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BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Avian and rodent responses to the olfactory landscape in a Mediterranean cavity community

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Abstract

Animals rely on cues informing about future predation risk when selecting habitats to breed in. Olfactory information may play a fundamental role in the assessment of predation threats, because predators produce characteristic body odours, but the role of odours in habitat selection has seldom been considered. Here, we test whether fear of predation induced by odour cues may affect the settlement pattern of a Mediterranean cavity-dependent community of rodents and non-excavator hole-nesting birds. To test this hypothesis, we experimentally manipulated the perception of predation risk on a scale of patch by applying either odours of a carnivore predator (risky odour treatment), lemon essence (non-risky odour treatment) and a control non-odorous treatment and studied bird and rodent settlement patterns. Nest-box occupation probability differed across treatments so that species in the community settled in more numbers in control than in non-risky and than in risky odour-treated nest boxes. Concerning settlement patterns, control nest boxes were occupied more rapidly than nest boxes with odour information. Birds and rodents settled earlier in control than in risky odour-treated nest boxes, but their settlement pattern did not significantly vary between risky odour and non-risky odour-treated nest boxes. Our findings demonstrate that olfactory cues may be used to assess habitat quality by settling species in this community, but we cannot pinpoint the exact mechanism that has given rise to the pattern of preference by nest boxes.

Keywords Birds · Cavity community · Fear ecology · Habitat selection · Olfactory landscape · Predation risk

Introduction

All animals are exposed to predation at some time through their life (Elton 2001). The risk of suffering a predation event is not random but more frequent in some habitats where predators concentrate or in some periods of life where individuals are more vulnerable. Habitat selection based on cues informing about the risk of predation has proved to be a widespread mechanism to reduce predation risk and, hence diminish or avoid predation, influencing survival and fitness (Lima and Dill 1990; Caro 2005). In birds, nest predation is the main cause of reproductive failure (Nice 1957; Martin 1993), and a large body of empirical evidence has shown that birds can perceive and react to a wide array of visual and vocal stimulus informing about predation risk when taking habitat settlement decisions (e.g., Eggers et al. 2006; Fontaine and Martin 2006; Peluc et al. 2008; Monkkonen et al. 2009; Emmering and Schmidt 2011; Parejo and Aviles 2011; Parejo et al. 2012b; 2018).

Olfactory information may play a fundamental role in the assessment of predation risk, as predators produce characteristic body odours which may act as modulators of memory and emotion in prey (Apfelbach et al. 2005; Parsons et al. 2018). Indeed, high-performance liquid chromatography analysis indicates enriched 2-phenylethylamine urine production by numerous carnivores, and that this volatile chemical detected in the environment can trigger stereotyped fear and avoidance responses in rodents (Ferrero et al. 2011), which may potentially have cascading effects on community dynamics (Brinkerhoff et al. 2005).

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Anatomical studies have shown that birds possess an olfactory apparatus similar in function and structure to that of other vertebrate species with known olfactory capabilities (Bang 1971; Wenzel and Sieck 1972; Zelenitsky et al. 2011). Recent comparative work has shown that inter-specific variation in the olfactory apparatus of birds reflect an interactive role of behaviour and ecology (Aviles and Amo 2018). Moreover, a growing body of behavioural work demonstrates that birds are capable of recognizing and responding to chemical cues in several relevant biological contexts including prey detection (e.g., Nevitt et al. 1995; Amo et al. 2013), orientation (e.g., Nevitt and Bonadonna 2005; Gagliardo 2013), and social interactions (e.g., Bonadonna and Nevitt 2004; Hagelin and Jones 2007; Caro and Balthazart 2010; Amo et al. 2012; Caspers et al. 2017; Rossi et al. 2017).

Avian olfaction may play a key role in the assessment of nest predation risk. Experimental studies have shown that birds can modulate their parental investment in response to the scent of mammalian predator urine placed in their nests (Amo et al. 2008; Whittaker et al. 2009; Stanbury and Briskie 2015), or even to odorous cues informing about recent predation attempts on their offspring (Parejo et al. 2012a). Surprisingly, although the study of chemical ecology in birds has considerably expanded in the last 2 decades, the role of predators' chemical cues in habitat selection of birds has been almost neglected. Eichholz et al. (2012) found that ducks were less likely to settle down their nests in plots where red fox *Vulpes vulpes* urine was applied than in control plots. Similarly, Forsman et al. (2013) found that the number of migratory passerine species and their total density were lower in patches where mammal's urine and faeces were sprayed compared to patches where water was sprayed as a control. However, mammalian urine is highly reflective in the UV part of the light spectrum that birds can detect (e.g., Cuthill et al. 2000) and, hence, as noted by the authors themselves, it cannot be discarded that ducks and passerines were cueing on visual rather than on chemical information when selecting breeding territories. Moreover, two recent studies have not found support for a role of olfaction in nest-box selection by European starlings *Sturnus vulgaris* (Blackwell et al. 2018) and in roosting site selection by great and blue tit (Amo et al. 2018). Hence, in the light of contrasting results and possible confounding effects of visual cues, it remains debatable if olfactory cues on predation risk may play a key role during habitat selection in birds.

