they host from 3 to 4 goats up to several hundred animals that seriously alter vegetation (Snogerup & Snogerup, 2004). Most of the islets are common lands belonging to the community of Skyros. In auctions that take place every 4 years, the community hires out islets to the highest bid. Tenants have the right to bring goats and use the islets they hire as pasture.

To evaluate grazing effect on lizards, we visited five biotopes: Palamari and Nyfi on the main island, and three islets, each of which has been subjected to different grazing pressures (Table 1) during a period of 6 years (2006–2011). Palamari is a semi-dunal biotope with sparse phrygana vegetation that has never experienced grazing and Nyfi is a smooth slope covered with maquis, which has experienced long-term heavy grazing. As for the islets, Mesa Diavates (hereafter Diavates) with its lush vegetation consisting of nitrophilous plants has remained ungrazed for the past 15 years, Lakonissi with its mixed vegetation of phrygana and

Table 1 Sea gull nests, grazing regime (occurrence or not), tick prevalence (% of infested lizards within the population) and geographic origin of the populations used in the study

	2006	2007	2008	2009	2010	2011	
Palamari (main island, 207)	–	–	–	–	–	–	Nests
	–	–	–	–	–	–	Grazing
	26.08	27.5	27.77	26.82	27.9	25.64	Tick prevalence
Nyfi (main island, 207)	–	–	–	–	–	–	Nests
	+	+	+	+	+	+	Grazing
	50.00	45.83	46.66	46.66	48.57	44.00	Tick prevalence
Diavates (0.019)	50	60	55	53	48	62	Nests
	–	–	–	–	–	–	Grazing
	14.7	16.21	16.66	14.63	13.15	14.28	Tick prevalence
Lakonissi (0.016)	10	5	6	12	7	4	Nests
	–	+	+	–	+	+	Grazing
	25.92	48.38	45.16	25.8	45.83	51.72	Tick prevalence
Valaxa (4.33)	5	8	6	12	7	15	Nests
	+	+	+	+	+	+	Grazing
	52.63	55.00	59.09	52.94	55.55	52.63	Tick prevalence

Number in parenthesis stands for the biotopes' area (in km²).

nitrophilous plants harbours 2–5 goats in a non-regular basis and Valaxa, with phrygana vegetation, hosts big flocks of goats (around 500 animals). Apart from grazing patterns, the islets also differ in the number of yellow-legged gull nests, *Larus michahellis*, which serve as carrier of nutrients during the breeding season. At each sampling, we recorded the presence/absence of goats and gulls' nests by covering the whole area of the biotopes under study.

Invertebrate abundance

We assessed prey availability using the quadrat counts method, which produces a good estimate within a narrow time window (Díaz & Carrascal, 1991*a*). Walking arbitrary transects within the study area, but taking care to cover as many types of microhabitats as possible, we tossed a 20×20 cm^2 wooden frame from a distance of 1.5 m. Afterwards, we counted arthropods contained within the frame during 1-min period. In each biotope, we processed 30 frame tosses. All prey items were identified to order. We should stress that this method does not take numbers of flying arthropods into account, although the diet of *P. gaigeae* comprises mainly terrestrial invertebrates.

Tick prevalence and infestation

For every noose-captured lizard we recorded sex, SVL and presence/absence of ticks. In cases of tick presence, we estimated infestation levels (mean number of ticks per lizard) and tick prevalence (the relative frequency of infested lizards within the population). We captured and assessed a total of 1047 lizards over the years. The annual field trips took place in late June when tick prevalence peaks (Bauwens, Strijbosch & Stumpel, 1983; Scali, Manfredi & Guidali, 2001).

Lizard population density

We employed the line transect method (Lovich *et al.*, 2012). The same observer (PP) walked the length of the trail (100 m) and recorded all lizards seen within a 4-m wide belt, 2 m on either side of the survey line (total area covered per trail 400 m^2). Four line transects were walked in each biotope (each five times, thus 20 transects per biotope). Line transects were chosen to cover as many different microhabitats as possible. Transect surveys were made only when environmental conditions were favourable for lizards and within a specific time-window (08:00–10:30 am) during which *P. gaigeae* summer activity is high (Pafilis, 2003), thus minimizing possible effects on density estimates (Castilla & Bauwens, 1991). Line transect method, which provides reliable data on the relative abundance of a population, is widely used in lacertid lizard studies (Martín & López, 2002; Díaz, Monasterio & Salvador, 2006).

