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Feeding habits of house and feral cats (*Felis catus*) on small Adriatic islands (Croatia)

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Abstract. The domestic cat (*Felis catus*), a globally recognised invasive predator, was introduced to the Adriatic islands (Croatia), but its feeding ecology and impacts on biodiversity in this region is unknown. We studied the feeding habits of house cats living in villages and feral cats on the outskirts of villages on two small islands (Olib and Silba) by analysing faecal samples collected in the spring and autumn periods. Our hypothesis was that the feeding strategies of cats as top mammalian predators vary in different environments, due to significant dissimilarities in their food resources. We surveyed the abundance of cats and their primary food types, e.g. small mammals, birds, rabbits *Oryctolagus cuniculus*, and lizards. Our results suggest that house cats fed most often on birds and household food, while feral cats ate mostly small mammals and lizards. Feral cats preferred the invasive mesopredator black rat (*Rattus rattus*) (Ivlev's index of preference, feral cats $E_i = 0.72$, house cats $E_i = 0.14$), suggesting that cats might have an effect-on rat populations. Common rabbits had a low density and were preyed on only occasionally. In both cat groups, predation on birds was more frequent during autumn migration when bird abundance was higher, than in the spring breeding period. Both groups were food generalists but in different ways, which is a fact that should be considered in planning predator pest control on the islands.

Keywords: invasive predator, domestic cat, Mediterranean island, prey abundance, rat preference

Running title: Feeding habits of domestic cats on small islands

Introduction

Species on islands generally have small populations, narrow distributions and restricted genetic diversity (Blondel 1995), and even small environmental changes can considerably affect their persistence (Vitousek 1988). Continuous human impacts which have influenced landscapes, habitats, and biodiversity are documented in the Mediterranean area, and also on the Adriatic islands for over 2 000 years (Blondel et al. 2010, Jelaska et al. 2010). Two major causes of the decline of biodiversity on the Adriatic islands are habitat degradation and the introduction of non-native predators, such as feral domestic cats (*Felis catus*), the black rat (*Rattus rattus*) and the small Indian mongoose (*Herpestes auropunctatus*) (Barun et al. 2008, 2010, 2011).

The domestic cat has a long history of coexistence with man (Fitzgerald 1988, Randi & Ragni 1991, Driscoll et al. 2009); having been transferred by humans to almost all parts of the world (Fitzgerald 1988, Dickman 1996a, Doherty et al. 2014) and they are considered to be one of the 100 worst invasive species in the world (Lowe et al. 2000). Feral domestic cats are principal predators of small-sized native animals (mammals, birds, reptiles and insects) as revealed in different climates, such as tropical, warm, temperate and sub-Antarctic islands or other inlands (Fitzgerald 1988, Dickman 1996a, 1996b, Pearre & Maass 1998, Nogales & Medina 2009, Bonnaud et al. 2011, Doherty et al. 2015). The cat as a predator may have a substantial effect on wildlife (Carss 1995, Dickman 1996a, Woods et al. 2003), e.g. causing local decline or extinction of many species (Dickman 1996b, Medina & Nogales 2009, Hervías et al. 2014). Cat eradication experiments are often effective in stopping such extinctions and in preserving biodiversity (Nogales et al. 2004, Bonnaud et al. 2007). However, in some cases the removal of the top predator can result in an increase in mesopredator numbers, based on the "mesopredator release effect" (Courchamp et al. 1999, Crooks & Soulé 1999, Russell et al. 2009).

Depending on the particular area, the most important prey for feral cats can be mammals such as rats (as mesopredators), mice or even rabbits (Liberg & Sandell 1988, Pearre & Maass 1998, Nogales & Medina 2009, Hervías et al. 2014). However, in cases of low availability of small mammals or in the breeding period of birds on islands, cats may alter their diet to feeding on birds or native amphibians during their breeding season (Fitzgerald 1988, Peck et al. 2008). The feeding ecology of domestic cats is less known on small Mediterranean islands (Clevenger 1995, Bonnaud et al. 2011), and on the Adriatic islands it has not yet been studied, especially where the cat is the sole carnivorous predator at the top of the food chain. House-based domestic cats (Liberg 1984) depend on food supplied by their owners; therefore, their populations are not limited by the availability of wild prey (Woods et al. 2003), although the domestic cat is still capable of moving from a tame to a feral state

(Liberg & Sandell 1988). In contrast to house-based domestic cats (hereafter: house cat), the diet of feral cats includes household food at low ratios or none at all (Liberg 1984, Doherty et al. 2015). Although a small part of scat samples collected within villages might originate from feral cats, and on the outskirts from house cats (Biró et al. 2004, 2005), in this study we distinguished the following two groups of cats: 1) house cats which are highly dependent on human households, and 2) feral cats which are independent of human households (Liberg & Sandell 1986, Pearre & Maass 1998).

In order to understand better the ecological role of the introduced domestic cat on small islands, the objective of this study was to carry out a comparative analysis of the diet composition and feeding habits of house and feral cats during the autumn bird migration and the spring nesting period on two islands in the Adriatic Sea. We assumed that the feeding strategies of cats as top mammalian predators on small Mediterranean islands vary in different environments, due to significant dissimilarities between the food resources of house cats living in villages and feral cats living on the outskirts of human settlements. According to the previous surveys (reviews: Fitzgerald 1988, Dickman 1996b, Bonnaud et al. 2011) we predicted that the feral cat, in comparison with the house cat, a) preys more frequently on wild-ranging prey species, such as rabbits, small mammals, birds, lizards and insects, and therefore b) has a more diverse food composition, and due to higher dependence on wild-ranging prey types, will be more food generalist and opportunistic than the house cat.

