



Response of a mesocarnivore community to a new food resource: recognition, exploitation, and interspecific competition

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Abstract

Mammalian carnivores with generalist feeding behaviour should trace and exploit new and predictable food resources quicker and more easily than more specialised species. On the other hand, if the new food resource is spatially and temporally predictable, interference or exploitation competition should arise among members of the carnivore guild, with the expectation that smaller species will not use the food resource or will change their foraging behaviour to avoid conflict with larger species. Here, we studied the response to a new food resource of a mammalian mesocarnivore community in south-western Iberian Peninsula. We installed artificial feeding points supplied with a novel food source and tracked them by camera trapping to investigate whether (1) the new artificial food resource was visited, recognised and exploited by the mesocarnivore guild species; (2) how frequently they used the food; and (3) in case of co-occurrence, if dominant species excluded or reduced the feeding options of subordinates. All target species except the badger recognised and exploited the novel food. More generalist species trended to visit feeding points more frequently and spent more time feeding than less generalist species, even though significant differences were not achieved in all cases. When co-occurring at the same feeding point, the arrival of larger species reduced either the visitation rates, feeding probability or time spent feeding of smaller species. Moreover, some smaller species showed a shift in their normal activity pattern at the feeding points when a larger competitor started to use the food source. Overall, we conclude that active avoidance combined with temporal segregation may help reduce agonistic interactions among competitors for shared resources.

Keywords Camera trapping · Food access · Foraging behaviour · Active avoidance · Mesocarnivore hierarchy

Introduction

Animal species have developed morphologies and mechanisms that allow them to forage and obtain food efficiently. While some species, called specialists, have specific and complex mechanisms for consuming very particular items (Freeland and Janzen 1974; Stiles 1981), others, known as generalists, consume a variety of food types (Stephens et al. 2007).

Carnivora is a mammalian order of which most species feed on other animals. They specialise in hunting or scavenging animal remains; however, not all are strictly carnivorous nor do they all predate on a single prey type. Within

Carnivora, different levels of specialisation exist. While some are strict carnivores (most of the felids and smaller mustelids), insectivores (some canids or herpestids) or even folivores (the giant panda, *Ailuropoda melanoleuca* or the ailurid red panda, *Ailurus fulgens*), many others are generalists and present different levels of omnivory (canids and some ursids, mustelids, herpestids and procyonids) (Boitani and Powel 2012). As dietary overlap increases between species with similar requirements, the strength of exploitation and interference competition also increases. Nevertheless, while the first describes indirect interactions, the second generates agonistic encounters that can escalate to interspecific killing (Holt and Polis 1997; Palomares and Caro 1999; Donadio and Buskirk 2006; Garvey et al. 2015).

Studying interference competition interactions among mammalian carnivores is important to understand how ecological communities and food webs are shaped (Palomares and Caro 1999; Garvey et al. 2015). These interactions are usually asymmetrical, with larger species being dominant

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over smaller ones (Schoener 1983; Garvey et al. 2015). Subordinate species lower their risk of agonistic encounters by segregating spatially or temporally (MacArthur and Levins 1967). If species with similar nutritional requirements coexist, changes in habitat use or activity patterns are expected in order to avoid exploitative or interference competition (Schoener 1974). However, high and predictable food concentrations may allow co-occurrence of different species through the establishment of dominant-subordinate hierarchies (Elbroch and Kusler 2018). Examples of these hierarchies have been observed at both interspecific (Barrull et al. 2014; Elbroch and Kusler 2018) and intraspecific levels (López-Bao et al. 2009).

This current work aimed to study how a carnivore guild behaves and structures itself around a new and allegedly unknown artificial food source. For this purpose, we installed artificial feeding points using dry cat food as bait and recorded the response of carnivore species with camera traps. The specific objectives were to determine (1) which species visited, recognised and were able to use the new resource; (2) if the species that used the feeding point exploited it sporadically or repeatedly; and (3) when several species exploited the same feeding point, whether they presented any kind of competition pattern.

Our study area in south-western Iberian Peninsula is dominated by a medium-sized carnivore guild. The most common carnivore species are red fox (*Vulpes vulpes*), European badger (*Meles meles*), Egyptian mongoose (*Herpestes ichneumon*), stone marten (*Martes foina*) and common genet (*Genetta genetta*), in addition to free-ranging domestic species such as cats (*Felis silvestris catus*) and dogs (*Canis lupus familiaris*) (Palomo et al. 2007). These species are considered to be trophic generalists, but some of them present more specialisation than others. The dog, the red fox and the European badger are the most generalist (Roper and Mickevicius 1995; Rosalino et al. 2005; Dell'Arte et al. 2007; Vanak et al. 2013a), even though some studies have reported local feeding specialisation in badgers (Kruuk and Parish 1981; Martín et al. 1995). The Egyptian mongoose and the domestic cat are less generalist, since they are more specialised in hunting animals than in consuming vegetable items, but their preys vary from different groups of vertebrates to invertebrates (Bandeira et al. 2018; Széles et al. 2018). On the Iberian Peninsula, the stone marten is a frugivorous-opportunistic species with a diet composed of, in order of importance, fruit, berries, small mammals, insects and birds (Genovesi et al. 1996). On the other hand, the common genet is considered the most specialist of all of these generalists as it preys mainly on wood mouse (*Apodemus sylvaticus*) and other small mammals (Virgós et al. 1999; Munuera and Llobet 2004).

