

Article

## Mammals and habitat disturbance: the case of brown hare and wildfire

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### Abstract

Ecosystem disturbances, such as wildfires, are driving forces that determine ecology and conservation measures. Species respond differentially to wildfires, having diverse post-fire population evolution. This study reports, for first time, the responses of brown hare (*Lepus europaeus* Pallas, 1778) to wildfires. Hare relative abundance, age ratio, diet quality, body condition, and diseases were studied. Fire influence on vegetation was calculated at a micro-scale level. Hare abundance was lower the first year after wildfires in burned relative to unburned areas. The reverse was found in the second year when hare abundance was higher in burned areas. Hare abundance in burned areas was also higher in the third and fourth years. In the fifth and sixth years after wildfire no significant difference was found in abundance. At a micro-scale level, higher numbers of hare feces were counted in places with greater wildfire influence on vegetation. Age ratio analysis revealed more juveniles in burned areas, but the same number of neonates in burned and unburned areas, indicating lower mortality of juveniles in burned areas. Reduced predation in burned areas provides the most plausible explanation for our findings.

**Key words:** diet, forest fire, lagomorphs, predation, vegetation.

The abandonment of traditional land uses in many Mediterranean areas has led to the growth of continuous forests and shrublands

that are susceptible to wildfires (Moreira et al. 2011). Wildfires can increase landscape heterogeneity by fragmenting continuous blocks

of dense woody vegetation (Vazquez and Moreno 2001). However, in some cases, wildfires are so extensive and severe that they decrease structural diversity and homogenize the landscape (Vazquez and Moreno 2001; Moreira et al. 2011).

Wildfire influences on wildlife species can be defined as either short term or long term (Quinn 1994). Short-term influences are displacement (Koprowski et al. 2006) and animal death directly caused by wildfire (Haim and Izhaki 1994) or indirectly caused through predation, starvation, and reduced reproductive success owing to habitat degradation (Haim and Izhaki 1994). In the long term, the evolution of an animal population after wildfire depends on parameters such as abundance of survivors, immigration, habitat, pathogens, predators, and the recovery of competitors (Quinn 1994; Haim and Izhaki 1994; Torre and Díaz 2004).

According to Quinn (1994) there are three basic types of post-fire population response in mammals: (1) species which were eliminated after a wildfire reoccupy the area after plant community has returned to an advanced stage of succession; (2) species which have low abundance before the wildfire increase their abundance for a period after the wildfire; and (3) species that appear for the first time in the area in a later stage of succession after wildfire. Not all species of mammals belong entirely to one of the three types of post-fire population evolution, but most species are better classified to one type versus the others (Quinn 1994).

The effects of wildfire on some mammals are well studied (e.g., Torre and Díaz 2004), but studies on lagomorphs are limited. Keith and Surrendi (1971) found more *Lepus americanus* in the burned area 1 year after a wildfire. In savannah grassland in East Africa, Ogen-Odoi and Dilworth (1984) determined that hare species (*Lepus* spp.) and medium-sized predators increased by over 300% and 124%, respectively, 3 months after prescribed burning. However, frequent prescribed burning has been reported to have a negative impact on *Lepus flavigularis* in Mexico (Lorenzo et al. 2011).

The response of hare species (genus *Lepus*) to wildfire has not been the subject of an in-depth study, although, hare species: (1) in many areas have low population densities (Delibes-Mateos et al. 2009) with high conservation importance due to the increased genetic variability

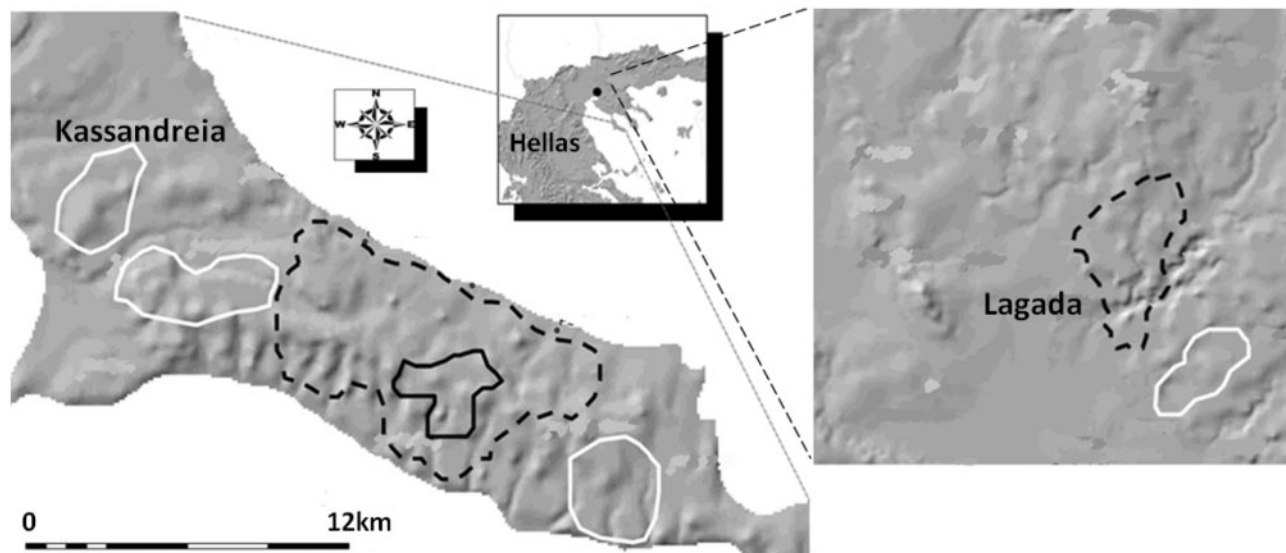
and geographical substructuring of populations in the Mediterranean region (Antonioni et al. 2013); (2) have fundamental roles in natural processes as prey of threatened predator species (Delibes-Mateos et al. 2009); and (3) are important species for rural human populations engaged in the hunting economy (Papasyropoulos et al. 2014). Legislation pertaining to hunting management after wildfires is not yet established in Mediterranean countries. Thus, hare hunting management after a wildfire is usually determined by local agencies without adequate scientific documentation (Zamora et al. 2010; Papasyropoulos et al. 2014). In Hellas, hunting is usually banned for a period of 2–5 years after wildfires (Papasyropoulos et al. 2014). In Spain this period lasts from 1 to 10 years (Zamora et al. 2010) and in Italy for 10 years, limited to the burned area (Francesco Santilli, personal communication).

