



Use of tree hollows by a Mediterranean forest carnivore



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ABSTRACT

Although tree hollows seem to be key structures for a wide range of forest mammals, their importance for Mediterranean forest carnivores remain poorly understood. Here we address this issue, by analysing daily resting site use by 21 radio-collared common genets. Tree hollows were used far more frequently during the wet season (October–April; 73.1% of daily locations) than in the dry season (May–September; 47.6%). Nests and underground dens were the second and third most frequently used resting sites, respectively, in both wet (17.5% and 9.4%) and dry (34.1% and 18.3%) seasons. Each individual reused a large percentage of its resting sites (65.7%). Some resting sites (17.3%) were used by more than one individual, but simultaneous sharing was exceedingly rare (0.56% of daily locations). Hollow use probability during the wet season varied little in relation to environmental variables, though there was a tendency to be higher away from riparian habitats (>50 m) and to be lower in sites with very high shrub cover (>80%). Environmental influences were responsible for more variability in the dry season, when hollow usage was highest in hot days, in days with precipitation, far from riparian habitats, close to sources of human disturbance, in landscapes dominated by continuous forest habitats, and in sites with low shrub cover. Results support the importance of tree hollows for Mediterranean forest carnivores, probably because they provide safe shelter against unfavourable weather, predators and human disturbance. However, results also revealed the importance of riparian trees, which offer support for building nests close to sources of water and food during the dry season. Considering home range size and the average number of hollow-bearing trees used by each genet, we recommend that management of cork and holm oak forests should strive to safeguard at least 4.6 hollow-bearing trees per 100 ha, while simultaneously maintaining large riparian trees. This will improve the resting habitat for common genets, while presumably favouring also other Mediterranean carnivores.

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1. Introduction

Tree hollows provide shelter for a range of forest mammals and thus appear to be an essential resource for the persistence of many species (Gibbons and Lindenmayer, 2002; Banks et al., 2011). This resource is declining due to modern forestry, which reduces the availability of large and old trees with cavities (Gibbons et al., 2008; Ranius et al., 2009). There is thus increasing interest in understanding how mammals use tree hollows, and how the shortage of hollows can limit their populations (Lindenmayer et al., 2012a). This information is essential for the sustainable management of forests, if these are to maintain habitat conditions

for hollow-dependent species (Gibbons et al., 2008; Manning et al., 2013).

Although many mammals are associated with tree hollows in natural forests, in at least some circumstances they may be able to persist despite reductions in hollow availability. For instance, den sharing in social mammals may overcome, at least partly, the shortage of hollows in managed forests (Banks et al., 2013). This strategy may be more difficult for solitary mammals such as most carnivores, where each hollow is generally used by a single individual at a time, with the exception of male and female pairs during the mating season, and of females with its cubs (Zielinski et al., 2004). In forest carnivores it is thus possible that shortage of hollows can be overcome through flexible behaviour allowing animals to use different types of resting sites. At present, however, information is still scarce on the flexibility of rest site use by forest solitary carnivores, and what factors influence such flexibility.

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Forest carnivores normally resting in tree hollows can also use a variety of other structures such as underground dens, green nests, raptor nests, rock piles, and human buildings (e.g. Palomares and Delibes, 1994; Zielinski et al., 2004; Birks et al., 2005; Slauson and Zielinski, 2009; Camps, 2011). However, three major resting site types appear to be used most regularly: (i) tree hollows, (ii) nests and (iii) dens (Zalewski, 1997b; Santos-Reis et al., 2004; Slauson and Zielinski, 2009; Camps, 2011). Nests are structures made by carnivores using plant material, which are often located in large tree branches, and are supported by climbing plants (Palomares and Delibes, 1994; this study). Dens are mainly located on burrows, often in riverbanks and surrounded by high shrub cover (Slauson and Zielinski, 2009). It is uncertain whether these three types of structures, can be used interchangeably, or whether each is associated with a specific set of environmental conditions. Clarifying this issue is important to find out under what circumstances the availability of tree hollows may be limiting for a species.

Several hypotheses may explain variation in resting site use by forest carnivores (Brainerd et al., 1995; Fernández et al., 2002; Birks et al., 2005; Purcell et al., 2009). Tree hollows may be used in more pristine habitats, whereas alternatives may be used in degraded and fragmented forests with few old and large trees (Zielinski et al., 2004, 2006; Manning et al., 2013). Variation may also be related to predation risk, because tree hollows may confer more protection than other rest-site types (Birks et al., 2005; Slauson and Zielinski, 2009). For instance, hollows may be used more frequently where understory shrub cover is lower and so predation risk may be higher, especially from avian predators (Zielinski et al., 2004; Popp et al., 2007; Banks et al., 2011). Seemingly, tree hollows may be used more often where human disturbance is high (Brearley et al., 2010; Banks et al., 2011; Bryant et al., 2012). Another possibility is that variation in rest site use is influenced by their capacity to offer protection against weather extremes such as high (or low) temperatures, and heavy rain events (Taylor and Buskirk, 1994). Tree hollows are judged to provide microclimate stability, and so they may be used more often under harsh conditions. On the other hand, nests may be a good alternative during hot periods, due to convective heat loss at upper canopy layers, while dens may provide fresh temperatures and insulation protection (Buskirk, 1984; Zabala et al., 2007; Lesmeister et al., 2008; Bryant et al., 2012). Finally, it is possible that rest-sites are used in relation to their proximity to critical resources such as mates, food and water, which greatly influence range use by forest carnivores (Brainerd et al., 1995; Purcell et al., 2009; Weir et al., 2012).