Here, we aim to test for the first time if fear of predation induced only by odour cues (i.e., excluding the possibility that prey would use UV clues) may affect settlement patterns in a Mediterranean cavity community composed of rodents and non-excavator hole-nesting birds. Rodents and birds can use cavities in trees as roosting or breeding sites, thus one group of species reduces the availability of holes for the other group of species simply by using them without interfering with one another (scramble competition sensu Dhondt 2012). Scramble competition is likely to be strong in Mediterranean holm oak *Quercus ilex* forests where long-term pruning activities have promoted a shortage of suitable holes for cavity-dependent species (Aviles and Parejo 2018). However, it is lowered in our study site due to a nest-box provisioning program which has resulted in a surplus of cavities (see Parejo et al. 2018). In this community, before the settlement of birds and rodents in cavities, we experimentally manipulated at the plot scale the perception of predation risk by applying odours of a carnivore predator (risky odour treatment), lemon essence (non-risky odour) and a non-odorous control and studied breeding settlement patterns by birds and rodents. We expected that settling avian and rodent individuals avoided nest boxes in plots (i.e., reduced their abundance and delayed settlement) with odours of predators, because this is likely to indicate dangerous areas.

Materials and methods

Study system

The study was conducted during the 2015 breeding season in the surroundings of the regional park of Sierra de Baza in south-eastern Spain (37°18′N, 3°11′W). The study area is an extensive agricultural landscape with scattered holm oaks where suitable natural holes for cavity-dependent species are very scarce (Aviles and Parejo 2018), and where 259 cork-made nest boxes were set up in 2010 allowing the settlement of a bird community composed of little *Athene noctua* and scops owls *Otus scops*, Eurasian rollers *Coracias garrulus*, common hoopoes *Upupa epops*, great tits *Parus major*, spotless starlings *Sturnus unicolor*, rock sparrows *Petronia petronia* and jackdaws *Corvus monedula*, which have regularly used the nest boxes as breeding sites (Parejo and Aviles 2011; Rodriguez et al. 2011; Parejo et al. 2012b; Aviles and Parejo 2018).

In addition, a proportion of next boxes are regularly occupied by two rodent species, garden dormouse *Eliomys quercinus* and wood mouse *Apodemus sylvaticus* (Table 1 Supplementary Material). No nest box was added during the study year, and hence both birds and rodents are likely to have previous knowledge of these nest boxes. All nest boxes had a base and roof surface of 24 × 24 cm, a height of 40 cm and an opening 6 cm in diameter, which is wide enough to allow easy entrance of all the species in the community. Nest predation rates (estimated as the percentage of nests of a given species where no chick fledged and all its content was removed by the predator) range between 7.7% for Eurasian rollers and 39.1% for spotless starlings (18.2%

for scops owls, 25% for hoopoes, 29.2% for great tits and 29.4% for little owls), and the most common nest predator in the study area was the ladder snake *Zamenis scalaris* (Avilés and Parejo. unpublished data).

Experimental design

Nearby nest boxes were assigned to plots (the mean number of nest boxes per plot was 5.07 and ranged from 3 to 8 nest boxes, $N = 259$ nest boxes in 51 plots, Table 1 supplementary material). Plots were separated by at least 300 m and nest boxes within each plot were separated by 50–100 m of each other. Aiming to avoid possible spatial influence on our experiment, plots were spatially grouped into triads. Within each triad, plots were randomly assigned to one of the following three treatments: (1) risky odour, in which we artificially increased perceived predation risk by applying the scent of a predator to all the nest boxes ($N = 17$ plots); (2) non-risky odour, in which we did not modify perception of predation risk but applied lemon essence as a control scent to all the nest boxes ($N = 17$ plots); and, (3) control, in which we did not apply scent but visited as frequently as risky and non-risky odour plots ($N = 17$ plots). The number of nest boxes per plot did not significantly differ among treatments (one-way Anova, $F_{2,48} = 1.90$, $P = 0.16$; average (± SD) number of next boxes: 5.47 (± 0.87) nest boxes in risky odour plots; 5.05 (± 1.08) nest boxes in non-risky odour plots; and 4.70 (± 1.40) nest boxes in control plots). We applied the same treatment to all nest boxes in a plot aiming to simulate the natural behaviour of mammal predators hunting within their territories.