Thus, for the first objective, we hypothesise that meso-carnivores with more generalist diets would be more likely

to recognise the artificial food resource and exploit it. Based on their generalist-specialist continuum position, we would expect the red fox, the badger and both domestic species to exploit the resource once discovered, the mongoose and the marten to at first distrust the food source but to then exploit it, and the common genet to show no or little interest. We expect the cat to behave like more generalist species because of the bait used. Regarding the second objective, we hypothesise that more generalist species would visit the feeding points more regularly and spend more time feeding than less generalist species. The more specialised a species is, the less flexibility it has to add new foods to its diet. We would expect the red fox, the badger and domestic species to regularly use the feeding points and the mongoose and the marten to use them less frequently. On the contrary, we would not expect the common genet to use the artificial feeding points. Finally, in the case of co-occurrence in exploiting the same feeding point, we would expect the establishment of a hierarchy based on species body size, where larger species would displace smaller ones. The expected hierarchy ranked from most to least dominant would be dog (> 10 kg) > badger (7.3 kg) > red fox (6.0 kg) > domestic cat (4.5 kg) > mongoose (2.8 kg) > genet (1.9 kg) > stone marten (1.5 kg) (Monterroso 2013).

Materials and methods

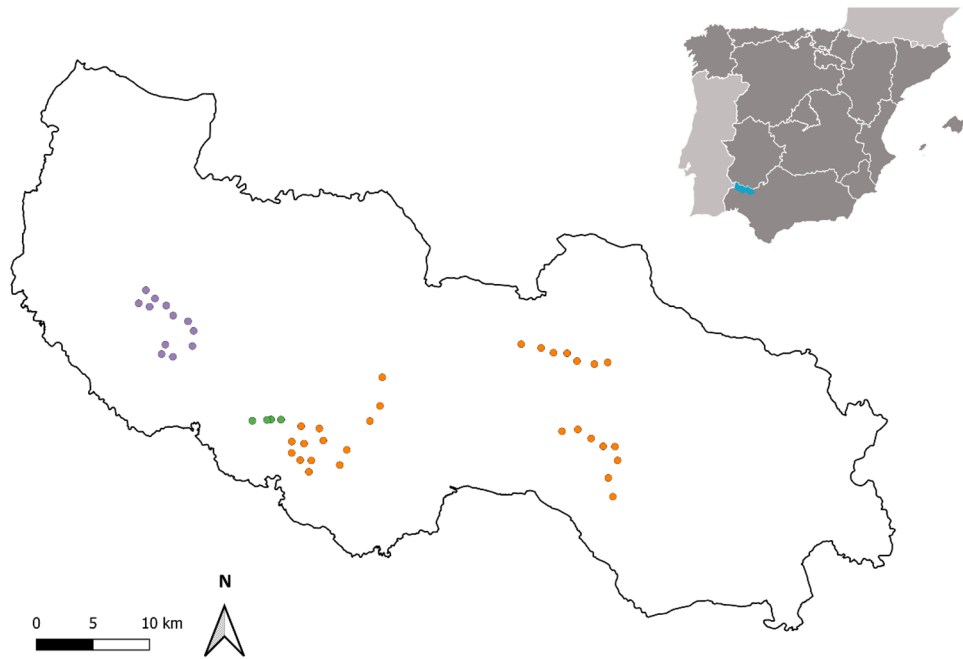
Study area

The study was carried out in the Natural Park of Sierra de Aracena and Picos de Aroche, located in the western part of Sierra Morena (N 37° 59' 42", W 6° 52' 23"), a province of Huelva in south-western Iberian Peninsula (Fig. 1). The park has a total area of 186,795 ha distributed in small municipalities of agricultural-forestry-livestock tradition. Its altitude range (460–1055 m.a.s.l.), and the annual rainfall variability (700–1000 mm) creates a large number of different habitats and environmental conditions. In addition to the previously mentioned carnivore species, other terrestrial species such as the wildcat (*Felis silvestris silvestris*), European polecat (*Mustela putorius*) and least weasel (*Mustela nivalis*) are also present, but in very low densities; therefore, they were not considered.

Feeding points

A total of 46 feeding points (hereafter FP) were deployed sequentially in different areas and habitats between March and August (spring–summer 2018 and 2020) to maximise the probabilities of recording all potential species of the carnivore community in the study area (Fig. 1). Each feeding point was formed by hand-made PVC pipes of

Fig. 1 Natural Park of Sierra de Aracena and Picos de Aroche in south-western Iberian Peninsula. Feeding point locations are represented with dots, with different colours for each sampling period: March–July 2018 (green dots), March–April 2020 (purple dots) and July–August 2020 (orange dots)



11-cm diameter and 50-cm long, tied to a tree with ropes and baited with approximately 1.4 kg of dried cat food pellet of any of two types (fish or meat flavoured) that were randomly assigned to each feeder. An experiment carried out in the same area with the same mesocarnivore guild by Amaya-Castaño and Palomares (2018) found that there was no difference in species response to different types of bait. Consequently, dried cat food was chosen due to its ease of acquisition.

The use by mesocarnivores of FPs was recorded with Bushnell Trophy HD camera traps set to distances of 2.5–8 m and tied to trees at 0.20–1 m above the ground. Cameras were programmed to take two pictures followed by a 30-s video during a 24-h period, with a 10-s delay between successive records. FPs were spaced 1283 ± 68 m (mean \pm SE) to maximise the probability of recording different individuals for each species.

As a rule, feeding points were left active for 1 month, but an adaptive strategy was followed based on relocating FPs when the response achieved was not useful (e.g. mainly visited by domestic species or wild boars), so some of them were active for less than 1 month. FPs were checked once a week to check batteries and to ensure constant food.