Here we examine factors influencing rest site use by the common genet (*Genetta genetta*) in Mediterranean oak forests. This species is considered a useful model for Mediterranean forest carnivores, because it is abundant within its range in south-western Europe, and it is relatively easy to trap and track using telemetry (Pereira and Rodríguez, 2010). Moreover, their predominantly arboreal habits and climbing skills make them suitable to study the importance of tree hollows as resting sites. The genet has a slender body shape, and so it may be affected by energetic constraints under climatic stress similar to those faced by other forest carnivores (Zielinski, 2000; Camps and Alldredge, 2013). Also, the genet occupies landscapes with a wide range of forest composition and fragmentation levels, making it particularly suited for analysing the effects of habitat conditions on rest-site use. Therefore, we carried out a detailed examination of rest-site use based on intensive radio-tracking of genets, aiming to: (i) identify the main types of resting sites; (ii) estimate seasonal variation in resting site use and (iii) quantify variation in tree hollow use in relation to forest composition and fragmentation, resource distribution, predation risk, human disturbance, and weather conditions. Results were

used to discuss Mediterranean forest management favouring the availability of resting sites for genets and other forest carnivores.

2. Materials and methods

2.1. Study area and species

The study was conducted in southern Portugal (38°32'24" to 38°47'33"N, 08°13'33" to 07°55'45"W), in an area of about 50,000 ha (Fig. 1). Climate is Mediterranean, with mean daily temperature ranging from 5.8 °C to 12.8 °C in winter, and from 16.3 °C to 30.2 °C in summer; annual rainfall averages 609.4 mm and is concentrated in October–March (Évora 1971–2000; IPMA, 2012). The relief is undulating (150–430 m above sea level) and the landscape is largely dominated (≈50%) by open to closed cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*) forests, where the understory may be herbaceous or shrubby depending primarily on grazing pressure. Understory shrubs are also frequently removed mechanically to reduce fire risk and for providing easy access to livestock. Agricultural areas are also important (≈45%), comprising mainly dry arable land and pastureland, with or without sparse oak trees, and olive orchards and vineyards.

Common genets (*Genetta genetta*), (mean adult weight ± SE: 1765.8 ± 34.8 g; this study) are widespread and abundant throughout the study area, though they are mainly associated with forested areas and riparian galleries (Zabala et al., 2001; Matos et al., 2009; Santos et al., 2011). They exhibit nocturnal activity, forage both on the ground and in the tree canopy, and select dense cover for breeding and resting (Palomares and Delibes, 1994; Santos-Reis et al., 2004; Camps and Llobet, 2004; Galantininho and Mira, 2009; Pereira and Rodríguez, 2010). Genets feed mainly on small vertebrates, mostly mammals (Virgós et al., 1999; Rosalino and Santos-Reis, 2002). The species is considered of least conservation concern in Portugal (Cabral et al., 2005).

2.2. Trapping and handling

Trapping was performed from May 2010 to December 2011, except in February–April 2011 and August–September 2011 due to logistic constraints and low capture success (Zabala et al., 2001). Trapping was carried out using 10–15 home-made box-traps (30W × 30H × 90L cm) groups, set at >500 m apart from each other, and baited with sardines in oil, fresh chicken eggs, and road-killed small mammals and passerines. Trap groups were spread all over the study area, in potential genet habitats (e.g. forest areas, riparian areas and shrubland areas; e.g. Zabala et al., 2001; Galantininho and Mira, 2009; Santos et al., 2011). Traps were checked every morning after sunrise to minimize animal stress, and bait was replaced whenever needed. Mean ± SE sampling effort in the wet season (October–April) was 33.9 ± 0.8 trap nights (696 total operative trap nights), and in the dry season (May–September) it was 123.0 ± 4.4 trap nights (1190 total operative trap nights).

Once an animal was captured, it was immediately carried to a nearby veterinarian hospital, where the animal was removed from the box, immobilised, and injected intramuscularly with a mix of ketamine hydrochloride (100 mg mL⁻¹) (Imalgene 1000, Lyon, France) and medetomidine hydrochloride (1 mg mL⁻¹) (Domitor, Pfizer, New York, NY, USA) (ratio of 2:1 by volume) at a dosage of 0.12 mL kg⁻¹ (Herr et al., 2010). Animals were weighted, sexed, and checked for sanitary disorders (e.g., parasites). Individuals were classified as juveniles, sub-adults or adults by analysing a combination of morphological traits such as tooth wear, body size, sexual development and overall body condition (Rodríguez-Refojos et al., 2011). All animals were marked with PIT (Passive integrated transponders) tags (model: TXP148511B, 8.5 mm × 2.12 mm,