In this study, in adjacent burned and unburned areas hares were compared in terms of: (1) relative abundance, (2) age ratio, (3) diet quality, (4) body condition, and (5) pathogens. Moreover, we investigated whether the severity of wildfire influences habitat use by hares at a micro-scale level. The survey of the population for 6 years following wildfire provides information about hare population evolution, whereas the measured demographic, dietary, and disease parameters contribute to our understanding of hare responses to wildfire.

## Materials and Methods

### Study sites

The study was conducted in burned and adjacent unburned areas in the Kassandra Peninsula of Chalkidiki Prefecture and in Lagada of Thessaloniki Prefecture in North Hellas (Greece) (Figure 1). The climate of both areas is classified as Mediterranean with hot and dry summers. In Kassandra, the mean annual precipitation is 581 mm and the mean annual air temperature is 16.3°C at altitudes ranging from 150 to 280 m a.s.l. In Lagada, the mean annual precipitation is 588 mm, with a mean annual air temperature of 12°C at altitudes of 200–520 m.



**Figure 1.** The two study areas in Kassandra (left) and Lagada (right). The dashed black line indicates the moderately burned areas and the solid black line shows the intensely burned area. The solid white line shows the neighbouring unburned areas where hares were counted.

The Kassandra Peninsula is covered mainly by forest vegetation of Aleppo pine (*Pinus halepensis* Mill) and broadleaved shrubs (*Quercus coccifera* L., *Smilax aspera* L., *Cistus* spp., *Pyrus spinosa* Forssk.), interspersed with scattered agricultural fields, mainly comprising olive groves, cereal, and a few vetch crops. The Lagada area is covered mainly by broadleaved shrubs (*Quercus coccifera* L. and *Pyrus spinosa* Forssk.) and secondarily by plantations of *Pinus brutia* Ten., as well as scattered cereal fields. The woody plants of both areas regenerated quickly after wildfires with re-sprouted shrubs reaching a height of half a meter in the first year after the wildfire (Birtsas et al. 2012).

Wildfire occurred in Kassandra on 21 August 2006 and the burnt area was 68.7 km<sup>2</sup>. In Lagada, wildfire broke out on 27 July 2007 and the burnt area was 29.17 km<sup>2</sup>. Due to very strong winds, wildfire severity was high with intensive crowning in both areas. In the centre of the burned region of Kassandra there is an intensely burned area of 18.3 km<sup>2</sup> where nearly all trees and shrubs were burned, whereas the remaining 50.4 km<sup>2</sup> is a moderately burned area with unburned stands (of about 0.1–0.5 ha), creating a mosaic of burned and unburned patches. Lagada is characterized as a moderately burned area. During the first year after the wildfire, most of the burned trees were felled in both areas. Some trunks were removed while others, together with their branches, were used for soil-erosion barriers.

Within both areas, hunters are interested mainly in hare and migratory birds. The hunting of red fox (*Vulpes vulpes* L., 1758) and stone marten (*Martes foina* Erxleben, 1777) is permitted but they are rarely hunted (Papasyropoulos et al. 2014). After the wildfire, hunting was prohibited throughout the Kassandra Peninsula until 25 November 2006 (for about 3 months), prompting objections from hunters. After this date, hunting was permitted only in the unburned hunting area of the Peninsula. In the burned area, the hunting ban continued for 2 years after the wildfire, with hunting permitted again during the third year. In Lagada, hunting was prohibited in the burned area and 200 m around the burned area. Hunting dog training was permitted in the area 3.5 years following the wildfire, especially, in order to facilitate the adaptation of hares to escape before hunting was opened. Local hunters prefer to use this area as dog training zone and thus hunting prohibition within the Lagada wildfire site continued until 2015.

### Study design

The influence of wildfire on hares was studied at three levels: (1) vegetation and diet quality; (2) age ratio, body condition; and disease; and (3) hare abundance. The above parameters were estimated and compared between burned and adjacent unburned areas of the same hare habitat (vegetation before the outbreak of wildfires, soil type, aspect, slope, altitude) and hunting management. The comparison of abundance between burned and unburned areas is a broad approach used in post-fire studies on the influences of wildfire on mammals (e.g., Borkowski 2004; Torre and Díaz 2004; Rollan and Real 2010). Hare population trends (for example due to weather) are at least locally similar (Marboutin and Peroux 1996), so that differences in abundance can be attributed to the independent variable of interest, which in this case is wildfire.

The study area of Kassandra stretches along the ridge of a peninsula and an unpaved forest road. The road has a total length of 22 km: 8.5 km passing through unburned areas, 9.5 km through moderately burned areas, and 4 km passing through intensely burned areas (Figure 1). In Lagada, the unpaved forest roads have a total length of 27 km: 12 km passing through unburned areas and

15 km through moderately burned areas. Taking into account that the hare is not a territorial species and the home range varies between 10 and 100 ha (Broekuizen and Maaskamp 1982; Homolka 1985; Reitz and Leonard 1994) the area sampled provides data that are presumably representative of the influence of wildfire on hare abundance and other parameters (Keith and Surrendi 1971; Cardarelli et al. 2011).