Data processing

Each sequence composed of two photos and one video when an animal came into the camera area was considered as a single record from which the following information was extracted: date, time, species, number of individuals, individual ID (mainly for domestic animals or wild animals with

fur patterning), behaviour observed and if the animal ate from the bait. The number of independent events was then estimated. Except in cases where individuals could be identified by their fur patterning or other features (injuries, marks, spots, tail shapes), the minimum time interval to consider two consecutive records of the same species in the same FP as an independent event was determined through the method of Yasuda (2004). This method is based on the analysis of different time intervals to determine at what point the curve that represents the proportion of events per species given by the chosen time interval in relation to the total number of records of that species stabilises. Intervals from 10 min up to 60 min with increases of 10 min and then intervals of 1 h up to 12 h with increases of 1 h were applied to build the curve.

Once the time interval was determined, a new database was created with independent events including the basic information from the initial database plus a total duration of events, record day from FP activation, presence/absence of bait and if the individual was aware of the FP. Total duration of events was calculated by subtracting the time of the first photo or video (first second) where the animal was detected from the time of the last photo or video (last second) where it appeared. Simultaneous appearance of several individuals was entered as different events, except for family-related groups (e.g. adults with cubs or just cubs). The starting time to denote a new recording day was set at 6:30 UTC. The threshold, corresponding to approximately 30 min before sunrise, was chosen based on a short time gap when most of the nocturnal carnivores had hidden but diurnal carnivores had not yet appeared. In this way, all events of both diurnal and nocturnal species could be included within the same day

allowing us to measure and compare rates of visits per day between seasons.

Data analyses

All statistical analyses were performed using R (version 4.0.2). Q-Q plots and Bartlett tests were used to test for normality and homoscedasticity of variables. When this was not achievable, non-parametric statistical tests and generalised linear models (GLMs) for non-normal distributions were performed.

Since the sampling effort differed among FP, data were standardised by dividing the number of independent events by the number of days a FP was active to achieve the species detection rate per 100 recording days (100RD). In addition, spatial autocorrelation was tested by means of Moran's I coefficient in order to validate the assumption that events across different sites were truly independent.

All events in which an individual passed rapidly at distance behind a FP, but without looking at it, were discarded from the analyses of use and intensity of use of the artificial food source because it was assumed they did not notice the FP.

To determine which carnivores visited and exploited the FPs, we counted feeding events discarding those without food available at the FP. The probability of eating and the duration of feeding events were then analysed as a function of the type of pellet and species using a binomial logistic regression and a GLM, respectively. Prospective analyses about the effect of type of pellets on the carnivore response were very small and heterogeneous (Figs. S2–S3 and Tables S2–S3), so we excluded this variable in further analyses to simplify results and their interpretation. To estimate the amount of time spent eating (exploitation time), the total duration of the events was taken into account under the assumption that the more time an individual spends eating and staying close to the feeder, the more it is interested in the artificial source of food. However, in no case does the measure indicate that it was eating *sensu stricto* the entire period. Tukey post hoc tests were performed and p values adjusted for multiple comparisons.

To assess which species visited the feeder regularly, a visitation rate per FP and species was calculated. Visitation rate was the number of visits/day from the day the feeder was discovered by a given species. Although likely rare, we were aware that in some occasions, the same FP could be visited by different individuals of the same species, and therefore, the visitation rate could be overestimated. However, since identification of all the individuals was not achievable, we decided to treat all data equally without distinction of individuals to reduce bias among species in the analysis. A Kruskal–Wallis H test was performed to compare

mean visitation rates between species. A Dunn post hoc test was used in the case of significant results for pairwise comparisons.

To determine if species became accustomed to the feeder, we analysed if the probability of eating varied over time once the FP was discovered. A binomial logistic regression was performed, consecutively numbering each of the visits to the feeder and specifying whether or not it ate and distinguishing between individuals when possible. The count of consecutive visits was made with or without available food although only those events with available food were considered in the regression. FP was added as a random factor to correct for repeated measurements.

To examine if the presence of some species changed the use of the FPs by other species, for each FP, the first species to use the feeder was taken as the owner (*sensu* Parker 1974), and its visitation rate, eating probability and mean time spent eating were calculated before and after the arrival of a second carnivore (the challenger *sensu* Parker 1974), only when the latter was considered to be dominant (i.e. larger) over the first. The marten and the genet were an exception, and the analyses were done in both directions due to their similar bodyweights. To determine if the response of the owners was by chance, we generated 1000 simulations by randomly distributing the different recorded days and the owner associated information. For each simulation, the measurements after the appearance of the challenger were calculated and then the percentage of times the observed value had been greater than that expected by chance was estimated. Higher or lower percentages would suggest attraction or avoidance, respectively. All of those species with visitation rates for a given FP lower than the first quartile of all visitation rates were not considered in the analyses since it was assumed that they did not visit the feeder with enough frequency to be affected by, or cause an effect on, the presence of another species.

Finally, to determine if the arrival of a dominant species shifted the time at which the subordinate visited the feeder, we fitted kernel density functions for the subordinate before and after the arrival of the dominant and compared them using the R package *overlap* (Ridout and Linkie 2009). To determine if the two functions were truly different, the activity overlap index (area shared under both curves) was calculated by means of Dhat1 equations when at least one of the sample sizes was lower than 50, and Dhat4 in the other cases as recommended in Meredith and Ridout (2020). Confidence intervals (95%) for overlap indices were estimated by bootstrapping 1000 samples from the kernel functions and the overlap index for each iteration within each pairwise comparison calculated using the same R package (Ridout and Linkie 2009). To test whether two activity patterns could be considered as significantly different, the R package *activity* (Rowcliffe 2019) was used to create a null distribution

Table 1 Number of records and independent events of each carnivore species. Percentage of FPs in which species were detected and detectability per 100 recording days considering the independent events are also shown

Species	Records	Independent events	% FPs that detected the species	Detection rate /100RD
Badger	135	107	47.7	9.6
Red fox	8417	1268	88.6	113.4
Mongoose	246	124	47.7	11.1
Genet	481	240	65.9	21.5
Marten	432	186	50.0	16.6
Domestic cat	1401	424	18.2	37.9
Dog	845	126	43.2	11.3
Total	11957	2476		

of 1000 random overlap indices using bootstrap samples that contain values taken indiscriminately from any of the two density distributions compared. The observed overlap index was then compared to this null distribution to check the probability that the index had arisen by chance (p).