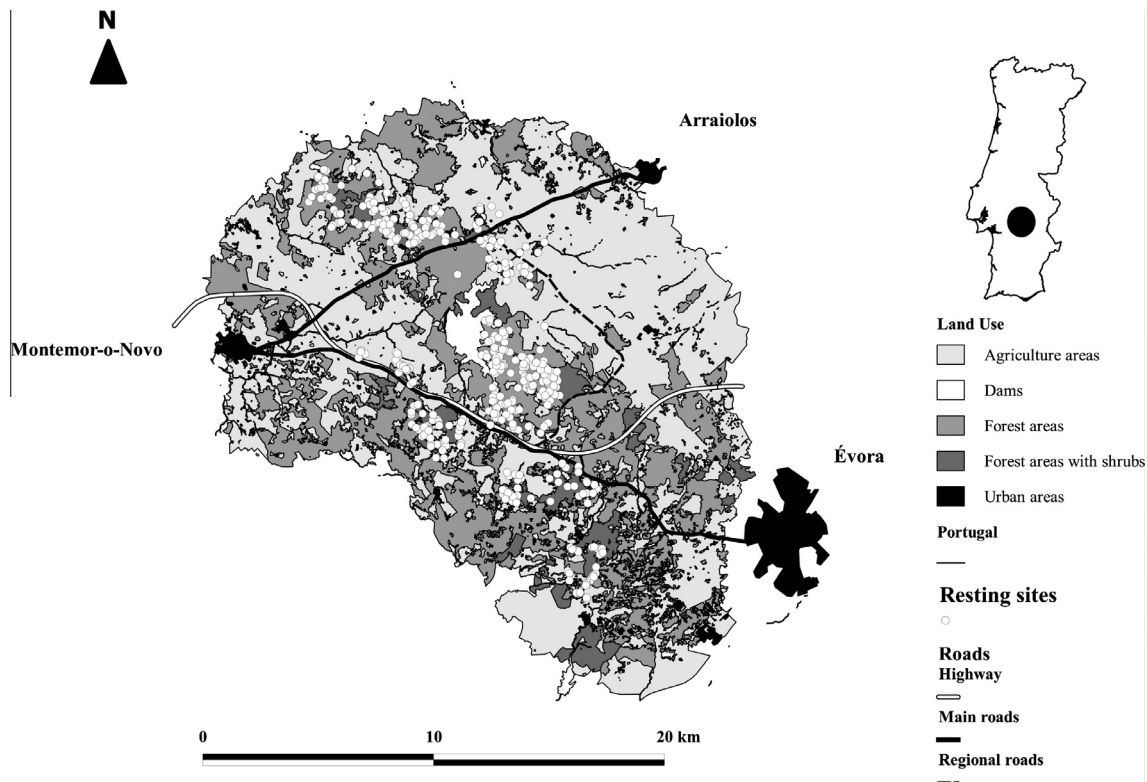


Fig. 1. Location of the study area, showing the main habitat types, roads, and spatial distribution of genet resting sites.

134.2 kHz ISO, 0.067 g, Biomark, Boise, USA) for individual identification. Adults and sub-adults were equipped with radio-collars (≈ 35 g) (models: lpm2700A, Wildlife Materials, USA and TW-3, BioTrack, Wareham, UK), if no more than 5% of their weight were added (Sikes et al., 2011). After handling, the individuals were released in the capture location once they had completely recovered their reflexes (1–3 h). Capture procedures and animal handling were in conformity with Portuguese legal regulations.

2.3. Study animals and data collection

Overall, 32 genets were trapped 36 times in 25 different trapping places. From these, 31 were fitted with radio-collars and one juvenile female was released without radio-collar. From all animals captured, females comprised 18 (12 adults, 5 sub-adults and 1 juvenile) and males 14 (7 adults and 7 sub-adults). Mean \pm SE adult weight for males and females was 1862.9 ± 56.3 g and 1709.2 ± 36.6 g, respectively. The study focused on the 21 genets tracked for at least 30 consecutive days (e.g. Zielinski et al., 2004), including 19 animals tracked in the wet season and 12 in the dry season. Each animal was monitored from the day of release until its death or when the radio-collar batteries finished, averaging (\pm SE) a monitoring period per animal of 183.2 ± 19.4 days (range: 36–389). Ten other animals could not be tracked for sufficiently long periods due to poaching (2 animals), roadkills (2), drowning (1), and radio-collar damage (5).

Resting sites were located by radio-tracking through the “homing” techniques, using a BioTrack receiver (model: biotrackSika, BioTrack, Wareham, UK) and an external 3-element Yagi directional antenna (Wildlife Materials, Inc.) (e.g. Millspaugh and Marzluff, 2001). Monitoring was performed on a daily basis, except on a few occasions due to logistic constraints. During an overall monitoring period of about 120 weeks, resting locations were checked in average (\pm SE) 6.4 ± 0.07 days per week. Although animals tend to remain on the same resting site in daytime, we

checked the location of each animal at different day hours, whenever it was logistical possible. Once the animal was located in the resting structure, we took a considerable care during the approach in order to not disturb the animal. To avoid wrong locations, a snake inspection camera (model: 8802 AJ GOSCAM, TFT-LCD 2.5 colour monitor) was used several times to guarantee the correct distinction between ground nests vs. dens, and tree hollows vs. nests. All locations (coordinates) were recorded using a GPS unit (model: Garmin Map 62; 2 m positional accuracy), and then a detailed microhabitat vegetation description was made (see below).

2.4. Explanatory variables

Analyses were based on nine explanatory variables reflecting landscape composition and configuration, resource distribution, predation risk, human disturbance, and daily weather conditions (Table 1), which were selected from previous studies reporting factors affecting resting site use by forest carnivores (e.g. Brainerd et al., 1995; Zielinski et al., 2004; Purcell et al., 2009; Slauson and Zielinski, 2009; Camps, 2011; Banks et al., 2011; Mergey et al., 2011). Landscape composition and configuration were estimated from the proportional cover and fragmentation of forest habitats within 1-km buffers (≈ 314 ha) of each resting site. We focused on forests because we expected the use of tree hollows to increase along with the extent and continuity of forest habitats (Santos-Reis et al., 2004). The buffer size was selected because it was close to genet mean (\pm SE) home range size in the study area (386.4 ± 40.1 ha; minimum convex polygon with 95% of locations [MCP95]), and it was much larger than the mean core range size (96.0 ± 12.0 ha; [MCP50]) (Slauson et al., 2007). Moreover, our daily data suggests that the average distance between resting sites was about 1 km (males: 1008.35 ± 95.18 m; and females: 1022.18 ± 102.89 m), so we believe that the buffer adopted in our study is likely to reflect a coarse spatial scale of resting site selection by common genets. Landscape composition was

Table 1

Description and summary statistics of explanatory variables used to analyse rest site selection by the genet in Southern Portugal.