Analysis

We performed a two-way analysis of variance (ANOVA) to examine the effects of biotope, year and their interaction on invertebrate abundance values for each biotope (quadrats pooled). Data were log $(x + 1)$ transformed. We also used two-way ANOVA tests (data log $(x + 1)$ transformed) to analyze differences in infestation levels and lizard densities among the biotopes and within the years. These analyses were followed by *post hoc* analysis [Fisher's least significant difference (LSD) test]. Mann–Whitney U-test was used to examine infestation levels between sexes due to the small sample size of females.

We performed a multiple regression approach using Akaike's information criterion with size correction (AIC$_c$) (Burnham & Anderson, 2002) to compare the 20 more predictive models. We used log-transformed values for the physical characteristics of the three islets (distance to main island and islet size) as well as habitat type, number of gull nests and grazing as independent variables and population density as the dependent variable. Furthermore, we conducted AIC weights to further evaluate model fit.

Differences in tick prevalence between sexes, among populations and within years were evaluated using χ^2 test. Relationships between tick prevalence and infested lizards were examined using Spearman rank correlation. All tests were two-tailed ($\alpha = 0.05$). Statistical analysis was performed according to Zar (1984). All statistical analyses were conducted using PASW-18.0 (SPSS Inc., Chicago, IL, USA).

Results

Invertebrate abundance

A total of 5490 individuals from 14 invertebrate taxa (including larvae as separate group – Supporting Information Table S1) were collected from all biotopes. Hymenoptera (notably ants), Coleoptera and Orthoptera were the most abundant orders, collectively comprising 64.5% of the fauna (ants 43.5%; Coleoptera 13.7%; Orthoptera 7.3%). Only the main prey groups of *P. gaigeae* (namely ants, Coleoptera, Orthoptera and larvae; Adamopoulou, Valakos & Pafilis, 1999) were included in further analysis.

Biotope and year had a significant effect on total invertebrate abundance, while analysis revealed no significant interaction between biotope and year [two-way ANOVA, data log $(x + 1)$ transformed, Table 2]. We failed to detect any statistically significant effect of year on prey groups. However, biotope indicating the grazing regime had a significant effect on all but the larvae groups (Fig. 1, Table 2).

Goats and gull presence

Goats were present in large numbers at Nyfi and Valaxa and absent from Diavates and Palamari (Table 1). Lakonissi harboured 2–5 goats every year with the exception of 2006 and 2009 when no goat was found on the islet.

The highest number of gull nests was recorded at Diavates and the lowest at Valaxa (Table 1). At Lakonissi, we detected more nests during the years without grazing. An interesting finding is that during the grazing years, nests were restricted to remote rocks in close proximity but not connected to the islet.

Table 2 Results of the two-way analysis of variance for invertebrate abundance, data log (x + 1) transformed

		Degrees of freedom	F–ratio	P
Total invertebrate availability	Biotope	4	12.154	0.00001
	Year	5	9.681	0.00001
	Biotope x year	20	0.810	0.702
	Error	870		
Ticks	Biotope	4	3.67732	0.0056
	Year	5	0.92082	0.466
	Biotope × year	20	0.41258	0.989
	Error	870		
Coleoptera	Biotope	4	12.7629	0.00001
	Year	5	2.0581	0.068
	Biotope × year	20	0.2139	0.999
	Error	870		
Orthoptera	Biotope	4	20.3268	0.00001
	Year	5	0.4221	0.833
	Biotope × year	20	0.7146	0.813
	Error	870		
Larvae	Biotope	4	1.60291	0.171
	Year	5	0.65895	0.654
	Biotope × year	20	0.35954	0.995
	Error	870		
Ants	Biotope	4	3.9923	0.00001
	Year	5	2.2348	0.0032
	Biotope × year	20	0.5609	0.939
	Error	870		

We found no nest at the main island (Nyfi and Palamari) during the study.