### Relative abundance of hares

No data on either the Kassandra or Lagada hare populations are available from before the wildfire events. After the wildfires, the relative abundance of hares was estimated using spotlighting and feces counts. Two methods were selected as increased relief, dense vegetation in unburned areas and burned vegetation may cause biases in census methods (Langbein et al. 1999). Burned and unburned areas with similar hunting statuses were compared, controlling for any influence of hunting. To minimize bias, spotlight and feces counts were performed by the same researchers.

### Spotlight count index

In the spotlight method, hares were counted from a 4-wheeled vehicle (see Sokos et al. 2015, for a detailed description). In Kassandra, usually one visit was carried out each month in periods 10/2006–9/2007 and 2/2008–8/2008 in addition to roughly two visits each month in period 10/2007–12/2007, for a total of 30 visits in the first and second years after wildfire. In Lagada six visits were carried out in summer of second year after the wildfire (6/2009–8/2009).

As most of the hares were seen initially or were approached later to a distance of less than 30 m, we distinguished which hares weighed more than 3 kg (developed hares) and which were less than 2.5 kg (juvenile hares), that is younger than 3 months old (Bray et al. 2002). Hares which could not be seen well or appeared to weigh between 2.5 and 3 kg, were excluded from this categorization of individuals.

### Belt transects for feces counting

Belt transects for feces counting were placed in sampling units along the length of the forest roads that were spotlighted using the previous method. Sampling units were positioned every 600 m following the random selection of the initial sampling unit (Calvete et al. 2004). The belt transects were set up in the same sampling units each year. In each sampling unit four sections of belt transect of 100-m length and 0.5-m width were installed (Fa et al. 1999; Calvete et al. 2004; Murphy and Bowman 2007). Two sections were located on each side of the road at a constant distance of 30 m from the road, and two more sections were located at a distance of 50 m from the road. In cases where obstacles (logs, dense shrubs, steep slope) were encountered, researchers went around those until 100 m of transect was completed. Consequently, feces were counted at a total distance of 400 m (4 sections × 100-m length) from each sampling unit. The sections were positioned 30–50 m from the road so as not to be influenced by negative factors (e.g., disturbances by cars or livestock), but not too far so that the data could be compared with that of the spotlight method.

This method is considered more effective than setting small plots as it covers a larger surface area and therefore it is more likely to count hare feces in an area with low hare density. In this way, one avoids zero values which would complicate the statistical analysis (Quinn and Keough 2002). The feces counting method was carried out once a year, so that the decomposition of the previous year's feces occurred in Mediterranean conditions (Palomares 2001). Feces disappearance

rates between burned and unburned areas are not expected to differ. Three months after wildfire in Kassandra (November 2006), the sampling method was tested by positioning five sampling units in the moderately burned area and five in the unburned area, later feces counts were performed each April for 6 years (2007–2012). In Lagada, feces counts were performed once at the end of August 2009, the second year after the wildfire.

In addition to the research described above, a number of hares were also kept in captivity and provided with herbaceous food. Collection of feces from those captive individuals revealed that feces of young leverets (until 2 months old) were usually smaller in size (typically smaller than half the size) than those produced by juveniles or adults. Therefore, the feces counted in Kassandra Peninsula were assigned into two size classes, large and small (Southgate, 2005; Rouco et al. 2012), to examine any differences in the ratio of young leverets/older hares between burned and unburned areas. Small feces were those that were smaller than one half of the size of large feces collected.

### Hare collection

In November 2007, 1 year after the wildfire in Kassandra, we requested and received permission from the Forest Service (Permission 5 September 2007, protocol number 98921/4798) to collect hares from burned areas and adjacent unburned refuges (in both areas hunting was prohibited). Twenty-two hares were captured in accordance with the guidelines for the use of wild mammals in research (American Society of Mammalogists 1998). Moreover, the number of hares collected was minimized to alleviate ethical concerns and to avoid upsetting members of the local community. Thus additional hares were collected by hunters in adjacent unburned areas during daylight adhering to legislation. The animals were inspected (hares that were collected at night were also weighed) and their sex was determined. Each hare was dissected to obtain one eye, one front leg, the stomach, the liver, the kidney, and the uterus (only 1 female was pregnant, and found in a moderately burned area). Eyes were preserved in 10% formalin and the other organs were frozen at  $-20^{\circ}\text{C}$ , 5–8 h following death.

To determine the age of each specimen, the crystalline lens was weighed according to Suchentrunk et al. (1991). Hares were divided into 3 age classes: leverets and juveniles with dried eye lens weights  $< 235$  mg, near adults with weight 235–279.9 mg, and adults with dried eye lens weights  $\geq 280$  mg (Suchentrunk et al. 1991). Hare body condition was determined using the kidney fat score on a 0–5 scale (Bonino and Bustos 1998; Banks et al. 1999; Jennings et al. 2006). Stomach contents were removed carefully so no residual stomach tissue remained, then were dried, weighed, and milled to 1 mm. Crude protein content was measured as Kjeldahl  $\text{N} \times 6.25$  (AOAC 2006), and crude fat and fibre contents were determined according to AOAC (2006). According to Banks et al. (1999) and Hackländer et al. (2002), high crude fat and protein levels together with low crude fiber content, indicate a nutrition-rich diet. Therefore, the ratio of crude protein and fat to crude fiber was used as an indicator of diet quality.