Materials and methods

Study area

The study was conducted on two similar islands, Olib and Silba located in the Adriatic Sea, Croatia (Fig. 1). These islands belong to the western part of the Zadar archipelago which is part of the National Ecological Network – areas important for birds in Croatia (Radović et al. 2005). Olib Island is 9.5 km long, stretching in a N-S direction. Its width is only 1.4 km in the middle, increasing up to 5.8 km, with a total area of 26.14 km^2 (0-71 m ASL). It is located 23.5 km from the mainland and the only settlement and harbour, Olib, has existed since Roman times (Magaš & Faričić 2002). The human population is low with only 140 inhabitants in 2011. The island of Silba, a smaller island (14.27 km^2, 0-77 m ASL), with similar natural history (Duplančić-Leder et al. 2004), is located about 1.8 km west of Olib. Its only settlement, Silba, had a population of 292 inhabitants in 2011. Current human activity (including tourism) is limited and restricted to the port area, where both islands have their villages. There are no surface water streams and the majority of the population's freshwater demand is supplied from rainwater reservoirs and tanker ships. The temperate Mediterranean climate on the island is characterised by mild and rainy winters with warm and dry summers (Magaš & Faričić 2002), with a mean annual precipitation of 970 mm and mean annual temperature of 15˚C. The vegetation consists of Mediterranean forests of Pubescent Oak (*Quercus pubescens*) and Holm Oak (*Q. ilex*) and their successional stages (Horvat et al. 1974). In the outer zones of the islands there are extensively managed olive groves and abandoned fields, whereas inside the village traditional gardening is practiced. Gardens and lands in the outer zones are bordered by traditional dry stone walls (Purger et al. 2012).

Populations of cats and their prey

A distance sampling method (line transect survey) using GPS was applied for estimating the population size of cats in autumn (October 2008) and spring (May 2009) within the same areas (Table 1). In order to reduce differences between detection probabilities depending on different habitats, two or three people performed the different surveys in parallel. In order to quantify cat abundances we used two survey methods. We calculated minimum cat density (D) along the total length of transect (L), based on the distance of cats (n) from the line, recording cats observed on the line and on its two sides within a 20 m strip width (w), using the line transect method (Krebs 1989), $D = n/(2wLp)$ and probability function. Cat occurrences were only taken into consideration within the 20 m strip. Individual distance data were divided into four quartiles (up to 4 m, 4.1-8 m, 8.1-15 m and above 15 m (max. 20 m). 100% probability was within the first quartile (which is approximately the road width), than decreased to 40.0%. Mean observation probability (p) was 68.1%. Due to terrain morphology (high stone walls along narrow and winding roads with dense woods and undergrowth along them) we counted cats during the day instead of the optimal night time (e.g. Peck et al. 2008), therefore we also used the density of scats (faeces) for drawing conclusions regarding dense or sparse cat occurrence. This method seemed to be justified by the fact that the hard and dry rocky soil found on the islands left the cats with limited possibility to bury their faeces, meaning that they remain exposed and observable. Relative scat density can potentially be used as an indicator of differences in population abundances between areas and periods if the data collection (survey) is standardised (Mason & Macdonald 1987, Gese 2001, Kamler et al. 2003). Therefore, to assess the "relative abundance of cats" we estimated a scat density index on the basis of scats found per line km (Table 1). Fresh or dry intact scat samples were collected inside and outside the two villages. Inside the villages samples were collected on both sides of the 4 m wide roads and outside the villages on the ca. 3 m wide dirt roads. All roads within villages and all approachable dirt roads outside villages were assessed.

We determined the abundance of small mammals of Olib Island by the capture-mark-recapture (CMR) method (Krebs 1989, Herczeg & Horváth 2015). In 2008 and 2009, we used 100 and 120 glass-door wooden live traps (size 180×70×70 mm), distributed along lines. In the village 20 traps were set in gardens in both years (10 and 5 nights, respectively), whereas in the habitats on the outskirts we used 80 and 100 traps. Sixty percent of these were in secondary closed canopy forests in abandoned fields and 40% in forests with open canopy, close to the coastline (10 and 8 nights in the two years, respectively). Traps were set every 10 m with maize as bait and the sites were checked twice a day. In order to avoid overestimating the number of captured animals, the fur on their head was trimmed as a marker. We standardised capture data as individuals captured per 100 trap nights. Rabbit (*Oryctolagus cuniculus*) abundance (number of rabbits observed per km) was estimated by relative index, on the basis of observed rabbits along transects (Table 1) surveyed for cats. We surveyed bird populations in the village of Olib, using a GPS device, along seven different transects (mean length ± SEM: 352 ± 33.9 m) of 50 m width, the total length of the route being 2466 m. In the outskirts transect the length was 800 m of 50 m width and the transect counts were repeated 7 times in autumn 2008, and 3 times in spring 2009. The total number of individuals was counted for each bird species in transects and on seasonal mean data the relative abundance was estimated (Bibby et al. 1992). We estimated lizard abundance, predominantly of the Italian wall lizard (*Podarcis sicula*), in the coastal area of Olib, and inland, along both sides of the roads, on ca. 1.5 m high stone walls, along a total of 15 different transect lines (200 m per line) in early summer.

Diet analysis

In order to determine the diet composition of the cat groups we analysed scat samples which we collected by walking on the same routes as described for cat density estimation (Table 1). The standard wet procedure was used to analyze samples (Jędrzejewska & Jędrzejewski 1998). Scats were soaked in water, washed through a sieve (0.5 mm mesh) and then dried. All food remains were separated and identified based on hair, bones, dentition, feathers, and arthropod exoskeletons under the microscope with the aid of keys, atlases (e.g. März 1972, Teerink 1991, Brown et al. 1993), and our own vertebrate, invertebrate, and plant reference collections. In the case of invertebrates, we only considered prey remains weighing more than 0.05 g, in order to avoid the counting of other indirect prey previously ingested by lizards, birds or rats (Medina & Garcia 2007). Vegetable food remains were also identified (as well as matter originating from litter), but, because cats are obligate carnivores (Bradshaw et al. 1996), these diet elements were excluded from the calculation of food composition (e.g. Hervías et al. 2014).