Tick prevalence and infestation levels

The species that parasitized *P. gaigeae* was the sheep tick (*Ixodes ricinus*). Ticks were almost always attached near the forelimb of the lizards. The majority of infested lizards carried a couple of ticks, although higher numbers were recorded in some adult individuals. Our measurements refer to the period during which ticks are more conspicuous in Mediterranean ecosystems (Asikidis, 1989; Scali *et al.*, 2001).
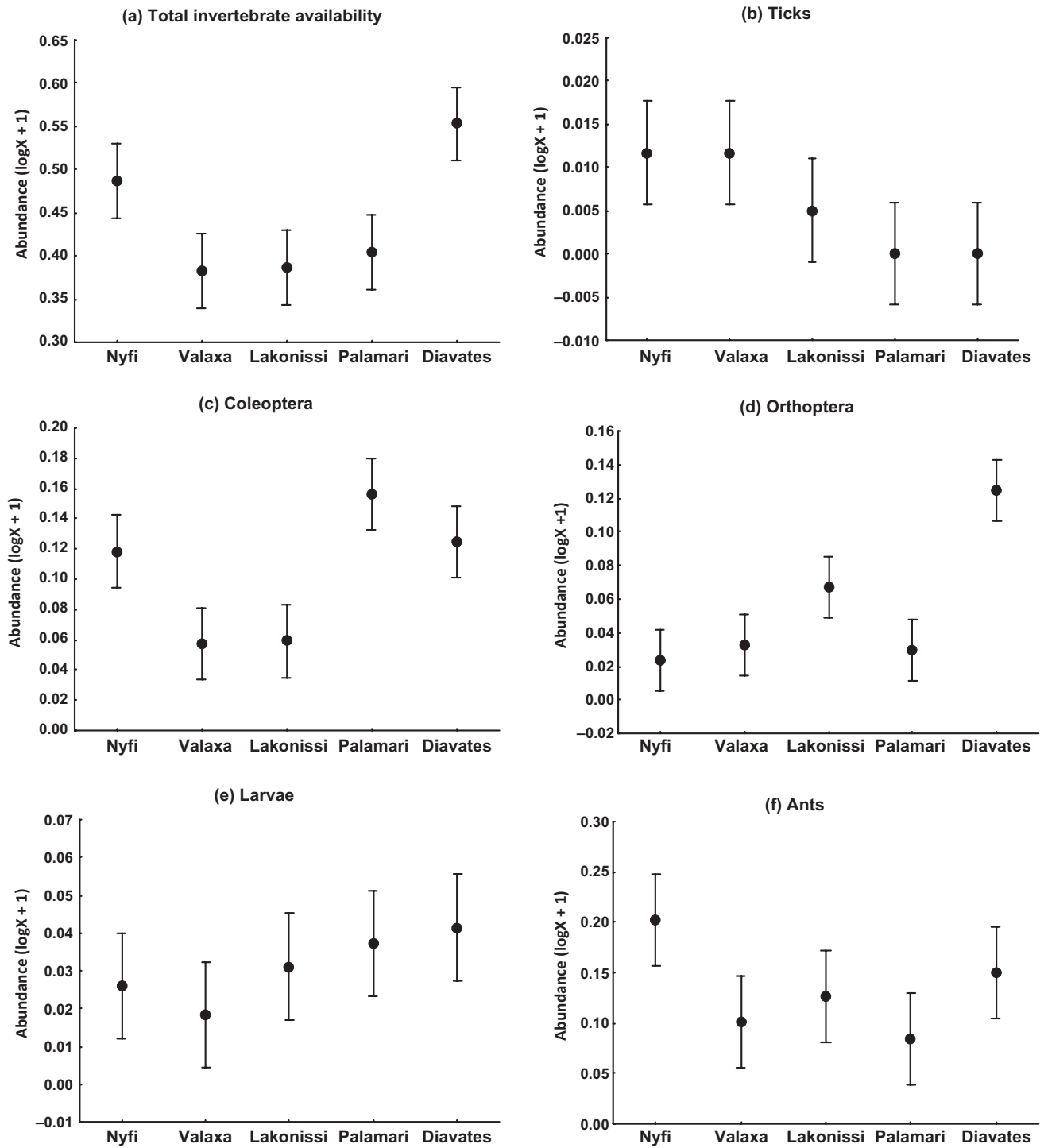
We found no significant differences between sexes in either tick prevalence (χ^2 test, $P > 0.05$ for all populations) or infestation levels (Mann–Whitney U-test, $P > 0.05$ for all populations) so data were pooled in all further analyses.