Results

Forty-four out of the initial 46 FPs installed provided useful data for the study even though some recordings were interrupted for short periods of time. A total of 1118 days of recording were available, for an average of 25.41 ± 1.39 days (range = 7–48) per FP.

A total of 13,758 records were obtained, and of these, 86.90% included the five target wild mesocarnivores and the two domestic carnivores (Table 1). Three FPs detected all wild species, and only one all wild and domestic carnivores. The weasel was detected once, and the Eurasian otter was detected 13 times at a FP located near a stream. Since the weasel was an isolated event and the otter was running up and down the stream completely ignoring the presence of the FP, we did not include them in the analyses. On average, each FP detected 3.6 (range = 1–7) of the target carnivore species.

After implementing Yasuda's (2004) method, the minimum time interval (intermission length) for considering two consecutive records of the same species as independent events was 40 min (Fig. S1), and the number of events was reduced to 2476 (Table 1). Moran's I coefficient was not significant for any species, thus confirming spatial independence of events between FPs (Table S1). Red foxes were the most detected carnivore, recorded in 89% of FPs, whereas domestic cats were detected only in 18% of FPs; the badger had the lowest detection rate (Table 1).

Use and intensity of use of the artificial food source

Carnivores took a median of 3 to 9 days to detect FPs, with the fox being the fastest and the dog the slowest. All the mesocarnivores fed from FPs, except the badger, which, from 107 independent events with available food, only ate once (Table 2). Therefore, the badger was not considered in subsequent analyses.

The first time species interacted with the bait, cats ate immediately 85% of the times, dogs and foxes did so 66% and 68%, respectively, while the marten and the genet did so between 48 and 50%. Contrarily, the mongoose behaved more distrustfully and only fed directly 25% of the times.

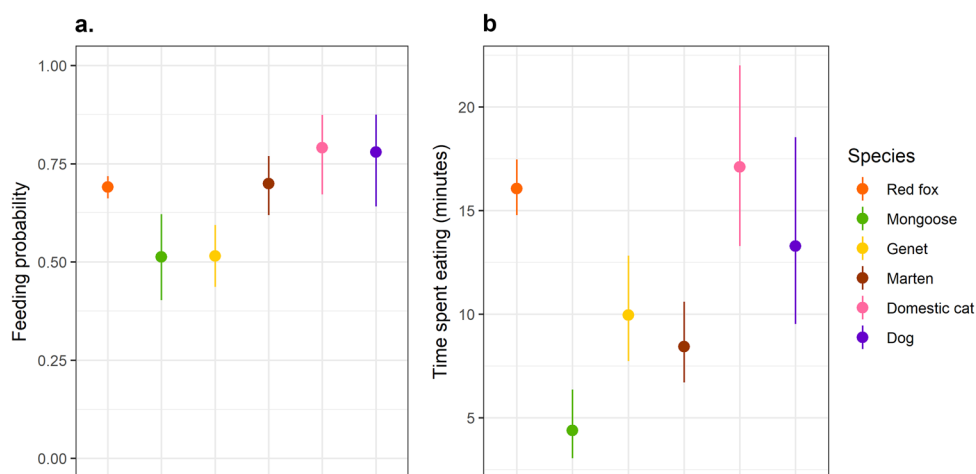
The probability of exploiting the new resource varied between species (binomial GLM $X^2_{11} = 55.20$, $p < 0.001$). Cats, dogs, foxes and martens presented values close to 0.75 whereas mongooses and genets showed a similar feeding probability (Fig. 2a), significantly lower than the other species (all Tukey test comparisons with mongoose or genet presented $p < 0.05$). In terms of exploitation time, differences also arose (GLM: $X^2_{11} = 85.54$, $p < 0.001$). Foxes and domestic species had the longest feeding events (13–17 min on average) while mongooses had the shortest ones (< 5 min; Fig. 2b).

All the species presented uneven visitation rates throughout the different FPs. While in some FPs visitation rates reached between 1.51 and 7.25 visits/day, in others, it was only 0.03–0.13 for the same species (Table 3), meaning that it just appeared once and never returned. However, all species showed the ability to use FPs regularly (Table 3). Median visitation rates were different among species

Table 2 Events with available bait at feeding points and number of times individuals of each species fed or did not feed

Species	Presence of bait	Feeding events (%)	Non-feeding events (%)
Badger	107	1 (0.93)	106 (99.07)
Red fox	1037	725 (69.85)	312 (30.15)
Mongoose	102	58 (56.86)	44 (43.14)
Genet	199	111 (55.78)	88 (44.22)
Marten	155	111 (71.61)	44 (28.39)
Domestic cat	346	228 (65.90)	118 (34.10)
Dog	74	55 (74.32)	19 (25.68)

Fig. 2 Overall differences between species in feeding probability (a) and time spent eating (b) in 44 experimental feeding points. Predicted means and 95% CI are shown



(Kruskall-Wallis test: $H_5 = 48.52$, $p < 0.001$), with foxes and cats having the highest rates (Table 3). Dunn's test pairwise comparisons indicated that domestic cat and fox had similar visitation rates ($Z = -0.195$, $p = 0.85$), these being significantly higher compared to the others (all $p < 0.05$), among which there were no differences (all $p > 0.16$).