For expressing diet composition, two methods were used: the relative frequency of occurrence (or RFO, number of occurrences of a certain food type expressed as a percentage of the total number of occurrences of all food items) and the frequency of occurrence (or FO, percentage of scats containing a food item). To avoid over- or under-estimating the importance of a given food item the minimum numbers of diet components identified from the scats were taken into account. Prey species have paired skeletal structures (e.g. jaws), that allow an assessment of the minimum number of individuals in a scat through the pairing of left and right sided bones of the same size.-RFO data was used for trophic niche calculations, and the basic data of FO calculations (cases) was used as input for log-linear analysis. The lack of exact (measured) body mass data for the species observed in the area did not allow us to calculate biomass values (e.g. Liberg 1984, Nogales & Medina 2009).

Trophic niche breadth was calculated in accordance with Levins (Krebs 1989): $B = 1/\sum p_i^2$, where p_i = the relative frequency of occurrence of the *i*th taxon; and standardized across food taxa: $B_A = (B - 1)/(n - 1)$, rating from 0 (dietary specialization) to 1 (broad diet). The following six main food taxa (types) were used in the calculations related to trophic niche and the comparative analysis of scat composition for cat groups: small-sized (< 0.5 kg) mammals, rabbit, birds, reptiles, invertebrates and human-linked (or household) food. The trophic niche overlap was calculated by means of the Renkonen index (Krebs 1989): $P_{jk} = [\Sigma n(\text{minimum } p_{ij}, p_{ik})]100$, where P_{jk} = percentage overlap between cat group *j* and cat group *k*; p_{ij} and p_{ik} = the proportion of resource *i* represented within the total resources used by cat group *j* and cat group *k*; *n* = the total number of resource taxa, rating from 0% (no overlap) to 100% (full overlap).

We applied Ivlev's index (E_i) of preference (Krebs 1989) according to the most important prey type i.e. small mammal species as follows: $E_i = (r_i - n_i)/(r_i + n_i)$, where r_i = percentage relative frequency of the given (*i*th) item in the diet and n_i= percentage relative frequency of the given (*i*th) item in the environment, derived from abundance index . Electivity varies from -1.0 to +1.0, where -1.0 indicates avoidance, and +1.0 indicates a preferred prey item.

Statistical analysis

We applied multivariate analysis of variance (MANOVA, GLM procedure with type III sum of squares, Bonferroni post hoc test) on abundance and density data, where density or relative abundance indices were dependent variables, whereas the time of the year (October and May), the island (Olib and Silba) and the habitat type (village or outskirts) were fixed factors. Log-transformation was performed on densities, relative abundance of cats and rabbits, birds and lizards. We used the Chi-square test for distribution analysis of the diet composition regarding plant matter and non-digestible food of the cat groups (house and feral) on both islands. We compared preference indices and trophic niche breadth values (normal distributions) using paired sample t-test between the two cat groups. General log-linear likelihood tests were used on frequency of occurrence data, to test for dietary differences between cat groups (house and feral), periods (October of 2008 and May of 2009) and islands. The unit of analysis was feral cat and house cat scats and the response variable was the presence or absence of the food item considered. We fitted the complete models using cat groups, period/season and island as independent variables and adjusted the level of significance to 0.0064 with a Bonferroni correction (Revilla & Palomares 2002). For the analysis of correlation between the resource and consumption of small mammals, rabbits and birds, the Pearson correlation was applied and the SPSS 10.0 for Windows (1999) statistical package was used for data processing.

Results

Abundance of cats and main prey types

The estimated relative abundance of cats (Table 1, estimated cat numbers per km^2) was significantly higher in villages than on the outskirts (180.7 *vs.* 0.42, MANOVA: $F_{1,1,1} = 106.45$, $p < 0.0001$). It was also higher in autumn than in spring (87.3 *vs.* 17.1, $F_{1,1,1} = 4.67$, $p = 0.033$), but there was no island-dependent difference (Olib: 70.4, Silba: 59.0, $F_{1,1,1} = 0.67$, $p = 0.416$). In accordance with these tendencies, the relative abundance of cats on the basis of scat index (Table 1, scats per km route) was also significantly higher in villages than on the outskirts (0.68 *vs.* 0.44, $F_{1,1,1} = 4.29$, $p = 0.048$), was higher in autumn than in spring (0.83 *vs.* 0.55, $F_{1,1,1} = 9.63$, $p < 0.0001$), and the difference between islands was not significant (0.83 *vs.* 0.55, $F_{1,1,1} = 1.59$, $p = 0.219$).

Small mammal relative abundance values (individuals captured per 100 trap nights, Appendix 1) were higher on the outskirts of Olib village than inside the settlement, and they were also higher in spring (outskirts: 23.63, village: 4.50) than in autumn (outskirts: 7.25, village: 1.63). The most frequently caught species was wood mouse (*Apodemus sylvaticus*), and the proportion within the small mammal community was 67.2% in autumn and 95.8% in spring. Substantial numbers of the black rat (*Rattus rattus*) were captured in the village in autumn and spring (15.4% and 22.2%), while the percentage of white-toothed shrews (*Crocidura suaveolens*) on the outskirts in autumn was 25.9%. No other species of small mammals were found in the traps. The relative abundance of rabbits was significantly higher on the outskirts than inside the villages (0.60 *vs.* 0.25, MANOVA, $F_{1,1,1} = 12.74$, $p = 0.0005$), but the difference was not significant between the autumn and spring periods ($p = 0.355$) or between islands ($p = 0.274$). The relative abundance of birds (Appendix 2) was significantly higher in Olib village than on the outskirts (MANOVA, $F_{1,1} = 8.29$, $p = 0.008$), and was higher during the autumn bird migration than in the spring ($F_{1,1} = 5.45$, $p = 0.028$). The calculated mean density of lizards in the breeding period of birds on Olib (mean ± 1SE) was 26.7 ± 5.79 lizard/km per transect.