Statistically significant differences were detected in the frequencies of infested lizards among the examined areas (χ^2 test, $P = 0.05$ among different populations). However, these differences disappeared when analysis took the presence/absence of goats into account (χ^2 test, $P > 0.05$). In grazed biotopes, tick prevalence ranged from 44 up to 59%, while in the case of ungrazed sites the equivalent values varied from 13 to 28% (Table 1). No statistically significant differences were found in tick prevalence among the years (Nyfi: $\chi^2 = 0.234$, d.f. = 5, $P = 0.99$; Palamari: $\chi^2 = 0.009$, d.f. = 5, $P = 1.00$; Diavates: $\chi^2 = 0.409$, d.f. = 5, $P = 0.99$; Valaxa: $\chi^2 = 0.01$, d.f. = 5, $P = 1$; Lakonissi: $\chi^2 = 8.04$, d.f. = 5, $P = 0.15$ – Table 1). In the latter case, a *post hoc* analysis (Fisher exact test) was employed to test whether grazing regime had an effect on tick prevalence

through the years. Tick prevalence differed significantly between years with and without grazing (z = 2.781, $P = 0.002$), whereas no differences were found among years with grazing ($\chi^2 = 0.052$, d.f. = 1, $P = 0.82$) and years without grazing ($\chi^2 = 0.307$, d.f. = 3, $P = 0.959$). Tick prevalence might be grouped in two different clusters according to grazing regime; the first included the years without grazing (2006 and 2009) during which tick prevalence was around 25%, and the second comprised the years with grazing (2007, 2008, 2010 and 2011) during which the percentages of infected lizards ranged between 45–51% (Table 1).

Infestation levels differed significantly among the examined biotopes (one-way ANOVA, $P < 0.001$, Table 3). *Post hoc* analysis (Fisher LSD test) indicated the existence of two distinct groups, one comprising the grazed and the other ungrazed biotopes, showing high and low infestation levels, respectively (Table 3). Interestingly, Lakonissi wavered from one group to the other over the years dependent on the presence of goats (Table 3). No statistically significant differences were found across the years for each of the examined biotopes, with the exception of Lakonissi (one-way ANOVA, $P < 0.001$). Once more, *post hoc* analysis (Fisher LSD test) grouped years according to grazing regime: one group comprised 2006 and 2009 (no grazing) and the other remaining years (Table 3).

Lizards from the grazed biotopes were infested with 0–17 ticks per individual, whereas lizards from the ungrazed biotopes hosted 0–6 ticks. Tick prevalence and infestation in the lizards were positively correlated (Spearman rank correlation coefficient, $r_s = 0.94$, $P < 0.001$).

(a) Total invertebrate availability

(b) Ticks

(c) Coleoptera

(d) Orthoptera

(e) Larvae

(f) Ants

Figure 1 Invertebrate taxa abundance (mean ± SD) from Skyros Island and islets (data log (x + 1) transformed).

Table 3 Results of the one-way analysis of variance (ANOVA) for infestation levels. Numbers in cells represent mean ± SE; range; number of examined lizards