Variables (abbreviation)	Description (transformation)	Wet season		Dry season	
		Mean ± SE	Range	Mean ± SE	Range
<i>Landscape composition and configuration (within 1 km of rest site)</i>					
Forests	Proportional cover by forests (>30% tree canopy density) (Asin[√x])	0.51 ± 0.007	0.0–0.95	0.44 ± 0.007	0.02–0.95
Forests with shrubs	Proportional cover by forests (>30% tree canopy density) with understory shrubs (Asin[√x])	0.18 ± 0.003	0.0–0.76	0.30 ± 0.006	0.0–0.76
Forest patch Size	Mean patch size (ha) of forest habitats (log10)	130.2 ± 2.1	3.5–304.3	146.3 ± 3.1	4.4–307.2
Forest edges	Density of (m/ha) of edges between forests and other habitats (log10)	49.8 ± 0.4	17.4–120.5	55.4 ± 0.7	26.4–113.0
<i>Resource distribution</i>					
Riparian	Distance (m) to the nearest riparian habitat (log10)	258.3 ± 5.3	0.2–1210.4	175.0 ± 6.9	0.1–848.2
<i>Predation risk</i>					
Shrub cover	Proportional cover by shrubs within a 25 m of each rest site (Asin(√x))	0.49 ± 0.009	0.0–1.0	0.67 ± 0.01	0.0–1.0
<i>Human disturbance</i>					
Human disturbance	Distance (m) of rest site to the nearest source of human disturbance (e.g., houses and roads) (log10)	846.9 ± 12.2	15.3–2263.0	723.5 ± 13.5	30.9–2263.0
<i>Weather</i>					
Maximum temperature	Maximum daily temperature (°C) (log10)	16.1 ± 0.1	5.7–33.4	28.8 ± 0.1	14.5–39.5
Precipitation	Daily precipitation (mm) (log10)	2.0 ± 0.09	0.0–32.8	0.5 ± 0.08	0.0–41.9

estimated in a Geographic Information System (Quantum GIS Development Team, 2011), based on detailed land cover maps prepared using digital aerial photographs from 2011 and field surveys. Landscape metrics were estimated using the Patch Analyst extension (Rempel and Carr, 2003) for ArcView 3.2 (ESRI, 1999).

Detailed information on the distribution of genet key resources (e.g., prey density) was unavailable, and so it could not be used to analyse the correlates of rest-site use. However, we used the distance to riparian habitats as a proxy for resource distribution, because they may be important sources of food and water, particularly during the hot and dry season (Matos et al., 2009). Likewise, detailed information on predation risk was unavailable, though it is likely that several predators occurring in the study area may kill or otherwise influence the behaviour of genets, including for instance domestic dogs (*Canis familiaris*), foxes (*Vulpes vulpes*), and eagle owls (*Bubo bubo*) (Larivière and Calzada, 2001; Carvalho et al., 2013). We used as a surrogate of predation risk the proportional cover by shrubs, estimated through detailed vegetation mapping within 25 m of each rest-site (e.g. Jerosch et al., 2010). Predation risk was assumed to vary inversely with shrub cover (Popp et al., 2007; Ordiz et al., 2011; Ross et al., 2012). The distance of rest-sites to houses and roads was used as a surrogate of human disturbance. Weather conditions were described from the maximum daily temperature and daily precipitation, using data collected in the nearest weather station (Mitra; CGE, 2012).

2.5. Data analysis

Prior to statistical analyses, skewed variables were transformed to approach normality and to reduce the influence of extreme values, using either angular or logarithmic transformations (Table 1). All variables were then standardised to zero mean and unit variance, to enhance comparability of effect sizes (e.g. Schielzeth, 2010). Collinearity was investigated using pairwise correlations, and one variable from each pair correlated at >0.7 was eliminated from further analyses (Dormann et al., 2013). All statistical analyses were performed using the R statistical package (R Project for Statistical Computing release 2.15.3 <<http://www.r-project.org>>).

The use of hollows vs. alternative resting site types was coded as a binary variable (1/0), and related to explanatory variables using generalised linear mixed effects models (GLMM), with binomial errors and logit link (Zuur et al., 2009). Wet and dry season data were modelled separately, because preliminary analysis

pointed out marked seasonal differences in resting site use. On the other hand, the two sexes were considered together because no significant effects were found in exploratory univariate analyses specifying sex as a binary variable in the fixed component of the GLMM model, in both the wet ($p = 0.489$) and the dry season ($p = 0.642$). Only tree hollows were explicitly modelled, because they accounted for most rest-sites recorded (65.1% out of 497), while each of the alternative types accounted for less than 25% of the rest-site and so they did not allow for separate analysis. In GLMMs, the animals were always included as random effects, to account for lack of independence resulting from eventual individual idiosyncrasies in resting site use. Model building of the fixed component was based on the information theoretic approach, and inference was based on model averaging (Burnham and Anderson, 2002). Candidate models were built based on all possible subsets of non-collinear explanatory variables, including the null (i.e., without explanatory variables) and the full (i.e., with all explanatory variables) models. Models were ranked according to their Akaike weights (w_i), and the average parameters and their unconditional standard errors (SE) were estimated based on the 95% confidence set of models (Burnham and Anderson, 2002). The relative importance of each variable was judged based on the sum of Akaike weights of models where the variable was included (w_+), and on the magnitude of the average model coefficient. GLMMs were fitted using the package lme4 (Bates et al., 2013), and multi-model inference was implemented using MuMIn (Barton, 2013).

Collinearity in model building was assessed by computing the variance inflation factor (VIF) of each variable in the full model, assuming that problems may occur if $VIF > 3$ (Zuur et al., 2009). Model adequacy was evaluated by plotting the residuals of the average model against the fitted values and each of the variables presented in the final model (Zuur et al., 2009). Model discrimination ability was assessed using the area under the remote operating characteristic curve (AUC), with values above 0.9 taken to indicate excellent accuracy (Rapacciuolo et al., 2012). To check for eventual autocorrelation problems, we computed the Moran's I based on spline correlograms for the raw binary response variable and the residuals from the average model, using the "spline.correlog" function with 1000 permutations from the R package "nfcf" (Bjørnstad, 2012). Additionally we run a mantel test of overall autocorrelation between the response variable and model residuals against distance between resting sites (Urban, 2003). Temporal autocorrelation was inspected by plotting the autocorrelation

function (ACF) with the model average residuals vs. the lag between monitoring days (Zuur et al., 2009), using the “acf” function from the R package “nlme” (Pinheiro et al., 2012).