Livers were examined for the presence of lesions and the method of reverse transcription–polymerase chain reaction (RT–PCR) was then applied to detect European Brown Hare Syndrome virus (EBHSV) (Spyrou et al. 2013, for a detailed description). Additionally, 29 serum samples were tested using the indirect immunofluorescence test (IFAT) for the detection of antibodies against *Francisella tularensis*, *Brucella* spp, and *Toxoplasma gondii*.

### Fire influence

Fire influence (FI) was estimated around each sampling unit (where belt transects for feces counting were set-up) within the Kassandra site. A  $600 \times 600$  m square (36 ha) was marked, with its centre on the sampling unit. These dimensions were selected so a high number of scent stations could be placed along the road and also to take into account the home range of hare (Homolka 1985; Reitz and Leonard 1994). The assumption was made that for any given  $600 \times 600$  m square, the combination of more burned area and higher aggregation of the remaining forest and shrubby patches, leads to greater FI (Birtsas et al. 2012):

$$FI = (BV \times CA)^{1/2}$$

where *BV* represents the burned vegetation and it is the sum of the percentages of the completely burned forest area and half of the completely burned agricultural area (because the wildfire in the agricultural area was not as intense as in the forested area), and *CA* is an indicator of woody cover absence after the wildfire (see Birtsas et al. 2012, for a detailed description).

### Statistical analyses

The number of spotlighted hares per kilometer and per visit was compared using the parametric Student's paired *t*-test or the one-factor within-subject analysis of variance (ANOVA). Using this approach, the effect of factors that may affect the detection of hares between visits, such as moon phase and wind were excluded. When the assumptions of using the parametric tests were not met (few observations, non-normal distribution) the nonparametric Wilcoxon paired-sample test and Friedman's test were used, respectively (Zar 1996).

The numbers of feces counted per belt transect (400 m) were compared using the independent samples *t*-test or one-factor between subjects ANOVA. In most cases, data were transformed using the equation  $\ln(x+1)$ . When assumptions were not met the nonparametric Mann–Whitney U-test and Kruskal–Wallis test were used, and post hoc tests were performed using the Bonferroni technique when the null hypothesis was rejected. At the micro-scale level, linear regression analysis was used to explore the relationships between the number of feces/belt transect and fire influence parameters in the moderately burned areas.

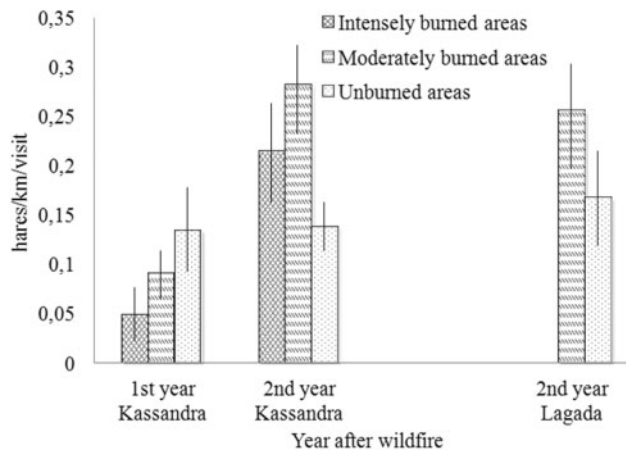
The parameters of diet quality and body condition were tested either by one- or two-factor (without interactions) between subjects ANOVA. The proportions of spotlighted hares in the different age classes and feces in the different faecal size classes were compared using the chi-squared test with the Yate's correction for continuity and, where the expected values in any cells of the contingency table were below 5, the Fisher's exact test (Zar 1996) was employed. Normality was investigated using the Shapiro–Wilk method and homogeneity of variances by Levene's test. Statistical analyses were performed using IBM SPSS 20.0. The level of significance was set to be  $\alpha = 0.05$ .

## Results

### Hare relative abundance in burned and unburned areas Spotlight count index

A total of 30 visits to the Kassandra study area identified 143 hares along a total distance of 837.8 km of forest roads (458.8 km in burned areas and 379 km in unburned areas). During the first year after the wildfire, the hares/km ratio was lower in burned areas than





**Figure 2.** Mean  $\pm$  SE of number of hares/per km/per visit during the first year ( $n=14$  visits) and second year ( $n=16$  visits) after the wildfire in Kassandra Peninsula, and the second year after wildfire in Lagada ( $n=6$  visits).

unburned areas. In the intensely burned area of Kassandra, no hares were recorded until spring 2007. In Lagada, 6 visits in summer of second year after the wildfire identified 35 hares along a total distance of 162 km of forest roads (90 km in burned areas and 72 km in unburned areas). In the second year, the hares/km ratio was higher in the burned areas compared with non-burned in both the Kassandra and Lagada study areas (Supplementary Table S1).

In the first year following wildfire, the number of hares/km/visit did not differ between burned and unburned areas (paired  $t$ -test,  $T=1.352$ ,  $df=13$ ,  $P=0.199$ ). Comparing the three areas, the hares/km/visit was marginally nonsignificant (Friedman  $\chi^2_2=4.98$ ,  $P=0.08$ ), with the number of hares/km/visit marginally lower in intensely burned compared to nonburned areas ( $P=0.071$ ) (Figure 2).

In the second year after the wildfire, the number of hares/km/visit was significantly higher in burned areas than in unburned refuge areas (paired  $t$ -test,  $T=2.58$ ,  $df=15$ ,  $P=0.02$ ). Comparing the three areas, the hares/km/visit was significantly different overall ( $F_{2,30}=5.9$ ,  $P=0.046$ ), with the number of hares/km/visit significantly higher in moderately burned compared to unburned areas ( $P=0.039$ ) (Figure 2). The study in Lagada showed similar results with more hares found in burned areas during the second year (paired  $t$ -test,  $t=2.99$ ,  $df=5$ ,  $P=0.019$ ).