Odour treatments were applied to each box by placing a scented paper hidden under a 10 × 3 cm piece of cork oak, attached with pushpins to the inner part of the nest box near the entrance. In control plots, we also attached a piece of cork oak but did not apply scent, so that the internal appearance of the nest box was not differently affected by treatments. Predator scent was obtained by placing clean absorbent papers under a cage with two male ferrets (*Mustela putorius furo* L.) for at least 3 days (see Amo et al. 2008, 2011). Although ferrets are not natural predators of cavity birds, they predate ground birds and small mammals (Bodey et al. 2011), and their scent is very similar to that of other common cavity avian predator mustelids inhabiting the study area, such as *Mustela erminea* or *Martes foina* (Brinck et al. 1983). Moreover, previous studies have consistently demonstrated that ferret scent is recognized as a predation threat by birds (e.g., Amo et al. 2008, 2011). As a control scent, we used lemon essence obtained diluting 0.5 g of scratch lemon in 1 ml of distilled water. The mixture was maintained 24 h in the fridge and then the liquid fraction was collected and used to drench absorbent papers to be used in the experiment. Lemon essence has satisfactorily been used as a control harmless and unusual odour in studies of scent recognition in breeding birds (Parejo et al. 2012a). We disregarded using natural or aromatic plants as a harmless control, because spotless starlings and great tits were known to carry them into their nests to enhance the aromatic environment of nests and/or as part of their sexual displays (Petit et al. 2002, Veiga et al. 2006), and this may confound the assessment of nest-box preference.

Based on phenological data collected in our study area during the previous years, we fixed the date of start of the experiment on 15 April. By this date, most bird species in the community are actively evaluating breeding territories but have not yet started reproduction. On that day, we found 23 nest boxes already occupied by birds (2 little owl, 10 spotless starling and 11 hoopoes nests), 50 nest boxes occupied by rodents (32 by wood mouse and 18 by garden dormouse), and 5 nest boxes with a honeycomb wasp. These 78 occupied nest boxes were removed from our analyses. The number of occupied nest boxes before starting the experiment did not differ between treatments once we control for the number of nest boxes in each plot (one-way Ancova, treatment effect: $F_{2,19} = 2.28$, $P = 0.12$; number of boxes effect: $F_{2,19} = 2.28$, $P = 0.12$; average (± SD) number of nest boxes: 1.23 (± 0.32) nest boxes in risky odour plots; 2.17 (± 0.46) nest boxes in non-risky odour plots; and 1.17 (± 0.25) nest boxes in control plots), suggesting that social cues are not likely to influence subsequent patterns of settlement after starting the experiment. Therefore, our analyses are based on the remaining 181 nest boxes that we were certain that were not occupied by birds or rodents by 15 April.

Treatments were applied every 2nd day for 20 days, i.e., from 15 April to 5 May, on alternative days in risky and non-risky plots and half of the control plots. However, response was limited to the time period lasting from 15 April to 10 May, because scents are highly volatile and hence cues were likely not available to inform settlement decisions after that period. For birds, a nest box was defined as occupied when at least one egg was laid in it. Rodents, however, can roost, stash their food or breed in nest boxes; hence we reported rodent occupation when we detected rodent presence, food stores or a nest in a nest box in two consecutive visits of the researchers.

Statistical analyses

Analyses were performed using SAS v.9.4 statistical software (SAS 2002-2008 Institute, Cary, NC, USA).

To evaluate whether the odour treatment affected the pattern of occupation of nest boxes at the end of the evaluation period, we first ran a binomial generalized mixed-effect model (GLMM hereafter) (GLIMMIX SAS procedure, link = logit) to model the occupation probability of a nest box by any species of the cavity community as binomial-dependent variable in relation to the odour treatment as a fixed term. In addition, we entered the presence of birds and rodents in the plot before the experiment (i.e., presence versus absence) as two additional fixed terms to control for a possible effect of social cues on breeding decisions of later settlers. Plot ID was included as a random intercept in the model to account for spatial clumping of nest boxes within the same plot. Pair-wise differences were checked by comparisons of least-squared means of each treatment using Scheffé test. Standard model validation graphs (Zuur 2009) revealed that model assumptions of homogeneity of variance and normality of residuals were fulfilled.

To assess nest-box settlement patterns in detail, we used Cox proportional hazard models (PHREG SAS procedure), which are a particular type of survival analysis regularly used to analyse time-to-event data (Austin 2017). Cox models allow us to predict the hazard or risk of failure (i.e., probability that a nest box will be occupied given that it has persisted to a given point in time) as a function of odour treatments. The nest-box level outcome in this analysis was the time in days from the start of application of treatments in the nest boxes (i.e., 15 April) to the occupation of a nest box. Nest boxes that were not occupied (zeros) were censored after 25 days (i.e. 10 May, the latest date the odour treatment was assumed to be detectable) if they were still available. The PHREG procedure allows for the incorporation of random effects into Cox proportional hazard models (frailty models sensu Austin 2017) and hence to account for within-cluster homogeneity of our experimental setup (i.e., plot ID) in hazards. We run first a Cox proportional hazard model predicting the hazard of a nest box to be occupied by any species in the community, and afterwards two separate models for bird and rodent occupations, as we were interested in knowing whether birds and rodents responded in a similar way to the experiment. We also entered the presence of birds and rodents in the plot before the experiment as two fixed terms in these models to control for a possible effect of social cues on settlement.