	2006	2007	2008	2009	2010	2011	ANOVAs
Nyfi (N)	2.7 ± 0.7; 0–11; 26	2.6 ± 0.8; 0–12; 30	2.6 ± 0.8; 0–17; 30	2.6 ± 0.7; 0–15; 30	2.7 ± 0.7; 0–14; 35	2.7 ± 0.7; 0–14; 25	$F_{5,164}$ = 0.06, P = 0.99
Palamari (P)	0.7 ± 0.2; 0–05; 46	0.7 ± 0.2; 0–05; 40	0.7 ± 0.2; 0–06; 36	0.7 ± 0.2; 0–04; 41	0.7 ± 0.2; 0–04; 41	0.6 ± 0.2; 0–05; 39	$F_{5,239}$ = 0.006, P = 0.99
Diavates (D)	0.2 ± 0.1; 0–02; 34	0.2 ± 0.1; 0–02; 37	0.2 ± 0.1; 0–02; 42	0.2 ± 0.1; 0–02; 41	0.2 ± 0.1; 0–03; 42	0.2 ± 0.1; 0–03; 42	$F_{5,228}$ = 0.04, P = 0.99
Valaxa (V)	2.7 ± 0.9; 0–14; 14	3.0 ± 1.0; 0–16; 20	3.0 ± 0.9; –17; 22	2.8 ± 0.9; 0–14; 18	2.9 ± 0.9; 0–14; 18	2.9 ± 0.8; 0–11; 19	$F_{5,109}$ = 0.04, P = 0.99
Lakonissi (L)	0.5 ± 0.1; 0–02; 27	1.8 ± 0.4; 0–07; 31	1.9 ± 0.4; 0–07; 31	0.5 ± 0.2; 0–03; 31	2.0 ± 0.5; 0–07; 24	2.0 ± 0.4; 0–07; 29	$F_{5,167}$ = 3.71, P = 0.003
ANOVAs	$F_{4,147}$ = 7.92, P = 0.000008	$F_{4,147}$ = 6.24, P = 0.00012	$F_{4,156}$ = 7.03, P = 0.000031	$F_{4,155}$ = 7.61, P = 0.000013	$F_{4,153}$ = 6.28, P = 0.00006	$F_{4,149}$ = 6.64, P = 0.00006	
Groups	{N,V};{P,D,L}	{N,V,L};{P,D}	{N,V,L};{P,D}	{N,V};{P,D,L}	{N,V,L};{P,D}	{N,V,L};{P,D}	
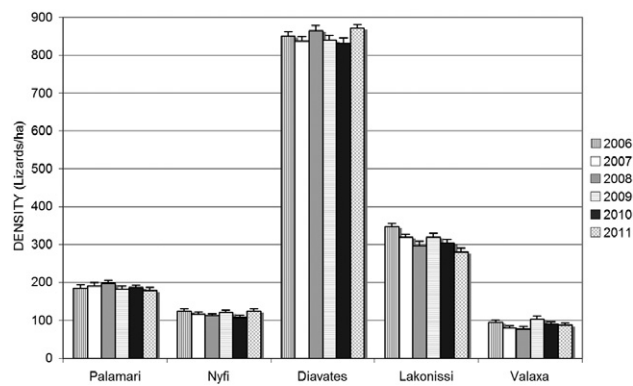
Figure 2 Density estimates (mean ± SE) in the biotopes under study during a period of 6 years.

Lizard population density

Population densities in each biotope fluctuated around a central value without significant deviations (Fig. 2). On the islets, the highest density was recorded on the ungrazed Diavates and the lowest on the heavily grazed Valaxa. The Lakonissi population had the second highest density among all biotopes, regardless of the grazing regime (although the highest density was recorded at 2006, a goat-free year). On Skyros Island, the ungrazed Palamari hosted a denser population than the heavily grazed Nyfi (one-way ANOVA, P < 0.001).

The model with the highest predictive value is the one using grazing regime and microhabitat type as predictors (model ID 1) (Table 4). However, the comparison of ΔAIC values of the candidate models indicates that the first two models gave equal support ($0 \leq \Delta AIC_c \leq 2$) (Burnham & Anderson, 2002). Further analysis revealed that grazing regime and microhabitat type were equally important in explaining population density (ANOVA, model 1 vs. model 11, P = 0.0098; model 1 vs. 14, P = 0.0087).

We found statistically significant differences among the examined populations (two-way ANOVA, $F_{20,569}$ = 2.62, P < 0.001). However, population densities in each biotope did not differ within the years (two-way ANOVA, $F_{20,569}$ = 2.62, P < 0.001) with the exception of Lakonissi islet. In the latter, case population density differed within the years depending the grazing regime (*post hoc* analysis Fisher LSD test, P = 0.045).