#### Belt transects for feces counting

In the first year following wildfire, the number of feces/belt transect was significantly lower in burned areas compared with unburned areas ( $t$ -test,  $t=2.83$ ,  $df=31$ ,  $P=0.008$ ) (Figure 3). Comparing the three areas, significant differences were found ( $F_{2,30}=3.887$ ,  $P=0.032$ ). Post-hoc comparison revealed that this difference was significant between unburned and moderately burned areas ( $P=0.039$ ), and also between unburned and intensely burned areas ( $P=0.022$ ). No significant difference was found between moderately and intensely burned areas ( $P=1$ ).

In the second year following wildfire, a comparison was made between the burned and adjacent unburned refuge areas. The number of feces/belt transect was higher in burned areas, however, this difference was not statistically significant ( $t$ -test,  $t=-0.899$ ,  $df=37$ ,  $P=0.374$ ). No differences were found between the three areas ( $F_{2,36}=0.436$ ,  $P=0.65$ ). In the summer at the Lagada site, we counted  $25.48 \pm 4.02$  feces/belt transect (mean  $\pm$  SE,  $n=21$ ) in the moderately burned area and  $13.39 \pm 2.49$  feces/belt transect

(mean  $\pm$  SE,  $n=18$ ) in the unburned area. This difference was found to be significant ( $t$ -test,  $t=-3.1$ ,  $df=38$ ,  $P=0.019$ ).

In the third and fourth years following wildfire, the hunting prohibition was lifted in the burned areas and the number of feces/belt transect was significantly higher in burned areas compared to unburned hunted areas (third year:  $t$  test,  $t=-2.146$ ,  $df=33$ ,  $P=0.039$  and fourth year:  $t$ -test,  $t=-2.095$ ,  $df=33$ ,  $P=0.044$ ). Comparing the three areas we found significant differences (third year:  $F_{2,32}=3.883$ ,  $P=0.031$  and fourth year:  $F_{2,32}=3.763$ ,  $P=0.034$ ). Post hoc comparison revealed that these differences were significant between unburned and moderately burned areas (third year:  $P=0.035$  and fourth year:  $P=0.039$ ). Between unburned and intensely burned areas no significant difference was detected (third year:  $P=1$  and fourth year:  $P=1$ ). Additionally, no significant difference was detected between moderately and intensely burned areas (third year:  $P=0.296$  and fourth year:  $P=0.297$ ).

The number of feces/belt transect did not differ between burned and unburned areas in the fifth year ( $t$  test,  $t=1.096$ ,  $df=33$ ,  $P=0.281$ ) or sixth year (Mann-Whitney  $z=-0.82$ ,  $P=0.412$ ) following the wildfire. No significant difference was detected when comparing the three areas in these years (fifth year:  $F_{2,32}=0.61$ ,  $P=0.55$  and sixth year: Kruskal-Wallis test  $\chi^2_2=0.895$ ,  $P<0.639$ ).

#### Micro-scale level study

In the moderately burned areas of Kassandra Peninsula, FI on vegetation was different between the 17 adjacent sampling units. The average FI on vegetation was 0.776 (range 0.38–1). In sampling units with high FI, the number of feces was greater in both years (1<sup>st</sup> year:  $R^2=0.42$ ,  $P=0.005$ , 2<sup>nd</sup> year:  $R^2=0.27$ ,  $P=0.034$ ). More specifically, this was found in the first year for the burned vegetation index (BV:  $R^2=0.28$ ,  $P=0.03$ ), and in both years for the absence of cover index (CA: 1<sup>st</sup> year  $R^2=0.398$ ,  $P=0.007$ , 2<sup>nd</sup> year  $R^2=0.286$ ,  $P=0.027$ ). Moreover, in the unburned area near the moderately burned area of Kassandra, we did not find an increased number of hares or their feces (Supplementary Figure 1).

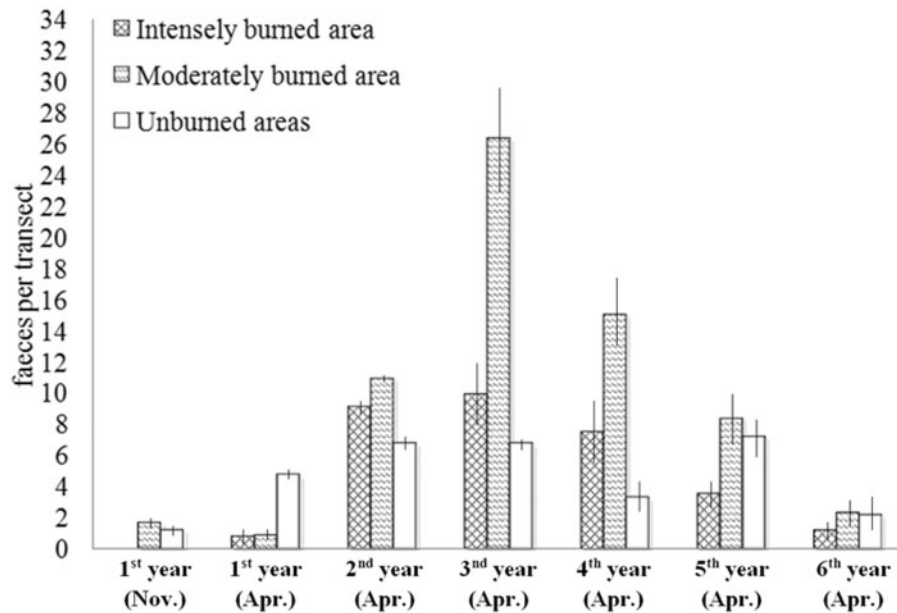
#### Age ratio

A total of 35 hares were collected in Kassandra. Eleven hares were collected in the burned area and eleven in the adjacent unburned areas. Thirteen more hares were collected in nearby unburned areas of Kassandra during the day. Age was determined for all hares. Adults were absent from the burned areas and the age ratio between burned (juveniles: 6, near adults: 5, adults: 0) and unburned areas (juveniles: 11, near adults: 2, adults: 11) was significantly different (Fisher's test,  $P=0.007$ ).