Diet, prey choice and trophic niche

A total of 578 scat samples were collected and analysed, and of these 325 samples were from Olib and 253 from Silba (Table 2). Total number of prey items was 838 (Olib: 496, Silba: 342). To this we added the number of plants and other food items, which were 99 and 74 on the two islands. The main prey type was small mammals (Fig. 1, Table 2). On both islands, the small mammal prey analysed from scats contained the Etruscan shrew (*Suncus etruscus*), in addition to the species caught with the traps. In the consumption of small mammals, the main effects (log-linear analysis) of cat group and island × period interaction were significant (Appendix 3), but not the island, period, cat group × island and cat group × period interactions. Feral cats, as compared to house cats, consumed small mammals more frequently (FO, 95.2% *vs.* 44.0%). Small mammal consumption on Olib was more frequent in the spring, whereas on Silba it was more frequent in the autumn (Table 2).

Regarding the available small mammal resource on Olib, cats preferred (E_i, Ivlev's index) black rats (feral cats $E_i = 0.72$, house cats $E_i = 0.14$), and slightly ate less (avoided) wood mice (feral cats $E_i = -0.18$, house cats $E_i = -0.08$) and shrews (feral cats $E_i = -0.30$, house cats $E_i = 0.00$). The preference for various small mammal taxa did not differ significantly between the two cat groups (paired samples t-test, black rat: $t_1 = 1.64$, $p = 0.349$, wood mouse: $t_1 = 2.35$, $p = 0.256$). Small mammals as a resource (individual per 100 trap nights) and their consumption (RFO) did not show a close relationship (Pearson correlation, $r_P = 0.79$, $p = 0.209$).

Among the birds consumed by cats, small passerines were present (on Olib: *Sylvia* sp., *Passer* sp., on Silba: *Erithacus rubecula*, *Regulus* sp.), and on Olib medium-sized species and eggs (egg shells) were also found in scat samples in spring. Regarding birds as food, the main effects of cat group and period were significant (Appendix 3). Birds were consumed more frequently by house cats than by feral cats (FO, 12.7%, *vs.* 7.3%), in autumn than in spring (FO, 15.9% *vs.* 4.1%). On Olib, bird abundance (n/km/day) showed a close relationship with bird consumption by cats (RFO) (Pearson correlation, $r_P = 0.999$, $p = 0.025$).

Among reptiles consumed by cats, the Italian wall lizard was the predominant species, but on Olib a few cases of snake consumption also occurred. In the consumption of reptiles, the main effects of cat group (Appendix 3), island, period and island × period interaction were significant. Reptiles were more frequently consumed by feral cats, as compared to house cats (FO, 21.7% *vs.* 2.7%), on Olib than on Silba (15.9% *vs.* 8.6%), and in the autumn than in the spring (15.8% *vs.* 8.7%).

Household food included fish (e.g. Percidae), food leftovers e.g. remains from ruminants and poultry, poultry eggs, and, most often, cat (or pet) food. In the consumption of household food, the main effects of cat group (Appendix 3), island, period and island × period interaction (were significant. The consumption of household food was more frequent in house cats than in feral cats (58.1% *vs.* 3.9%), on Silba than on Olib (41.3% *vs.* 20.6%), and in the autumn than in the spring (36.0% *vs.* 26.0%).

The effect of cat groups (feral and house cat) was not important in the consumption of rabbits (FO, 4.3% *vs.* 1.5%) and invertebrates (3.9% *vs.* 6.0%), nor were the other main effects significant (Appendix 3). Relative rabbit abundance (n/km) did not show a strong correlation with the consumption of rabbits (RFO) (Pearson correlation, $r_P = 0.46$, $p = 0.248$).

Among invertebrate prey, we found locusts (Acridoidea), European mole cricket (*Gryllotalpa gryllotalpa*), beetles (*Cetonia* sp., Scarabeidae) and snails (Gastropoda) on both islands, and bees and wasps (Hymenoptera), scorpions (*Euscorpius* sp.), seashells and starfish (Asteroidea) on Olib.

House cats consumed plant matter more often than feral cats on both islands (Chi-square test, Olib: $\chi^2_1 = 8.92$, $p = 0.003$, Silba: $\chi^2_1 = 9.97$, $p = 0.002$). Plant matters found in scats from feral cats were mostly leaves of grass, and on two occasions olive fruit were found on Olib. On the other hand, in the case of house cats we also found debris of plant matter, and fruit peelings, as well as grapes from the village.

The scat samples of house cats from both islands more frequently contained non-digestible substances and litter (20 types, including plastic, rubber, fabric, aluminium foil, paper, paint, wax pieces and lead shot), than those of feral cats (three types: nylon, plastic fibre, paper) (Chi-square test, Olib: $\chi^2_1 = 36.28$, $p < 0.0001$, Silba: $\chi^2_1 = 9.81$, $p = 0.002$).

We identified altogether 20 different animal species or taxa in the diet of feral cats, and 24 in that of house cats. The trophic niche was not significantly broader in house cats than in feral cats (mean ± 1SE, $B_A = 0.27 \pm 0.070$ *vs.* 0.17 ± 0.049, paired-samples t-test: $t_3 = 1.68$, $p = 0.191$). The trophic niche overlap between the two cat groups was moderately low (35.6-41.5%), except for Olib where its value in spring was higher (74.3%).