3. Results

3.1. Resting site use

A total of 497 different resting sites were used by the 21 genets tracked during 28 months. Most sites (82.7%) were used by a single individual (not shared), while the others were shared by 2 or 3 individuals. Simultaneous use of the same rest-site by two individuals occurred rarely (0.56% out of 3334 daily locations) and involved a small proportion of the rest-sites (2.8%). The simultaneous use of resting sites occurred among the following pairs: adult male/adult female, adult female/sub-adult male, adult male/sub-adult male, and two sub-adults male/female. Individuals used from 12 to 45 different resting sites, corresponding to an average (\pm SE) of 28.2 ± 2.3 rest-sites per individual. Resting sites reuse (percentage of resting sites used more than once by an animal) occurred quite often, both in wet ($63.9\% \pm 2.8$) and dry ($54.7\% \pm 2.9$) seasons. Reuse of rest-sites occurred predominately in tree hollows (60.9%), followed by nests (22.6%) and dens (16.5%).

Genets rested most often in tree hollows (65.1%), which were mainly located in cork oaks (50.6%), and holm oaks (42.5%), while

ash (*Fraxinus angustifolia*), poplar (*Populus* spp.), and large and old olive trees (*Olea europaea*) were used rarely (6.9%). In average (\pm SE), tree hollows were located 3.5 ± 0.1 m above the ground. Nests were the second most frequent resting site (22.7%). Most nests were located above the ground (84.2%), at an average height (\pm SE) of 3.4 ± 0.4 m, and they corresponded to vegetation beds made with grass and leaflets supported by tree branches (most ash and poplar trees) and/or climbing plants. Nests at ground level were always under shrub cover and they were similar to grass beds. Dens (11.2% of resting sites) were found in riverbanks under high shrub cover, and they were mainly located on burrows excavated by other animals (97.9%), or under tree roots. Most burrows had been excavated by rabbits (*Oryctolagus cuniculus*), though genets were also found in a few occasions in unoccupied red fox and badger (*Meles meles*) burrows. Other types of resting sites were used rarely (1.0%), including rock piles and one habited farmhouse. From 2291 daily locations recorded during the wet season, there were 73.1% in tree hollows, 17.5% in nests, and 9.4% in dens. In contrast, from 1043 daily locations during the dry season, there were 47.6% in tree hollows, 34.1% in nests, and 18.3% in dens.

3.2. Correlates of resting site use

The only pairwise correlations >0.7 were between forest cover and mean patch size ($r = 0.88$ and 0.82 , using wet and dry season data, respectively), and between forest edge density and mean