No differences were detected in the ratio of small/large feces between areas in the first ( $\chi^2_c=0.765$ ,  $df=1$ ,  $P=0.382$ ) or second year ( $\chi^2_c=0.554$ ,  $df=1$ ,  $P=0.457$ ) following the wildfire. Similarly, according to the spotlight counts, the ratio of hares younger/older than 3 months old did not differ between areas in the first ( $\chi^2_c=0.62$ ,  $df=1$ ,  $P=0.401$ ) and second year ( $\chi^2_c=0.47$ ,  $df=1$ ,  $P=0.57$ ) following the wildfire.

#### Body condition, diet quality, and disease

Thirty-four kidneys and 33 stomachs were collected and analyzed (2 stomachs were rejected as 1 contained milk and the other blood). Analyses took into account hare age, sex, and the time of day (day or night) they were collected. No differences were found in hare



**Figure 3.** Mean  $\pm$  SE of number of hare feces per belt transect (400 m) in Cassandra Peninsula. Three months after wildfire (November), the sampling method was tested by positioning five transects in the moderately burned area and five in the unburned area. In subsequent visits, 7, 17, and 9–15 transects were taken in intensely, moderately, and unburned areas, respectively.

body condition between burned and unburned areas ( $F_{1,18} = 0.169$ ,  $P = 0.685$ ).

Body condition was not influenced by the dry weight of the stomach contents ( $R^2 = 0.06$ ,  $P = 0.182$ ). Regarding diet quality, crude protein had a positive effect and crude fiber a negative effect on kidney fat, but these were not found to be significant ( $P > 0.136$ ). Fat in the diet favourably affected body condition, although this was marginally non-significant ( $P > 0.052$ ). The diet quality indicator showed a positive correlation with body condition ( $R^2 = 0.243$ ,  $P = 0.0048$ ). No significant difference was detected (Figure 4) between burned and unburned areas in diet components and the diet quality indicator ( $F_{2,25} < 1.56$ ,  $P > 0.229$ ).

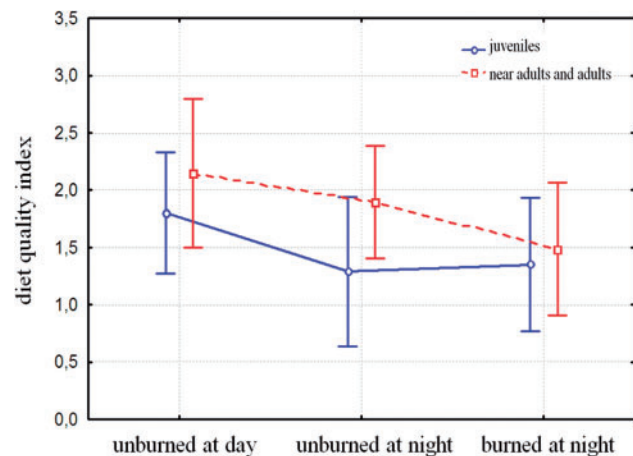
Using PCR, two hares were found to be positive for EBHS. One of these was found in the burned area and the other in the unburned area. No antibodies were detected against any of the pathogens tested by IFAT.

## Discussion

### First year after wildfire

The wildfire in Cassandra was more severe at sites where woody vegetation was abundant, though agricultural fields scattered within the forest contributed to the formation of unburned stands. These sites, located in moderately burned areas seemed to provide refuge for hares during the wildfire and for their recovery after wildfires. In moderately burned areas, hares were counted from the first visit to the study area (1.5 months after the wildfire). Keith and Surrendi (1971) did not find any population decline in moderately burned areas. However, in this study reduced abundance was observed relative to adjacent unburned areas, possibly due to the higher severity of the wildfire in Cassandra.

Increased numbers of hares in unburned areas proximate to moderately burned areas were not observed (Suppl Figure 1), which supports the view that major population dispersal out of burned areas did not occur, or that hares soon returned to the burned areas after the



**Figure 4.** Means and confidence intervals (95%) for the diet quality index [(protein + fat)/fiber] for adult and juvenile hares collected day or night in burned and unburned areas.

wildfire. Keith and Surrendi (1971) also observed no dispersal from moderately burned areas to unburned areas. Hares avoid making home range movements of more than 1 km (Reitz and Leonard, 1994), exhibiting a pronounced homing instinct (Jeziński 1968), with natal dispersal less than 1.5–3 km for the majority of young hares (Reitz and Leonard 1994; Bray et al. 2007; Avril et al. 2011). Furthermore, after the rains of September (about 1 month after the wildfire) the herbaceous vegetation grew and could provide adequate nutritious food. It is probable that hares which moved from the burned areas, mainly the intensely burned areas, returned to their pre-fire home ranges, however, this requires further investigation.