Discussion

It has been claimed that grazing has a negative influence on lizard populations (James, 2003). However, species that prefer open areas increased their populations after grazing provided places for thermoregulation and foraging (Smart, Whiting & Twine, 2005). Our results revealed that grazing had a clearly negative impact on lizards. Namely, in grazed biotopes prey availability declined, gulls stopped nesting (cease of marine subsidies), tick prevalence and infestation levels increased and lizard densities were lower.

Table 4 Akaike's second-order information criterion (AIC$_c$) results for 20 candidate models

Model parameters	Model ID	k	ΔAIC$_c$	W_{AIC}
Grazing + Microhabitat	1	4	0.00	0,14
Density + Grazing	2	4	0.11	0,13
Distance + Grazing	3	4	0.29	0,12
Density + Microhabitat	4	4	0.44	0,11
Grazing + Microhabitat + Area	5	5	0.76	0,09
Density + Distance + Microhabitat	6	5	0.96	0,08
Density + Grazing + Microhabitat	7	5	2.03	0,05
Density + Distance + Grazing	8	5	2.04	0,05
Distance + Grazing + Microhabitat	9	5	2.06	0,05
Grazing	10	3	2.14	0,05
Distance + Microhabitat	11	4	2.40	0,04
Grazing + Area	12	4	2.87	0,03
Density + Distance + Grazing + Microhabitat	13	6	4.08	0,02
Density	14	3	4.41	0,02
Density + Distance	15	4	5.08	0,01
Density + Distance + Grazing + Microhabitat + Area	16	7	6.32	0,01
Distance	17	3	6.64	0,00
Microhabitat	18	3	8.29	0,00
Microhabitat + Area	19	4	8.81	0,00
Area	20	3	14.72	0,00

Number of ticks was used as the response variable, microhabitat type, islet area (log transformed), distance from the main island, grazing regime and population density were used as predictor variables. Random-effects ANOVAs was performed to evaluate the differences between populations.

Models are ranked by ΔAIC$_c$. k represents the total number of parameters in each model; W_{AIC} is the Akaike weight.

Changes in vegetation structure affect habitat selection and decrease invertebrate communities (Rambo & Faeth, 1999; Martín & López, 2002). The majority of lacertid lizards are insectivorous, although many insular species are omnivorous, and thus any change in the dynamics of invertebrate populations influences lizard communities directly (Díaz & Carrascal, 1991*b*; Fisher, Suarez & Case, 2002). Vegetation on the islets surrounding Skyros has been seriously affected by chronic grazing (Bohling, Greuter & Raus, 2002; Snogerup & Snogerup, 2004). This decline is reflected in a prey availability gradient among the five sites: at the one extreme (lower food availability) were islets that experienced long-term (Valaxa) or aperiodic (Lakonissi) grazing, main island sites were located in the middle of the gradient, regardless of the grazing regime, and at the other extreme was the goat-free Diavates with the highest prey availability.

The negative role of grazing on prey availability was clear in the case of islets where goat presence resulted in low invertebrate densities (Fig. 1a). However, on Skyros, the grazed biotope (Nyfi) had a higher total arthropod abundance than the ungrazed one (Palamari). The underlying reasons for this seeming contradiction should be sought in the type of the biotopes. Palamari is a semi-dunal ecosystem with few phrygana, unable to support livestock thus, one of the few goat-free places we found on the island. The overall productivity of dunes is lower than maquis ecosystems, and this is reflected in the higher invertebrate availability at Nyfi (Fig. 1a). Nonetheless, when we focused on the arthropod groups comprising the main trophic sources for *P. gaigeae*, such as coleoptera, orthoptera and larvae, Palamari had either higher (Fig. 1c,e) or the same (Fig. 1d) values with Nyfi. This should come as no surprise since insect groups like coleoptera are more vulnerable (Gardner *et al.*, 1997).