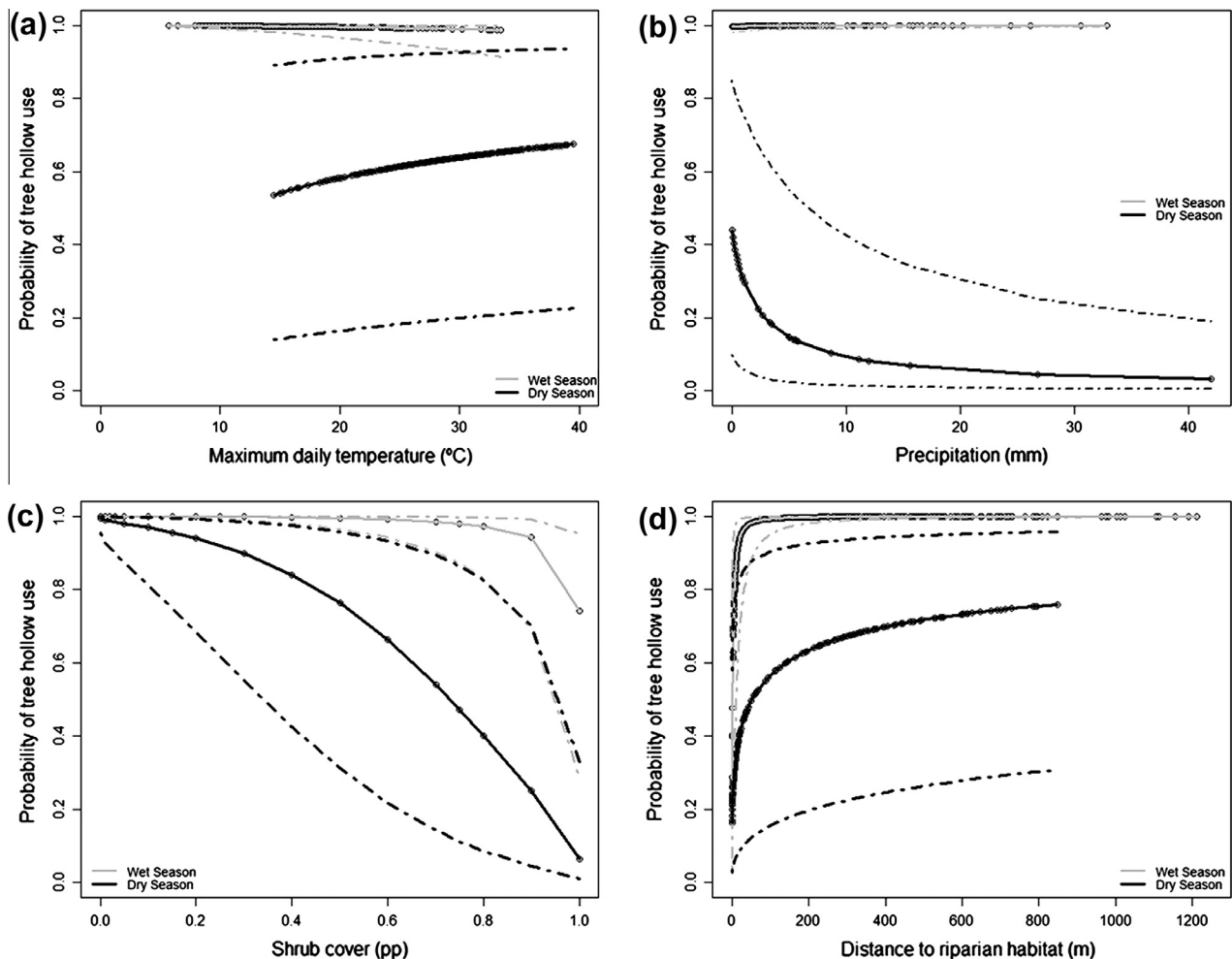


Fig. 2. Probability of tree hollow use (with 95% confident limits) predicted from dry and wet season average GLMM models (see Table 2), in relation to: (a) maximum temperature, (b) precipitation, (c) shrub cover, (d) distance to riparian habitat, (e) human disturbance, (f) forest cover, (g) cover by forest with shrubs, and (h) forest edge density. For each variable and season, response to one variable was extracted from the model by maintaining all the other variables at their median values. Models were fitted on transformed and standardised data, but are depicted on the original scale.

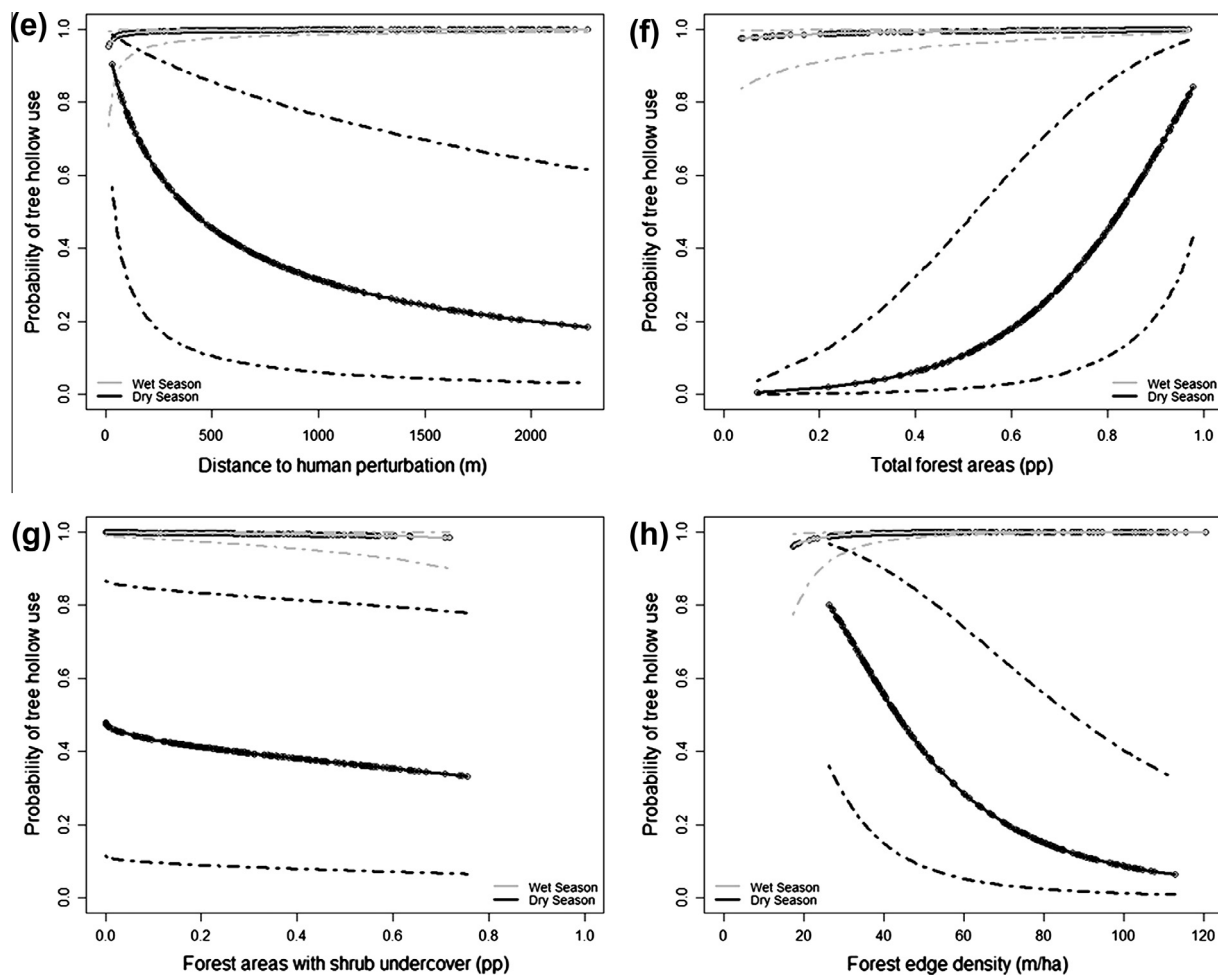


Fig. 2 (continued)

patch size (0.71; dry season). Therefore, mean patch size was removed from subsequent analysis to reduce collinearity problems. The GLMM model developed for the wet season indicated that the use of tree hollows prevailed across the range of variation of the explanatory variables (Fig. 2), though the probability of tree hollow use increased to some extent with distance to riparian habitats and to human disturbance, with forest cover and edge density, and with precipitation (Table 2). Hollow use declined with shrub cover around resting sites, forest with shrubby understory, and maximum daily temperature (Table 2). The strongest effects observed, were the declines in tree hollow use in areas very close (<50 m) to riparian habitats and high local cover (>80%) by shrubs (Fig. 2d and c). The wet season model had high discrimination ability (AUC = 0.944) (Supplementary Fig. S4a), and it did not show any problems resulting from collinearity (VIFs < 3), outliers or extreme values and deviations from linearity assumptions in the logit scale. Although there was high spatial autocorrelation in the raw binary variable, this was no longer observed in the correlogram of average model residuals (Supplementary Fig. S1) and in the Mantel test ($p = 0.17$). Temporal correlogram suggested that residuals were correlated for resting sites monitored in the same day, but correlations declined to close to zero afterwards (Supplementary Fig. S3a). There were also significant correlations in the residuals for time lags of 13 and 26 days.