Discussion

Differences between cat groups

Feral cats prey more frequently on small mammals and lizards

We found differences between feral and house cat groups in the consumption rates of four important food taxa.

For both cat groups, small mammals were the most important prey, but they were caught more often by feral cats than by house cats. The primary importance of small mammal prey was reported in most of the studied islands (Fitzgerald 1988, Peck et al. 2008, Nogales & Medina 2009, Bonnaud et al. 2011, Hervías et al. 2014). The difference between the two cat groups was explained by the availability of small mammal resources, regardless of whether they were fed on household food or not. The frequency of small mammal consumption by the two cat groups in the autumn in Olib village and on the outskirts differed between the groups, which reflected the differences in small mammal availability between the two habitats. In the spring, however, both cat groups had similar frequencies of small mammal consumption. The changes in small mammal consumption frequencies are probably due to the fact that small mammal availability was higher in the spring than in the autumn in both types of area, while the difference between the two types of area remained constant regarding their actual small mammal resource.

The consumption of small mammals by cats on the study islands did not depend on the small mammal supply. This suggests the presence of an unlimited food resource (Carbone & Gittleman 2002) for the cats. Our study shows that with such an abundance of small mammals, the overwintering lower population of cats preferred hunting for common small mammals (e.g. wood mice) to hunting for birds. The less pronounced predation by cats on native species (such as lizards) in the Adriatic islands may be due to the presence of small rodents as a primary food source, similar to the effect of rabbits in New Zealand (Norbury 2001). This moderating effect is particularly important in the case of the feral cat group which, compared to house cats, fed more often on lizards, as well as on small mammals. Feral cats showed a preference for black rats, an invasive mesopredator of particular importance (Courchamp et al. 1999, Bonnaud et al. 2007, 2011), suggesting the possibility that this predation may regulate (Fitzgerald et al. 1991) or at least effect rat populations.

Our studies revealed that there were lizard remains in the scat samples of one in five feral cats. Lizard consumption by cats inhabiting islands is either occasional or regular (Nogales & Medina 2009, Bonnaud et al. 2011), however, in our studies, cats consumed lizards less frequently than in other cases at lower latitudes (Fitzgerald 1988). Based on cat density data on the Adriatic islands studied and regarding the 1 scat per day defecation rate (Liberg 1984), the observed predation rate on lizards is higher even than that found in most other studies performed in warmer climates (Juan de Nova Island: Peck et al. 2008; Canary Islands: Nogales & Medina 2009), except in Australia (Doherty et al. 2015).

With a view to the rich reptile fauna of the Adriatic islands (Tvrtković 2006), the high rate of lizard consumption by feral cats is worrying, and this may also indicate the vulnerability of the food network. The lower rate of lizard consumption observed in the case of house cats is due to the fact that they can utilise food resources that are much more readily available for them (Fitzgerald 1988, Norbury 2001, Corchamp & Caut 2005). The difference can also be due to other factors, e.g. cats often hunt without actually being hungry (Mertens & Schär 1988), and in such cases they can leave the prey without eating it (Carss 1995, Woods et al. 2003).

House cats consume more frequently household foods and birds

The group of house cats took domestic food 15-22 times more often than the group of feral cats, meaning that the feeding strategies of the two groups were sharply dissimilar in this respect. Feral cats do not depend on household food (Dickman 1996b), yet they may occasionally take such food (Liberg 1984, Pearre & Maass 1998). This food might have been taken, apart from when occasionally visiting the settlements (Biró et al. 2004, 2005), from sources further off from the settlements (dumping grounds, food leftovers).

The Adriatic islands, including the two study areas, are important in bird migration and in the wintering of a number of bird species, but they are also important habitats for nesting of several rare bird species (Radović et al. 2005). The diet of cats was influenced by the fact that the number of birds, important components of the wildlife of these islands, varied seasonally. Feeding on birds by house cats was more pronounced at the time of the autumn migration (Olib, high bird abundance). In addition to direct predation (Purger et al. 2008), predation of songbirds may have been assisted by the attraction of birds to the sticky flowers of common leadwort (*Plumbago europaea*) which was flowering in that period (Purger et al. 2012). This was especially the case for small (4-7 g) goldcrests (*Regulus regulus*) which arrived in high numbers (Appendix 1). The feeding rate on birds was relatively low in both cat groups, especially when compared with other islands (Bonnaud et al. 2011, Hervias et al. 2014), continents (Fitzgerald 1988; Biró et al. 2005) or urban environments (Heezik et al. 2010).

During the bird breeding season when the numbers of birds were lower, house cats on Olib did not consume birds, and feral cats did so only occasionally. On Silba, bird consumption was relatively rare (<9%, RFO), irrespective of season or cat group. The fact that it was possible to find the remains of egg shell in cat faecal samples despite the limitations of the faecal analysis method (Reynolds & Aebischer 1991) indicates that cats may have a role in nest predation on the study islands. The low rates of bird consumption in both cat groups only partially support our prediction in this matter. The relatively low frequency of predation on birds could be caused by the easier availability of other food sources such as house food and small mammals.

Importance of other food types

Rabbits, arthropods, plants and kitchen waste were supplementary cat food sources with low importance on the study islands. The rabbit population of the islands was said by locals to have dropped substantially as a result of an epidemic of myxomatosis in the years prior to our studies. Feeding on rabbits was occasional in the studied period, although it can be a frequently taken food for domestic cats during periods of high rabbit abundance (Corbett 1979, Liberg 1984, Carss 1995, Medina et al. 2006).