Tick prevalence and infestation levels were strongly correlated with grazing regime. Lizards caught at sites with heavy grazing had the higher values of tick prevalence (Table 1) and higher infestation levels (Table 3). In contrast, lizards from the goat-free Palamari and Diavates had fewer ticks per individual and infestation was lower. From this evidence, we inferred that grazing speeds up the spread of ticks. Results from Lakonissi corroborate this assumption. Although tick prevalence and infestation levels were similar to the heavily grazed Nyfi and Valaxa, they spectacularly decreased during the years 2006 and 2009 when no goats were released on the islet (Tables 1 and 3). The numbers of free-ranging ticks (prior to lizard infection) further highlighted the significant role of goats in spreading ectoparasites. Quadrat counts yield the lower numbers in the two ungrazed sites while the highest values were recorded at Valaxa and Nyfi (Fig. 1b). Lacertids are common hosts of ticks (Scali *et al.*, 2001). Infected lizards experience numerous disadvantages that may reduce viability (Bauwens *et al.*, 1983) and jeopardize the survival of small, isolated populations.

Gulls may subsidize insular populations with sea-derived food (Polis & Hurd, 1996) and enhance the soil with nutrients (Anderson & Polis, 1999). Nesting seabirds are known to increase nitrogen and phosphorous content, the main limiting factors for terrestrial systems (Wait, Aubrey & Anderson, 2005). Gull guano and decaying carcasses increase soil fertility and, through this bottom-up pathway, support dense islet populations (Kolb *et al.*, 2010).

In general, gull nest density is negatively correlated with island size (Vidal *et al.*, 2001). This pattern was verified in our study system where not a single nest was found on the main island and only a few ones were detected on Valaxa, the largest islet of the Archipelago. On the other two islets, the number of nests depended on grazing regime. Diavates hosts a thriving gull colony with many nests while Lakonissi had fewer nests, the number of which doubled in the grazing-free years (Table 1).

The absence of gulls had a negative effect on lizard densities. Population density is the result of many ecological components, the most important of which are predation and food availability. Predation pressure in the Skyros Archipelago is rather relaxed (there are only three snakes on the main island of Skyros, none of which is found on the islets, Pafilis *et al.*, 2009*b*); food is probably the main driving factor, and this may depend on marine subsidies on the islets. Grazed biotopes had lower lizard densities, while the ungrazed sites higher ones (Fig. 2). We believe that the nitrophilous vegetation of Diavates is maintained through natural fertilization of the soil by guano and decomposition of sea gull carcasses (Pafilis *et al.*,

2011). It seems that this increased primary productivity leads to a richer invertebrate prey, which may account for the highest lizard density of the Archipelago. A striking deviation from this pattern comes from Lakonissi, which had the second densest population, despite the fact that it regularly hosted goats. This finding should be attributed to the irregular nature of grazing there, during the non-grazing years gulls nested on the islet, supporting nitrophilous plants and terrestrial arthropods. Thus, the main prey groups of *P. gaigeae* are represented in high frequencies (Fig. 1d,f), providing food to a dense population. The small difference between Palamari and Nyfi could also potentially be attributed to food availability. Although Nyfi is subject to intense grazing, its higher total arthropod abundance can support a sufficient lizard population.

In sum, our findings, despite their limitations (few sampling sites, no direct measurement of extinction risk or grazing pressure) suggest that the introduction of goats changes the particular conditions on the islets. Goats introduce ticks that attenuate lizards' fitness and, most importantly, chase out gulls, thus stopping the flow of sea nutrients.

Grazing has been practiced on Mediterranean islands for millennia (Geeson, Brandt & Thornes, 2002), shaping both the landscape and local fauna. In view of the long history of the activity, we do not believe that grazing on the main island of Skyros represents any hazard to *P. gaigeae*. Co-evolution may smooth interactions between native reptiles and introduced species, minimizing the impact of alien species (Case & Bolger, 1991). However, grazing effect on the islets is strong and could have dramatic consequences. Islet lizards differ from their mainland counterparts in many features and to understand the dynamics of their populations, it is important to assess interactions with the other species, native or introduced, of their particular ecosystem (Castilla & Herrel, 2009). Further research on the impact of goats on lizard communities (including experimental manipulation of grazing and quantitative analysis of grazing pressure) in the islets of this Archipelago but also in other similar systems around the Mediterranean is required to unravel the nature of this compound ecological effect.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1 Arthropod abundance in the biotopes under study