In the intensely burned areas of Cassandra, the first presence of hare was recorded 8 months after the wildfire (Supplementary Table S1). Similarly, Keith and Surrendi (1971) found no hares in intensely burned areas for 1 year after the wildfire. In the intensely burned

area of Kassandra, the hare population was likely to have been low before the wildfire due to the small number of forest openings and fields (Paci et al. 2007; Karmiris and Nastis 2007). Lower hare density was found in the intensely burned areas in the following years. This does not, however, adequately account for the total absence of hares for the first 8 months after the wildfire. It is possible that in the intensely burned area, the higher severity of wildfire caused mortality and a more permanent dispersal of hares, as adequate shelter and food was absent. Several researchers provide evidence of mortality by wildfires for *Lepus americanus* (Hakala et al. 1971) and *Sylvilagus floridanus* (Erwin and Stasiak 1979).

The intensely burned area is located within the moderately burned area and hare range expansion and any other interaction is presumably more probable between these two areas than between the intensely burned and the unburned area. Therefore, the study design was not able to isolate any influence of adjacency. However, using the distinction of moderately and intensely burned areas, the differences due to wildfire influence were further investigated.

### Second year after wildfire

The effects on hare abundance observed during the first year after the wildfire in Kassandra were reversed in the second year (Figures 2 and 3). The spotlight counts showed more hares present in burned areas from autumn 2007, one year after the wildfire in Kassandra. Similar results were observed in the Lagada during the second year after the wildfire, where higher hare abundance was found inside burned as opposed to unburned areas. Keith and Surrendi (1971) report more hares in burned areas 1 year after wildfire. Other researchers also report lagomorph population increases at certain time periods after the occurrence of wildfire or prescribed fire (Gates and Eng 1983; Ferron and St-Laurent 2008; Rollan and Real 2010; Amacher et al. 2011)

One population can be larger than another because reproduction and immigration rates are higher and mortality and emigration rates are lower. Hares rarely disperse more than 1.5–3 km from their birth place (Reitz and Leonard 1994; Bray et al. 2007; Avril et al. 2011). Most hare abundance data for burned areas were collected at distances greater than 3 km from unburned areas, and thus immigration was predicted to be low. Therefore, the most probable explanations for increased population size in the second year are increased reproduction and reduced mortality rates. In burned areas of Kassandra, we collected a higher number of juveniles and near adults than in unburned areas. This indicates that more neonates were produced and/or more juveniles survived.

Increased reproduction and survival rates could occur because of improved food quality and quantity (Hill 1972; Hackländer et al. 2002). The herbaceous biomass had increased considerably 2 years after the wildfire. However, in the Kassandra study area in the autumn of 2007, about 1 year after the wildfire, the diet quality did not differ between burned and unburned areas for all three components considered: crude protein, fat, and fiber. Wildfires generally increase herbivore diet quality. This increase occurs immediately after the wildfire, but quickly diminishes, and after an interval of 1–2 years, there is no difference between burned and unburned areas (Hobbs and Spowart 1984; Carlson et al. 1993). The results of this study showed that the wildfire did not affect diet quality after 1 year. Moreover, body condition did not differ between hares occupying burned and unburned areas.

According to Sinclair et al. (1982), snowshoe hares require about 11% crude protein to maintain body weight. Studies in Central Europe found that the chemical composition of stomach contents

consisted of 19.43% crude protein, 4.14% crude fat and 15.36% crude fiber (Hackländer et al. 2002). In the present study, the diet quality was similar or better in our burned and unburned areas in comparison with Central Europe. Recorded values of mean crude protein were 26.7% in burned areas and 23.73% in unburned areas, with mean crude fat measuring 5.55% in burned areas and 9.1% in unburned areas, and mean crude fibre measured at 19.71% in burned areas and 19.68% in unburned areas.

Diet quality may have been higher in the first months after the wildfire, and thus the initially fewer hares in burned areas could have increased their reproduction rates. Hill (1972), states that the soil fertility increased the number of embryos of *Sylvilagus floridanus* by improving diet quality. However, in Kassandra, according to the feces counts and spotlighting, the ratios of younger (2- to 3-month-old) to older hares were not significantly different between areas in the first or second years after wildfire, thus indicating that the fecundity and production of neonates did not differ.

Lower mortality in burned compared to unburned areas may be attributable to reduced predation, less disease, and various anthropogenic factors such as hunting, poaching, agricultural practices, and roads (Smith et al. 2004; Santilli and Galardi 2007). Anthropogenic influences did not change between the 2 years of research in the burned areas of Kassandra and Lagada. Additionally, the hunting influence was excluded as counting took place in adjacent wildlife refuges where hunting was prohibited.

Among possible diseases, EBHS is one of the most important diseases for hare populations (Frölich and Lavazza 2008). Juveniles have lower susceptibility to EBHS (Frölich and Lavazza 2008), and thus the influence of EBHS is expected to be lower in burned areas over the first 2 years following wildfire when the population has a high percentage of young hares as this study found. However, no differences were detected for the infectious diseases examined and no disease symptoms were observed in collected hares. Wildfire seems not to influence EBHSV prevalence between burned and unburned areas 1 year after the wildfire. The year 2007 is characterized by a low EBHS prevalence of 5.7% over the entire Kassandra Peninsula. A few years after the wildfire, between 2010 and 2012, EBHSV prevalence was higher (28.6%) and yet no difference in EBHS prevalence was detected between burned and unburned areas (Sokos 2014).