Invertebrates normally have a minor role in the feeding of cats, mostly due to their small size. The small pieces of invertebrate remains found in cat faecal samples could also originate indirectly from consumed lizards (Medina & Garcia 2007), even though it is well known that cats do prey on rare, endemic invertebrate species too (Fizgerald 1988, Medina & Garcia 2007). As has been found on other islands (Medina & Garcia 2007; Peck et al. 2008; Nogales & Medina 2009), their food included mostly easily caught species (Fitzgerald 1988) of greater size (e.g. locusts that often stay on roads). Individuals of the small-bodied, moderately poisonous scorpion species of the islands were directly taken by house cats, in spite of the fact that scorpions are normally seldom taken by cats (Bonnaud et al. 2011). Although cats only occasionally eat plant matter (Fizgerald 1988, Biró et al. 2005), house cats in our study fed more frequently on vegetable food. In the case of feral cats, the digestive tract of various prey items is more likely to contain the vegetable nutrients and vitamins essential for cats (Fizgerald 1988), and this may explain why plant matter was eaten less frequently.

Trophic niche and opportunism

The trophic niche values of the two cat groups did not differ significantly. So our prediction that the trophic niche of feral cats will be broader because of more frequently predation on wild prey types could not be confirmed.

Besides household food, house cats practically took all the other food types eaten by feral cats. Although the hunting abilities of the two cat groups are very similar, their feeding niche overlap was smaller than in the case of wild cats (*Felis silvestris*), hybrid wild cats and feral cats on the mainland (Biró et al. 2005). This suggests that the difference between food compositions is due to the difference between feeding strategies. Both cat groups studied can be regarded as generalist predators (Fitzgerald 1988), because they adapt to the food resource available in the particular habitat, and take a variety of food types, as found in other studies (reviews: Fitzgerald 1988, Bonnaud et al. 2011). Yet, the preference by feral cats for black rats still indicated an ability to specialise (and potentially regulate or effect other species populations). When the subjects of such specialisation are endangered endemic small mammals, such as the San Jose Island kangaroo rat (*Dipodomys insularis*) (Bonnaud et al. 2011), this may be a serious species conservation concern. Our studies confirmed the different feeding behaviour with both generalist and opportunism (and trophic flexibility) being shown in each of the two cat groups. This should be considered when predator control measures are taken in these islands.

Implications for conservation on small Mediterranean islands

The removal of predators from sensitive ecosystems is often a successful solution even in itself (Nordström et al. 2003, Nogales et al. 2004, Smith et al. 2010). In seriously altered habitats with a number of introduced species, cascade mechanisms function on trophic levels. According to Courchamp et al. (1999), in the three-species system (prey – mesopredator – superpredator) the eradication of feral domestic cats (as super- or apex predator) is not always the best solution to protect prey (e.g. endemic birds) when rats (as mesopredators) are also present. Similarly, in an urban setting where cats are important predators of introduced species (house mouse, rats, certain bird species), controlling cat numbers or reducing their night time activity would need to be accompanied by rat control (Heezik et al. 2010). Although no such investigations or interventions have been performed in the Adriatic islands our study showed that cats prefer the introduced and common black rat in their feeding, suggesting that the question of nature conservation-oriented habitat management in the islands is complex and has to be carried out carefully.

The frequent consumption of lizards by cats (especially by feral cats) can mean a threat to the native lizard populations of the Adriatic islands. In islands where endemic subspecies (e.g. *Podarcis melisellensis melisellensis*, *P. sicula adriatica*) also occur (Tvrtković 2006), lizard predation by cats can be critical during certain periods.

The abundance of rabbits introduced to the Adriatic islands can decrease due to diseases (myxomatosis; Flux, 1993), and their population can be kept at low levels by hunting (Norbury 2001). By that means, the number of predators (cats) can be reduced, which can indirectly help the survival of native lizard populations, and directly serve the preservation of native plant species (Courchamp & Caut 2005). On the other hand, decline in rabbit abundance may result in cats' switching to other prey groups, such as lizards and small mammals (Norbury 2001, Doherty et al. 2015). The complexity of the predator-prey systems on islands is likely to be important in multi-species management (Courchamp et al. 1999, Doherty et al. 2015).

Cats are common domestic animals on the Adriatic islands. Partly due to tourism, the human population of the islands grow in the summer months, but when autumn comes, a significant proportion of even the local inhabitants move to the mainland. Cats left behind on the islands mean a continuous supply to add to the feral cat population.

Currently, the possible functional and numeric response of intensive rat and rabbit control on various cat groups on small Adriatic islands is unknown. Based on models and the mesopredator release effect hypothesis (Courchamp et al. 1999, Norbury 2001, Russell et al. 2009, Heezik et al. 2010) we assume that the most successful method for preserving the native fauna of the Adriatic islands would be a combination of feral cat control accompanied by intensive rat control (rats being both an important food and predator), and moderate rabbit control (rabbits being an occasional food source). Because the feeding strategies of the two cat groups are different, it is reasonable to look for different management techniques to be applied inside human settlements and outside them.

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Table and Figure captions

Table 1. Estimated density and relative scat density indices of cats in Olib and Silba islands (mean ± 1SE).

Table 2. Diet composition of feral cats and house cats on two small Mediterranean Islands (Olib and Silba, Adriatic Sea, Croatia).

Figure 1. Geographic location of the study areas in the Adriatic Sea, Olib and Silba islands.

Figure 2. Diet composition of feral cats (black bars) and house cats (open bars) on a) Olib and b) Silba islands (Adriatic Sea, Croatia). RFO (%) – percentage relative frequency of occurrence (mean ± 1SE). Food types: Sm – small mammals, Ra – rabbit, Bi – bird, Re – reptile, In – invertebrates, Ho – household food.

Appendix 1. Abundance of small mammals based on numbers captured per 100 trap nights by CMR technique on Olib island (Adriatic Sea).

Appendix 2. Abundance and dominance of birds observed on Olib Island.