Regarding the analysis to see if species get used to the feeder, none of the species showed a significant habituation to the food over time, although some trends could be observed (Fig. S4).

Interspecific competition at the feeding points

When dogs appeared in FPs after a smaller species had started using it ($n = 12$), several effects were observed. A decrease in visitation rates was observed (i.e. observed variable was lower or smaller than expected by chance in $> 60\%$ of simulations) in all cases except in one with domestic cats, one with genets and another two with foxes. Similarly, a decrease in the probability of eating was observed except in two cases with marten and three with fox. A decrease in the mean time spent eating was also observed, except in two marten cases and two fox cases (Table 4). When foxes were the challenger ($n = 12$), visitation rates of owners decreased in all except one case with domestic cat, one with mongoose

and three with genets; the probability of eating decreased except in the case of one cat, one mongoose, two genets and one marten; and the mean time spent eating decreased except for one mongoose, one genet and one marten (Table 4). In the only FP in which a cat was the challenger, a significant decrease in the number of daily visits by marten occurred, but did not affect either its eating probability or the time spent feeding. In fact, the latter increased significantly (Table 4). The marten and the genet showed a mutually negative effect on each other in the number of daily visits, eating probability and mean time spent eating, since for all them the percentage of observed values was lower than expected by chance in more than 84% of simulations (Table 4).

When comparing activity patterns of owner species before and after the arrival of a larger species, the cat was the only species with a significant shift in its activity due to the presence of dogs, while this also seemed to cause a constriction in the activity pattern of both foxes and martens (Fig. 3). The arrival of foxes caused a significant change in genet and mongoose activity patterns, but neither cats, mongooses nor genets influenced the activity of their putative subordinate species (Fig. 3). Martens affected genets, even though genets were considered to be dominant over martens due to their slightly larger size (Fig. 3).

Table 3 Number of FPs in which each species was detected, and median and range of the visitation rates per day

Species	Number	Median (visits/day)	Range
Red fox	38	1.11	0.13–4.22
Mongoose	20	0.19	0.03–1.78
Genet	28	0.20	0.03–1.97
Marten	22	0.22	0.04–3.19
Domestic cat	8	1.08	0.06–7.25
Dog	19	0.32	0.08–1.51

Discussion

We experimentally examined the reaction of a mesocarnivore community, mainly formed by trophic generalists, to a new food source with the aim of investigating whether a species was able to exploit the new food source, how often they did so and what happened when several species co-occurred at the same point. Overall, we proved that most mesocarnivores were able to detect and exploit the new food resource repeatedly, and described how subordinate species maintained feeding at a FP through active avoidance and

Table 4 Visitation rate, eating probability and mean time spent eating per visit observed for each owner, before and after the arrival of the putative dominant species (the challenger). Means expected by chance obtained through simulations are also shown for post-measurements. Percentages indicate the number of times each observed value was lower than expected by chance

Challenger	Owner	Pre-challenger										Post-challenger									
		Visitation rate observed	Eating prob. observed	Mean time spent eating observed	Visitation rate (visits/day)					Eating probability					Mean time spent eating (minutes)						
					Observed	Expected	% Obs < Exp	Observed	Expected	% Obs < Exp	Observed	Expected	% Obs < Exp	Observed	Expected	% Obs < Exp					
																	Observed	Expected	% Obs < Exp	Observed	Expected
Dog	Fox	2	1	28.27	1	1.13	74.20	0.67	0.79	74.20	15.93	22.24	100.00								
	Fox	1	1	36.43	2.20	2.01	0.00	0.71	0.77	86.10	21.84	24.27	70.00								
	Fox	0.50	0	-	0.68	0.67	58.70	0.33	0.30	43.50	6.03	6.37	8.76								
	Fox	3	0.66	22.34	2.53	2.55	66.90	0.90	0.89	19.30	25.62	25.45	24.80								
	Fox	2.30	0.71	11.04	1.59	1.67	85.30	0.53	0.56	2.50	4.79	6.07	100.00								
	Fox	0.81	0.88	8.65	0.57	0.70	83.60	0.25	0.69	93.10	0.60	7.14	99.40								
	Domestic cat	5.40	0.65	12.15	5.76	5.60	38.30	0.56	0.59	86.30	11.30	11.6	61.50								
	Mongoose	1	1	32.64	0.18	0.57	100.00	0	0.90	100.00	-	32.95	100.00								
	Genet	1	1	14.52	0.53	0.55	49.50	0.43	0.50	84.00	4.04	6.60	94.30								
	Marten	1.25	0.40	6.11	0.75	1	68.10	1	0.66	0.00	6.34	6.20	44.00								
Fox	Marten	2.50	0.71	10.91	0.73	1.57	99.90	0.50	0.67	89.50	8.68	10.72	89.60								
	Marten	2	0.50	0.28	0.25	0.31	93.90	0.50	0.50	2.90	9.34	7.10	0.00								
	Domestic cat	4	0.75	14.87	5.71	5.62	25.30	0.59	0.60	71.10	11.39	11.61	79.90								
	Domestic cat	6.33	0.53	25.82	3.72	4	85.30	0.71	0.68	2.50	13.98	15.56	97.10								
	Mongoose	0.75	0.50	1.07	1.96	1.79	10.50	0.83	0.81	21.90	5.87	5.76	48.20								
	Genet	0.20	0	-	1	0.83	1.20	0.84	0.80	20.30	5.77	5.74	49.50								
	Genet	2.35	0.63	19.42	1.46	1.96	93.90	0.47	0.58	97.60	12.68	17.49	94.90								
	Genet	1.70	0.64	16.16	1.13	1.30	79.40	0.50	0.56	80.40	6.96	11.10	95.90								
	Genet	1	1	25.42	0.26	0.28	76.60	1	1	0.00	5.75	10.64	95.80								
	Genet	1	1	14.52	0.53	0.55	44.90	0.43	0.50	83.70	4.04	6.64	94.20								
Domestic cat	Genet	0.50	1	20.32	0.79	0.76	32.20	0.33	0.38	89.30	9.00	10.97	82.90								
	Marten	2	0.88	3.58	0.60	0.84	98.50	0.33	0.58	100.00	0.71	2.69	100.00								
	Marten	3.50	0.79	11.94	3.12	3.20	62.10	0.93	0.89	4.50	13.95	13.4	38.40								
	Marten	1	1	1.03	0.11	0.14	100.00	-	1	100.00	-	1.03	100.00								
	Marten	2	0.50	0.28	0.25	0.31	91.80	0.50	0.51	4.20	9.34	7.06	0.00								
	Mongoose	No data available																			
	Genet	Marten	2.36	0.71	10.91	0.70	1.58	99.80	0.50	0.67	87.80	8.68	10.67	84.90							
	Marten	Genet	2.35	0.63	19.42	1.46	1.95	94.00	0.47	0.58	97.90	12.68	17.41	94.60							