Predation depends on predation risk, which is controlled in part by predation pressure (Torre and Diaz 2004; Paci et al. 2007). Hares deposit their feces in their feeding places (Litvaitis et al. 1985; Karmiris et al. 2010), and by counting feces we found that hares prefer to feed in areas with greater wildfire influence (FI). This holds primarily in the absence of woody vegetation (CA) and less to burned vegetation (BV). Therefore, hares preferred to feed in burned sites with more and larger openings, without woody vegetation. This has also been found in other studies on hare and reflects the lower predation risk in these sites compared with sites with woody vegetation (Paci et al. 2007; Karmiris and Nastis 2007; Karmiris et al. 2010). In southern Hellas 2 years after a wildfire, Karmiris et al. (2010) found that as woody vegetation was decreasing due to burning, the number of hare feces was increasing.

Trees provide perch sites for raptors and are used by martens, so it is expected that the destruction of trees by wildfire will reduce the presence of these predators (Torre and Diaz 2004; Tapia et al. 2008). Further, during the second year post-fire, the rapid growth of herbaceous vegetation, together with the presence of branch soil-erosion barriers and branches from logging of burned trees, may have provided improved shelter for hares relative to what was present before the wildfire.

Stone marten were not detected in the burned areas during the second and third summers after wildfire in Kassandra (Birtsas et al. 2012) and fewer eagle owl (*Bubo bubo* L.) individuals were recorded during spotlight counts in burned than in unburned areas (unpublished data). However, Birtsas et al. (2012) found that during the second and third summers after Kassandra's wildfire, red fox had higher visitation rates at scent stations positioned in the intensely burned area. Increased fox presence in the intensely burned areas may contribute to the lower abundance of hares in intensely burned compared to moderately burned areas.

### Third to sixth year after wildfire

Two years after wildfire, the local Forest Service rescinded the hunting ban enforced in burned areas of Kassandra due to the increased hare abundance in burned areas and the fact that shrubs had largely regained their pre-fire height. Following the hunting season, hare abundance was again higher in burned areas in the third and fourth years. Thus, hunting did not strongly influence the increased abundance of hares in burned areas even though more hunters visited these areas in comparison with unburned areas. According to game wardens about 30% more hunting excursions took place in burned areas.

The research team visited the area accompanied by experienced local hare hunters to observe how the hounds *Canis lupus familiaris* behave in both burned and unburned areas. Observations showed that the initial detection of hares by hounds did not differ between burned and unburned areas. However, dogs appeared to experience greater difficulty when chasing hares after flushing, due to the relative impermeability of the thicker vegetation in burned areas at the height of dogs (numerous young shoots and fallen branches). According to discussions with seven experienced local hunters, the hunting effort and success does not seem to change in an unburned and a burned area after the second year from wildfire, however, this requires additional study.

In the fifth and sixth years following wildfire, hare abundance did not differ between burned and unburned areas. This is expected as the regrowth of woody vegetation again creates unfavourable conditions for hares by covering openings and increasing in height. Moreover, predator populations of species like stone marten likely recover owing to the presence of suitable habitat.

### Conclusions and management implications

Hares are widely distributed throughout Mediterranean ecosystems. In this study, in two Mediterranean areas, the relative abundance of hares was lower during the first year after wildfire in burned areas relative to unburned areas. Population abundance was even lower in the intensely burned area where wildfire severity was higher and the wildfire completely destroyed all woody vegetation. This relationship was reversed, however, in the second year, where hares were more abundant in burned areas than unburned areas. Thus hare populations are adversely affected initially by wildfire, but recover rapidly after this severe habitat disturbance, resulting in an increased abundance in burned areas until the fourth year after the wildfire. In the fifth and sixth years, no differences in abundance were found between burned and unburned areas.

Diet quality, body condition, and diseases were not found to differ between burned and unburned areas 1 year after the wildfire. The reduced abundance of some predator species, the opening of forest vegetation, and the higher presence of juveniles and near-adults in burned areas, with a stable presence of neonates, suggest

reduced predation in burned areas compared with unburned areas. Thus, predation appears to be an important limiting factor for hare populations, and wildfire disturbance decreases its impacts.

Additionally, post-fire forest treatments may influence predation risk on hares. Post-fire tree logging is the most commonly applied practice in burned forests. The dispersion of branches was not found to prove beneficial for wild rabbit (*Oryctolagus cuniculus* Lilljeborg, 1873), but their aggregation seems to provide valuable shelter (Rollan and Real, 2010). In our study area, many branches were gathered to form soil-erosion barriers, a practice which we believe provides valuable cover for hares. A future study should focus on optimizing the provision of suitable cover for mammals after wildfires.

Hare populations are a renewable natural resource important to the hunting economy (Zamora et al. 2010; Papaspyropoulos et al. 2014), and thus responsible agencies should monitor their populations after a wildfire using appropriate counting methods. Of the two methods used in this research, feces counts proved more economical than spotlighting, as reported previously by Newey et al. (2003). Additionally, the prohibition of hare hunting should be examined for the first year after wildfire in a moderately burned area, or, until the second year for an intensely burned area. After 1 year, the population density of hares in burned areas exceeds that found in wildlife refuges, a fact that may increase the risk posed by certain pathogens (Gortázar et al. 2006).

The formation of dense scrublands and woodlands has led to diminishing hare populations in mountainous areas of the Mediterranean (Delibes-Mateos et al. 2009). The main change after the wildfire was the change of vegetation structure (reduction of woody cover from 83% to 7% in Kassandra burned area). The results presented here appear to support the statement that land abandonment is one of the main factors explaining the current trend toward the declining abundance of many wildlife species in the Mediterranean region (Sokos et al. 2012). This study highlights the utility of prescribed burning, grazing, logging, and farming within forests as tools promoting the conservation of biodiversity in Mediterranean ecosystems by reducing forest biomass.

### Supplementary Material

Supplementary material can be found at <http://www.cz.oxfordjournals.org/>.

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