During the dry season, the GLMM suggested that variation in the probability of tree hollow use in relation to explanatory variables was much larger than in the wet season (Fig. 2).

The probability of genets using tree hollows increased with distance to riparian habitats and forest cover, and it declined with

Table 2

Average models describing the estimated effects of explanatory variables on the probability of tree hollow use by genets in the wet and dry seasons. For each season, multi-model averaging was based on the 95% confidence set of models. For each variable, we show the standardised regression coefficient (β), the unconditional standard errors (SE), the 95% confidence interval of coefficient estimate (CI), and the selection probability (w_+). Variables selected in the best models are underlined and coefficient estimates whose 95% CI exclude zero are in bold.

Parameters	β	SE	CI	w_+
Wet season				
Intercept	4.469	0.981	(2.546, 6.392)	–
<u>Maximum temperature</u>	–0.562	0.130	(–0.817, –0.307)	1.000
<u>Precipitation</u>	0.298	0.114	(0.075, 0.522)	0.940
<u>Shrub cover</u>	–3.209	0.271	(–3.742, –2.678)	1.000
<u>Riparian</u>	2.315	0.243	(1.839, 2.791)	1.000
<u>Human disturbance</u>	0.662	0.229	(0.215, 1.110)	1.000
<u>Forests</u>	0.633	0.285	(0.075, 1.191)	0.820
<u>Forests with shrubs</u>	–0.649	0.331	(–1.297, –0.002)	0.730
<u>Forest edges</u>	0.988	0.304	(0.392, 1.583)	1.000
Dry season				
Intercept	0.286	0.993	(–1.661, 2.232)	–
Maximum temperature	0.103	0.153	(–0.198, 0.403)	0.320
<u>Precipitation</u>	–0.398	0.156	(–0.704, –0.092)	0.930
<u>Shrub cover</u>	–2.679	0.260	(–3.188, –2.169)	1.000
<u>Riparian</u>	0.788	0.179	(0.438, 1.138)	1.000
<u>Human disturbance</u>	–0.671	0.250	(–1.161, –0.181)	1.000
<u>Forests</u>	1.127	0.321	(0.498, 1.756)	1.000
Forests with shrubs	–0.151	0.254	(–0.650, 0.348)	0.310
<u>Forest edges</u>	–1.181	0.477	(–2.215, –0.247)	0.890

forest edge density, local shrub cover, distance to human disturbance, and precipitation (Table 2). Temperature and cover by forests with shrubs had low selection probabilities ($w_+ < 0.35$), and so their effects were very little supported (Table 2). The dry season model had high discrimination ability ($AUC = 0.901$) (Supplementary Fig. S4b), and it did not show any problems resulting from collinearity ($VIFs < 3$), outliers or extreme values, and deviations from linearity assumptions in the logit scale. Although there was high spatial autocorrelation in the raw binary variable, this was no longer observed in the correlogram of average model residuals (Supplementary Fig. S2) and in the Mantel test ($p = 0.37$). The temporal correlograms suggested that residuals were correlated for resting sites monitored in the same day and, to a much lesser extent, for time lags of one and two days (Supplementary Fig. S3b).

4. Discussion

Our study evidenced the importance of tree hollows as key resting sites for genets inhabiting Mediterranean oak forest. Tree hollows were particularly used during the wet season, whereas alternative resting sites (nests and dens) were also heavily used during the dry season. In line with expectations, explanatory variables reflecting landscape composition and configuration, resource distribution, predation risk, human disturbance and weather affected the probability of tree hollow use, though these effects were most marked during the dry season. Overall, our daily based results support the view that tree hollows may be an important resource for Mediterranean solitary forest carnivores, in line with observations for other forest carnivores elsewhere (e.g. Brainerd et al., 1995; Zalewski, 1997a, 1997b; Zielinski et al., 2004; Isaac et al., 2008; Purcell et al., 2009; Slauson and Zielinski, 2009; Camps, 2011; Weir et al., 2012).

4.1. Resting site selection

The use of tree hollows vs. that of alternative resting site types (i.e., nests and dens) was significantly related to the explanatory variables analysed, but the strength and shape of the relationships varied considerably across seasons, suggesting that the mechanisms of resting site selection may change across the annual cycle. During the wet season, genets were found almost exclusively in tree hollows, with variation in the explanatory variables only causing very small changes in hollow use probability. There was thus evidence for a largely inflexible resting site selection strategy, suggesting that during the wet season tree hollows may be more suitable for genets than the alternative resting site types. Reasons for this are uncertain, but they may be related to tree hollows providing relatively stable microclimates and dry conditions in a period when temperatures are relatively low, and there is high probability of precipitation. This view is supported by other studies suggesting that unfavourable climate conditions during the winter are among the key factors affecting resting site selection by forest carnivores (Taylor and Buskirk, 1994; Isaac et al., 2008). Another possibility is that resting site selection was driven by human disturbance (e.g. Ordiz et al., 2011), because hunting in the region occurs through most of the wet season. Although genets are not legally hunted, it is possible that animals prefer to shelter in more secluded sites such as tree hollows when there are hunters and their dogs in the vicinity. Despite the dominant use of hollows, however, genets used alternative resting sites more frequently in areas with very high shrub cover (>80%), and very close (<50 m) to riparian habitats. These relationships are similar to those observed during the dry season, albeit less pronounced, and may reflect predation risk avoidance and resource distribution (see below).