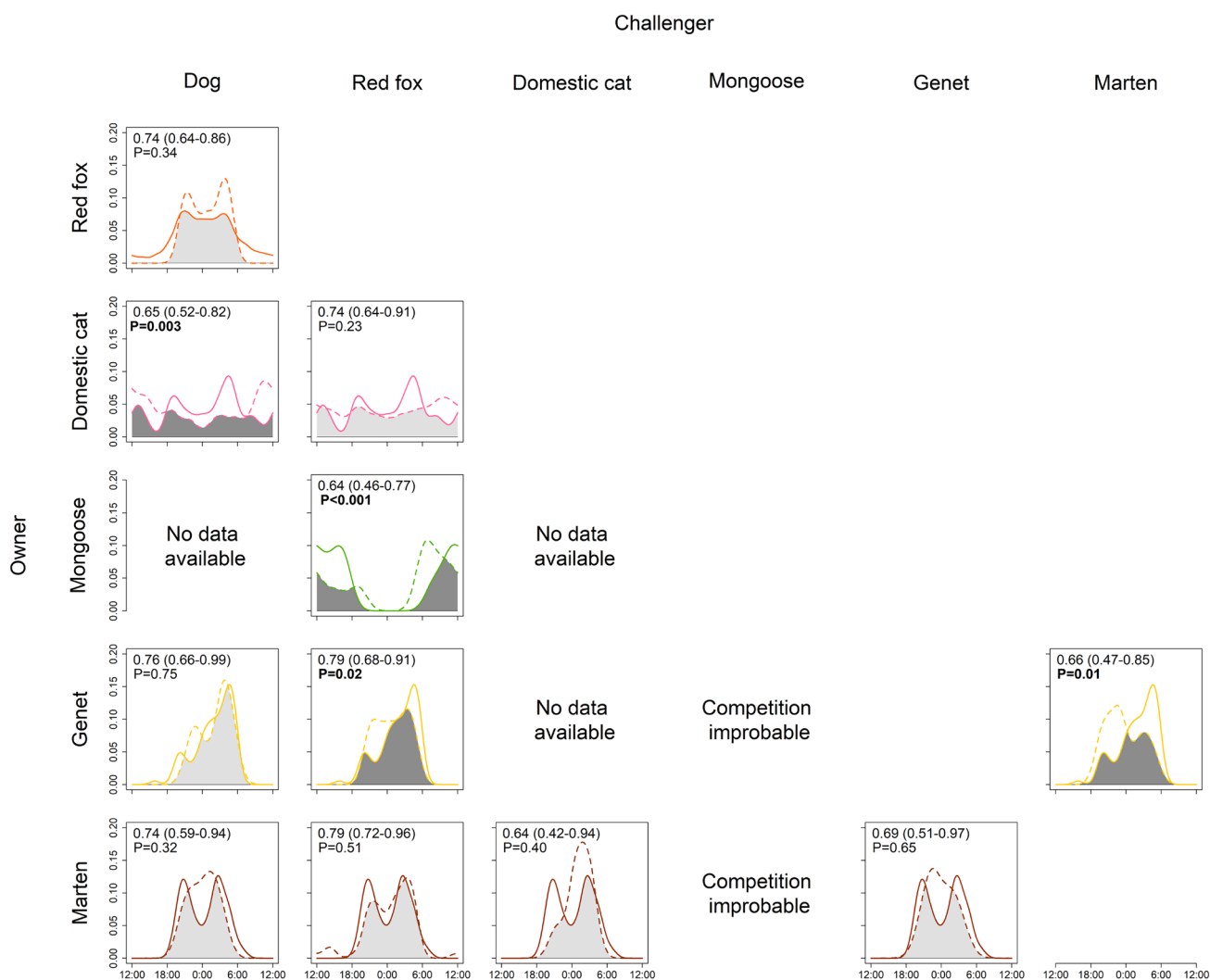


Fig. 3 Comparison of the putative subordinate species (owner) activity patterns at the feeder before (solid line) and after (dashed line) the arrival of a putative dominant species (challenger). At the top left of each graph: Dhat1 activity overlap index (except Dhat4 for genet with fox as challenger) obtained by comparing both activity patterns with

its 95% CI and p values showing significant differences between the two density functions. Hours expressed in UTC on the x -axis and kernel density estimate on the y -axis. Competition improbable: pairs of species with completely opposite activity pattern; no data available: pairs with insufficient events to build the kernel density function

temporal shifts in activity despite being negatively affected by the appearance of a dominant.