Appendix 3. Results of log-linear models for the frequencies of occurrence of food types in the scats of domestic and feral cats during autumn (2008) and spring (2009) in the Adriatic Sea, Olib and Silba islands, for the effect of cat groups, periods, islands and their interaction. Numbers in italics indicate significant values (Bonferroni correction).

Table 1

Island	Habitat	Season	Surveyed lines	
			No. of lines	Sum. length (km)
Olib	Village	Autumn	18	9.42
		Spring	8	10.77
	Outskirts	Autumn	36	32.72
		Spring	12	20.65
Silba	Village	Autumn	9	8.17
		Spring	6	14.53
	Outskirts	Autumn	12	10.05
		Spring	7	13.41
			Estimated cat density (n/km^2)	Scat index (n/km)
Olib	Village	Autumn	266.6 ± 131.22	8.9 ± 1.31
		Spring	40.7 ± 25.71	6.2 ± 1.35
	Outskirts	Autumn	0.6 ± 0.63	4.6 ± 1.27
		Spring	0.4 ± 0.43	2.9 ± 0.98
Silba	Village	Autumn	191.6 ± 35.37	17.0 ± 8.28
		Spring	46.9 ± 20.21	3.8 ± 0.37
	Outskirts	Autumn	0	10.0 ± 3.51
		Spring	0	5.1 ± 2.20

Table 2

Food items	Olib								Silba							
	Autumn				Spring				Autumn				Spring			
	Feral cat		House cat		Feral cat		House cat		Feral cat		House cat		Feral cat		House cat	
	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO
Wood mouse *Apodemus sylvaticus*	24.3	41.8	11.0	15.3	68.5	78.3	57.4	62.7	26.3	31.6	7.1	10.3	29.4	42.4	10.3	11.3
Black rat *Rattus rattus*	27.2	49.3	10.0	13.9	21.7	29.0	9.8	11.8	51.3	68.4	21.2	30.8	35.3	50.8	14.7	16.1
Mus sp.	0.8	1.5									0.9	1.3				
Lesser white-toothed shrew *Crocidura suaveolens*	4.5	6.0					3.3	3.9								
Etruscan shrew *Suncus etruscus*	2.9	5.2									0.9	1.3				
Soricidae, indet.	0.8	1.5														
Rabbit *Oryctolagus cuniculus*	2.1	3.7			1.1	1.4	4.9	5.9	2.6	3.5			5.9	8.5		
Robin *Erithacus rubecola*									1.3	1.8						
Typical warblers, *Sylvia* sp.			1.0	1.4												
Crest, *Regulus* sp.											1.8	2.6				
Sparrow, *Passer* sp.			1.0	1.4												
Small passerines, indet.	4.5	8.2	23.0	31.9					3.9	5.3	7.1	10.3	7.1	10.2	2.9	3.2
Medium-sized bird, indet.	0.4	0.7			1.1	1.4										
Bird egg					1.1	1.4										
Wall lizards, Lacertidae	23.9	42.5	4.0	5.6	5.4	7.2			6.6	8.8			15.3	22.0	2.9	3.2
True snakes, Colubridae	2.9	5.2					1.6	2.0								

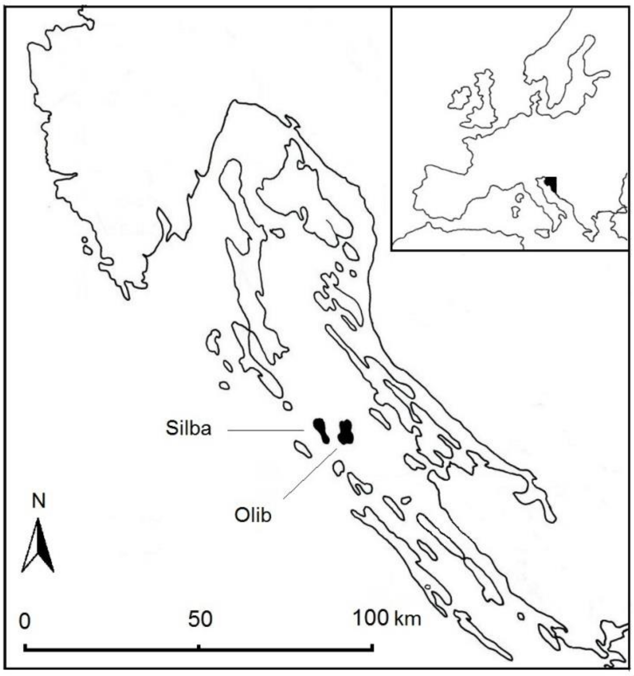
Table 2 continued

Food items	Olib								Silba							
	Autumn				Spring				Autumn				Spring			
	Feral cat		House cat		Feral cat		House cat		Feral cat		House cat		Feral cat		House cat	
	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO	RFO	FO
Locusts, Acridoidea	2.5	4.5	1.0	1.4			1.6	2.0	2.6	3.5	1.8	2.6	2.4	3.4		
Scorpion *Euscorpius* sp.							3.3	2.0								
Other invertebrates	1.23	2.2	6	8.3			1.64	2.0	2.6	3.5	1.8	2.6				
Fish, Pisces	1.6	2.2	22.0	16.7	1.1	1.4	4.9	5.9	1.3	1.8	8.8	12.8	3.5	5.1	8.8	9.7
Poultry			5.0	6.9									1.2	1.7	2.9	3.2
Poultry egg			1.0	1.4					1.3	1.8	3.5	5.1				
Domestic ungulate offal	0.4	0.7	5.0	6.9			4.9	5.9			8.8	12.8				
Cat (pet) food			10.0	13.9			6.6	7.8			36.3	52.6			57.4	62.9
Number of scats (n)	133		72		69		51		57		78		59		59	
Number of items	243		100		92		61		76		113		85		68	
B_A	0.25		0.47		0.04		0.18		0.13		0.26		0.24		0.17	
Fruits (N)	1		8		1						4					
Other plants (N)	16		13		16		14		8		20		3		13	
Other materials (N)	3		23		1		3		2		17		2		5	

Scat samples collected in October 2008 and May-June of 2009. RFO – relative frequency of occurrence, FO – frequency of occurrence. B_A – standardized trophic niche breadth value. Empty cells mean that the given taxon was not detected.