In contrast to the wet season, there was a high flexibility in resting site use during the dry season, with variation in several explanatory variables causing major changes in hollow use probability. Hollows were used most frequently in hot days, in days with precipitation, far from riparian areas, close to sources of human disturbance, in landscapes dominated by forest habitats and with low forest edge density, and in sites with low shrub cover. The relationships with temperature and precipitation supported the importance of climate conditions on resting site selection, suggesting that tree hollows provided insulation against extreme temperatures, and dry conditions during rainy days (Taylor and Buskirk, 1994; Weir et al., 2004; Isaac et al., 2008). The higher use of tree hollows close (<500 m) to sources of human disturbance (e.g., roads, farmhouses) also supported the view that hollows may be particularly suitable to offer secure shelter from human activities (e.g. Ordiz et al., 2011). Tree hollow availability was probably another factor affecting resting site selection, as suggested by the higher usage of hollows in landscapes with more cover and less fragmentation of forests. The higher usage of alternative resting sites in areas with high shrub cover is in line with the prediction that resting site selection should reflect predation risk avoidance (Purcell et al., 2009; Slauson and Zielinski, 2009; Broekhuis et al., 2013). In fact, shrub cover probably reduced predation risk due to the lower accessibility by flying raptors and owls, and poorer scent detectability for other ground carnivores such as foxes and dogs (Popp et al., 2007; Slauson et al., 2007; Mangas et al., 2008; Ordiz et al., 2011; Caryl et al., 2012), thereby relaxing the need to find safe shelter in tree hollows. Close to riparian areas genets were found resting primarily in nests and, to a much lesser extent, in underground burrows, suggesting that riparian trees may offer little shelter in hollows. The use of these trees was probably related to the distribution of key resources such as water and food, which are largely concentrated in riparian habitats during the Mediterranean dry season (Matos et al., 2009; Sabino-Marques and Mira, 2011).

4.2. Forest management implications

Results from this study supported the view that the conservation of carnivores in Mediterranean forests may require the preservation of hollow-bearing trees, as it has been shown for a range of forest mammals elsewhere (e.g. Brainerd et al., 1995; Zalewski, 1997b; Zielinski et al., 2004; Isaac et al., 2008; Purcell et al., 2009; Slauson and Zielinski, 2009; Camps, 2011; Weir et al., 2012). In particular, the study underlined the need to maintain large and old oak trees, both cork and holm oaks, which accounted for the vast majority of genet rest sites recorded. This idea is supported by a previous study showing a strong association between genet latrines and large oak trees in Mediterranean forests (Espírito-Santo et al., 2007). Although these results derived from the study of a single species, there is some evidence that they may apply to other carnivores (e.g. Zalewski, 1997b; Santos-Reis et al., 2004; Birks et al., 2005), including for instance the critically endangered Iberian lynx (*Lynx pardinus*) (Fernández et al., 2002) and the endangered wild cat (*Felis sylvestris*) (Jerosch et al., 2010).

Considering the average number ($\pm SE$) of hollow-bearing trees used by each genet (18 ± 3.4), and their average home range size (386.4 ± 40.1 ha), we suggest that a minimum of 4.6 hollow-bearing trees per 100 ha should be maintained in cork and holm oak forests, though further research is needed to assess whether the same threshold applies in other habitat types. Even in cork and holm oak forests, there may be variation in the density of tree hollows required by genets, depending on local environmental conditions and management practices. For instance, management aiming to reduce fire hazard involves the widespread clearing of undergrowth woody vegetation (Santana et al., 2011), which may

reduce protection against predators and thus increase the use of tree hollows. Also, higher tree hollow densities may be required due to human disturbance, as anecdotal information suggested that some potentially suitable trees may become temporally avoided by genets due to silvicultural operations such as cork stripping and pruning. Finally, it should be stressed that a much larger density than that identified in this study is probably required to maintain the full variety of species associated with hollow-bearing trees, such as reptiles, birds and bats (e.g. Gibbons and Lindenmayer, 2002; Fischer et al., 2010), though information to confirm this is largely lacking for Mediterranean forests. In fact, little is known about the typical densities of hollow-bearing trees in Mediterranean forest landscapes and the factors affecting these, and about the densities required by different species of vertebrates. Clearly, these issues require further research in order to inform the sustainable management of Mediterranean oak forests (Gibbons et al., 2008; Lindenmayer et al., 2012b).

This study also identified large trees along riparian galleries as another important resource for genets, which used them as support for nest building, particularly during the dry season. This result is in line with other studies on Mediterranean carnivores, which have shown a heavy use of riparian areas (Virgós, 2001; Matos et al., 2009; Santos et al., 2011). Large riparian trees probably provided safe microclimatic refuge, and allowed the efficient exploitation of water and food resources that are concentrated along stream and river margins during the dry and hot summer season (Ruggiero et al., 1998; Zielinski et al., 2004; Pereira and Rodríguez, 2010; Santos et al., 2011). Hollow-bearing oaks and large riparian trees may thus be complementary resources, both of which are needed to assure habitat conditions for genets across the annual cycle. Maintenance of large riparian trees may thus be important for the conservation of genets and eventually other Mediterranean carnivores (Fernández et al., 2002; Birks et al., 2005; Camps, 2011), further adding to the importance of riparian forests for biodiversity conservation in Mediterranean landscapes (Gibbons and Lindenmayer, 2002; Pereira and Rodríguez, 2010; Lindenmayer et al., 2012a).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.12.013>.

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