Camera trapping was a useful method to record the use of FPs by the carnivore community under study. This technique has been commonly used to study species occurrence, abundance and other demographic parameters (Sollmann 2018), but has also been used in behavioural studies to investigate food choices and feeding habits in urban areas (Cronk and Pillay 2018), intraspecific competition for high-quality patches (Dorning and Harris 2017) and ecological drivers of spatial coexistence (Monterroso et al. 2020). Nevertheless, the limitation of the visual field to a few metres around the feeder was a drawback that allowed us to only observe the behaviour of the species close to FPs, but did not allow

observations of individuals or species exhibiting cautious behaviour some metres away. In fact, on some occasions, flight or vigilant reactions from the recorded individual were observed but could not be attributed to anything observed in the camera's visual field. Therefore, our results on the potential interspecific competition or interference due to the new food source should be considered in respect to the nearby surroundings of the FPs.

Use and intensity of use of the artificial food source

All the target species visited, recognised and exploited to a greater or lesser extent the artificial food except the badger, even though it is considered one of the most generalist

trophic species in the studied carnivore guild. The same response was observed by Amaya-Castaño and Palomares (2018) with several food types in the same study area. One explanation for this badger behaviour could be that although it has been shown that it can feed on several food items (Roper and Mickevicius 1995), it tends to locally specialise when its main prey abundance allows it (Virgós et al. 2004). In numerous studies across Europe, badger specialisation in eating earthworms stands out (Kruuk and Parish 1981). Moreover, similar studies carried out in the Iberian Peninsula have found that despite the lower abundance of earthworms during dry summers, badgers manage to maintain an important percentage of them in their diets (Virgós et al. 2004). Therefore, perhaps badgers are less flexible than assumed in incorporating new food items into its diet, and only do so when its main prey is scarce.

Regarding the other species, as expected, more generalist species such as the fox and domestic species exploited the artificial food more than the less generalist species. Contrary to our expectations, genets also exploited the food resource. The response seen in domestic species could be explained by their likely familiarity with the foods provided in our experiment, since few of the individuals appeared to be feral. On the other hand, foxes are opportunistic carnivores that feed on almost anything. This has allowed the fox to become one of the most common urban carnivores in European cities (Contesse et al. 2004; Dorning and Harris 2017), and would explain how they easily took advantage of the new source. A similar argument could apply to martens, which despite their tendency toward fruit specialisation, are considered opportunistic and flexible feeders that adapt their diets to potential food sources and availability (Genovesi et al. 1996; Zhou et al. 2011). Although they present some reluctance to consume anthropogenic resources even when they are found inhabiting urban environments (Herr 2008), they have been observed doing so in some studies (Duduš et al. 2014). Additionally, the habit of many homeowners of feeding their pets outside could mean that the bait used in our study was already known to these two species, which have the ability to forage in humanised areas. The observed response of the mongoose was expected for a species with a diet more focussed on consuming animals than alternative items, but with an opportunistic behaviour of consuming the most available resource in the moment (Palomares 1993). Conversely, even though genets focus primarily on preying on the wood mouse (*Apodemus sylvaticus*) (Virgós et al. 1999; Amroun et al. 2014; Bandeira et al. 2018), their response towards the new food resource was similar to that of mongooses. This could indicate two things: that using our FPs containing easy-to-consume and abundant food outweighed the benefits of hunting their preferred preys or that the abundance of wood mouse in the study area during the trapping months had been lower than our resource, making our food

source more likely to be consumed. However, analysis measuring prey availability in the area would be necessary to test these hypotheses.

All species that made use of the new resource used it repeatedly in at least one FP, thus demonstrating an ability to learn that the source was spatiotemporally stable. However, less generalist species showed lower visitation frequencies than more generalist species, probably because they do not rely on new food sources to meet their energetic requirements and prefer to keep foraging for the prey or food item in which they specialise. Indeed, the fact that the probability of eating did not increase over time showing some habituation process could mean that species maximise the use of a trophic resource when they find it, as they do not know how long it will remain available in the environment. Moreover, although our experiment was carried out in a natural area, generalist species may have behaved around FPs as their urban counterparts (Dorning and Harris 2017), temporally reducing home ranges and centring their activity around predictable patches, thus increasing visitation rates. This explanation fits with the behaviour displayed by some species. For example, foxes spent long periods of time exhibiting vigilance behaviour and circling around the feeder, and cats rested and exhibited grooming behaviour at FPs. Some long events may have been split into multiple occurrences due to the limited visual field, thus increasing visitation rates of these two species. Additionally, some high visitation rates may have been overestimated due to challenges in distinguishing between different individuals. For instance, a minimum of two different cats appeared in 5 out of 8 FPs where they were detected. In foxes, groups of two or three individuals were also detected in at least 14 FPs, but were impossible to individualise due to their fur homogeneity. Despite being a generalist, dogs visited FPs less frequently than expected. This pattern of use could be explained by their manner of eating, usually consuming all the bait in a single visit, yielding long feeding times (Fig. 2b) but resulting in lower visitation rates. However, we hypothesise that if constant food could have been ensured in FPs, dogs would have presented frequencies similar to those of foxes and cats.