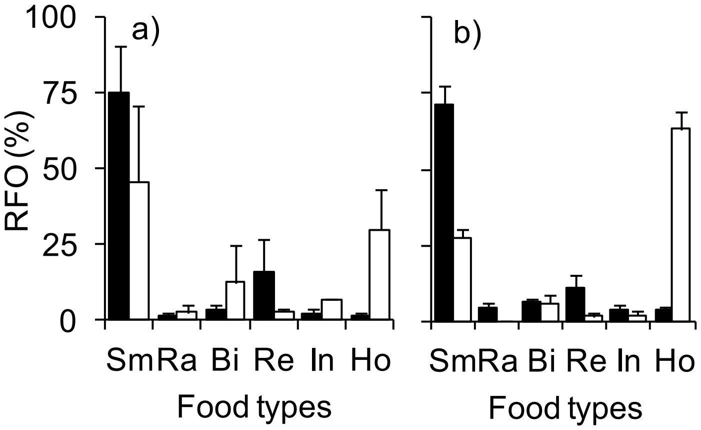
603 Figure 1

604



605

Figure 2


a)
b)
100
75
50
25
0
RFO (%)
Sm
Ra
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In
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Food types
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Food types

Appendix 1

Species	Autumn		Autumn		Spring	
	Outskirts		Village		Outskirts	
	N	%	N	%	N	%
Accipiter nisus	9	1.3	2	0.2		
Alcedo atthis	1	0.1				
Apus apus					1	0.6
Buteo buteo	1	0.1				
Columba livia			1	0.1		
Columba palumbus	65	9.2				
Corvus cornix	39	5.5	16	1.7	12	7.5
Dendrocopos major	2	0.3				
Erithacus rubecula	279	39.5	42	4.6		
Fringilla coelebs	39	5.5	67	7.3		
Hirundo rustica					13	8.1
Larus michahellis	21	3.0	6	0.7	51	31.9
Luscinia megarhynchos					17	10.6
Motacilla alba	1	0.1				
Parus major	36	5.1	10	1.1		
Passer domesticus			18	2.0		
Phalacrocorax aristotelis					2	1.3
Phasianus colchicus	3	0.4			10	6.3
Phoenicurus ochruros	2	0.3	17	1.8		
Phylloscopus collybita	2	0.3	1	0.1		
Regulus regulus	113	16.0	85	9.2		
Saxicola rubicola			1	0.1		
Serinus serinus	1	0.1	25	2.7		
Streptopelia decaocto			12	1.3	3	1.9
Streptopelia turtur					1	0.6
Sturnus vulgaris	2	0.3	612	66.4		
Sylvia atricapilla	15	2.1			4	2.5
Sylvia cantillans					38	23.8
Sylvia communis	1	0.1	2	0.2		
Troglodytes troglodytes	43	6.1	2	0.2		
Turdus merula	24	3.4	1	0.1	8	5.0
Turdus viscivorus	7	1.0	1	0.1		
Summarized number	706		921		160	
Bird abundance (n/km/day), mean	126.1		434.4		66.7	
± 1SE	8.04		169.70		12.49	

Appendix 2.

Small mammal species	Autumn		Spring	
	Village	Outskirt	Village	Outskirt
	Individuals captured per 100 trap nights			
Apodemus sylvaticus	1.25	4.88	3.50	22.63
Rattus rattus	0.25	0.50	1.00	1.00
Crocidura suaveolens	0.13	1.88		
Summarized	1.63	7.25	4.50	23.63

Appendix 3.

Item	Effect	df	χ^2	P
Small mammals total	Cat group	1	*208.7*	*<0.0001*
	Period	1	5.0	0.0258
	Island	1	7.9	0.0093
	Cat group × period	1	0.1	0.7402
	Cat group × island	1	3.5	0.0619
	Period × island	1	*20.0*	*<0.0001*
Birds	Cat group	1	*8.2*	*0.0043*
	Period	1	*16.8*	*<0.0001*
	Island	1	1.6	0.2003
	Cat group × period	1	7.4	0.0065
	Cat group × island	1	1.5	0.2169
	Period × island	1	5.8	0.0161
Reptiles	Cat group	1	*64.3*	*<0.0001*
	Period	1	*15.1*	*<0.0001*
	Island	1	*12.7*	*0.0004*
	Cat group × period	1	2.1	0.1469
	Cat group × island	1	0.4	0.5461
	Period × island	1	*29.6*	*<0.0001*
Household food	Cat group	1	*233.1*	*<0.0001*
	Period	1	*11.2*	*0.0008*
	Island	1	*36.4*	*<0.0001*
	Cat group × period	1	1.3	0.2537
	Cat group × island	1	2.1	0.1519
	Period × island	1	*12.1*	*0.0005*
Rabbit	Cat group	1	3.7	0.0529
	Period	1	1.6	0.2062
	Island	1	0.1	0.7759
	Cat group × period	1	2.5	0.1132
	Cat group × island	1	4.6	0.0314
	Period × island	1	0.7	0.3910
Invertebrates	Cat group	1	1.5	0.2277
	Period	1	4.5	0.0332
	Island	1	1.9	0.1649
	Cat group × period	1	0.3	0.5797
	Cat group × island	1	3.1	0.0805
	Period × island	1	<0.1	0.9563