Interspecific competition at feeding points

As hypothesised, in most cases observed, the arrival of a larger species negatively affected the feeding activity of the species already feeding at an FP. The arrival caused a reduction in either subordinate visitation rate, eating probability or time spent feeding. This finding is in accordance with similar studies in which dominant species or individuals displaced subordinates and monopolized resources (López-Bao et al. 2011; Dorning and Harris 2017; Cronk and Pillay 2018). However, while in the most extreme case, a subordinate species stopped eating and reduced its visitation rate to a

minimum, in many cases, a reduction in one of the measures was offset by an increase in another. A reduction in the visitation rate was often solved with an increase in the probability of eating and/or longer feeding bouts or the opposite, an increase in visitations to compensate for shorter feeding bouts. This behavioural adaptation to continue feeding at the same FP could be an indication that subordinate species were aware of the dominant's proximity to the FP. Subordinates may have maximised food input when dominants were far away from FPs, thus avoiding or reducing the probability of agonistic encounters. This response is known as active avoidance, and some studies suggest that it helps subordinates exploit the same food source (López-Bao et al. 2011) without the need for temporal or spatial segregation. López-Bao et al. (2016) observed how wolverines and lynx were able to feed on the same lynx-killed reindeer carcasses using active avoidance. Similarly, Vanak et al. (2013b) found that leopards and cheetahs minimised lion encounter risk using fine-scale avoidance behaviours to keep feeding in the same prey-rich areas. Also, in López-Bao et al. (2016), wolverine presence was seen to shorten lynx feeding bouts around carcasses. This effect can be compared to observations made in some of our events where, despite not observing a competitor in the vision field of the camera, an individual from a given species ate for a short period of time and then left, with another species appearing shortly afterwards. The lack of replicas for most owner-challenger pairs did not allow us to evaluate whether the magnitude of the changes induced on the owners was dependent on the challenger's visitation rate. Much more effort deploying FPs would have been needed in order to reach a representative sample with different visitation rates for each pair of species. However, we hypothesise that the increase in the visitation rate of the dominant species would lead to a reduction in the activity of the subordinate species around the feeder, to a point where it would no longer be worthwhile to be constantly aware of the dominant's activity, so that the subordinate would stop coming to the FP.

Although active avoidance could be an important mechanism to reduce agonistic interactions, some degree of temporary shift was also observed. This indicates that food-sharing within a carnivore guild may be the result of several strategies to avoid competitors.

As predicted, free-ranging dogs were clearly the top carnivore of our guild, as they negatively affected at least one individual of each species. Although the observed dogs may not compete with wild species for foraging resources, they do represent a threat to many species, since they can be an important source of mortality (Palomares and Delibes 1992; Revilla and Palomares 2002; Vanak and Gompper 2010). The mongoose seemed to suffer the most marked effect. In the only FP in which the dog appeared after the mongoose, the latter stopped eating and reduced its visitation rate from 1 to 0.18 visits/day. Additionally, domestic cats modified

their activity patterns, shifting their peak at midday probably to avoid the peak of dogs at dawn (Fig. S5). Domestic cat and mongoose were probably the most affected due to their diurnal behaviour, making them more likely to co-occur with or be attacked by dogs, in comparison to more nocturnal species. In our study area, some foxes were found to be active almost throughout the 24-h period. Although the change was not significant, the appearance of a dog caused a narrowing in the fox's activity pattern, becoming more nocturnal (Fig. 3), probably to reduce the probability of agonistic encounters (Fig. S5). Similar behaviours have been reported in foxes both in the presence of free-ranging dogs (Silva-Rodriguez et al. 2010) and with other wild canids (Mitchell and Banks 2005).

The fox caused greater negative changes in use of the food source by martens and genets compared to mongooses and cats, probably due to greater overlap in activity and greater size differences. Determining competitive ability based on body size can be challenging between similar-sized species and can depend on factors such as sex and age of the individuals (Palomares and Caro 1999). However, the negative effect associated with the higher competitive ability of the larger species tends to increase with size difference from the opponents. The presence of foxes also affected the activity patterns of mongooses and genets, which could be explained by subordinate species visiting the feeders outside their preferred hours. The fox's diurnal activity previously mentioned could have caused even the mongoose, a diurnal carnivore, to widen its daily activity interval in order to visit the feeder at different times.

Concerning cats, we only collected interaction data with martens, but hypothesise that the negative effect of cats would be similar with mongooses and genets, since the bodyweight ratios oscillate between 1.68 and 2.47, respectively (Monterroso 2013). The activity pattern of the marten did not change significantly, but the slight advance in its second peak of activity suggests it may have been avoiding overlap with the activity peak of the cat.

An unexpected bidirectionality between genets and martens was observed. Both caused a reduction in the frequency and exploitation of the feeder in the other species when they acted as owners. Although genets have a higher average weight and size than martens, the bodyweight ratio is very small (1.27; Monterroso 2013) which means that both species could hold the dominant status depending on age and sex of the individuals. However, in terms of activity overlap, the marten eventually displaced the genet, causing it to move its activity from dawn to evening. In this case, although the results suggest that the marten holds a higher rank in the hierarchy, we believe that genet specialisation on small mammals would cause it to avoid unnecessary competition for non-preferred items once martens appeared at the FP. The marten's foraging strategy and opportunistic behaviour

would make it more willing to compete for the FP than the genet (Lopez-Martin 2006).

In conclusion, the mesocarnivore community of SW Spain, with the exception of the badger, successfully recognised and regularly exploited the new artificial food resource. Overall, generalist species were more likely to exploit the food directly the first time, visiting it more frequently, eating with a higher probability and spending more time feeding than less generalist species. However, one of the hypothesised most generalist species, the badger, appeared to be the most specialist, and species we had hypothesised to be the most specialist (e.g. genet) effectively exploited the new resource. When co-occurring at the same FP, the arrival of larger species affected the way smaller species were using it but did not completely exclude them. Active avoidance of dominants combined with some degree of temporary shift could allow subordinate species to forage at the same feeders as dominant species, while reducing competition and the probability of agonistic encounters.

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Declarations

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