A central assumption of Cox regression is that covariate effects on the hazard rate, namely hazard ratios, are constant over time. Violations of the proportional hazard assumption may cause bias in the estimated coefficients as well as incorrect inference regarding significance of effects. We used the assess statement with the *ph* option in PHREG procedure in SAS to assess the proportional hazards assumption for each treatment category both graphically and numerically. Stated another way, the assumption of proportional hazard was verified (i.e., none of the observed score processes looked particularly aberrant, and the supremum tests are non-significant ($P > 0.24$)).

Results

In total, 54 out of the 181 nest boxes were occupied by at least 1 cavity community species during the experimental time (i.e., from 15 April to 10 May, Table 1 appendix), rendering an occupation of 29.8%. Considering only occupied nest boxes, 29 were occupied by birds (53.7%) and 25 (46.3%) by rodents.

Community responses to olfactory cues

Probability of occupation of a nest box at the end of the experimental time was influenced by odour treatment and was not influenced by bird or rodent occupation of plots before starting the experiment (Table 1). Pair-wise comparisons revealed that control nest boxes had significantly higher probability of being occupied by any species in the community than non-risky odour-treated and risky odour-treated nest boxes (Fig. 1).

Table 1 Results of a generalized mixed-effect model of nest-box occupation in relation to odour treatment and previous occupation by birds and rodents

Fixed effects	*df*	*F*	*P*	Level	Coefficient	SE	Lower 95% CL	Higher 95% CL
Nest-box occupation probability								
Intercept	143.8	2.24	0.03		− 1.28	0.57	− 2.44	− 0.12
Treatment	243.8	6.19	0.004	Control	1.63	0.48	0.71	2.65
				Non-risky odour	0.69	0.50	− 0.32	1.70
				Risky odour	0	–	–	–
Bird presence	140.7	0.72	0.40		− 0.40	0.47	− 1.35	0.55
Rodent presence	142.3	0.19	0.66		− 0.17	0.40	− 0.99	0.64
Random effects	σ^2	SE	*Z*	*P*				
Plot ID	0.27	0.35	0.79	0.22				

Degrees of freedom for fixed effects were estimated using the Kenward-Roger approximation. $N = 181$ nest boxes. Non-significant effects were removed one by one starting with the less significant (i.e., high *P* value)

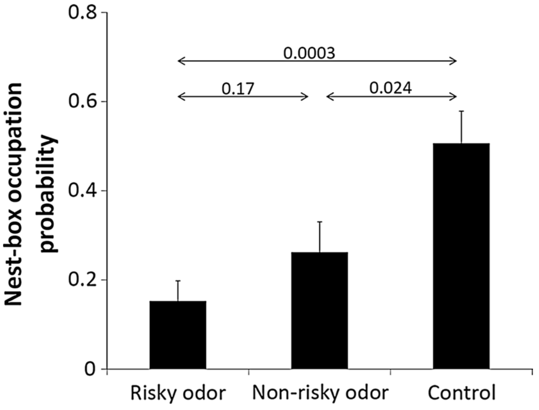

Fig. 1 Nest box choice in relation to olfactory cues informing on predation risk. Least square mean (±standard error) probability of occupation of a nest box by cavity community species in relation to odour treatment. *P* values for tests of pair-wise differences are shown on top of arrows designating each pair

A Cox proportional hazard model on temporal next-box occupation by any species in the community showed that the hazard function varied in relation with odour treatment and was not influenced by bird or rodent occupation before starting the experiment (Table 2). In particular, the state of being non-occupied disappeared more rapidly for nest boxes without odour information (i.e., control) than for non-risky odour-treated and risky odour-treated nest boxes (Table 2). Among the nest boxes with olfactory information, occupation tended to be faster, but not significantly (Table 2), when odour does not inform on a predator threat (Table 2, Fig. 2a).

A second Cox proportional hazard model, which examined the hazard of a next box to be occupied by birds, showed that there was not a significant effect of odour treatment ($P=0.08$, Table 2), and that the hazard function was not influenced by bird or rodent occupation before starting the experiment (Table 2). A close examination of the hazard ratios comparing treatments revealed that the state of being non-occupied disappeared more rapidly for nest boxes without odour information (i.e., control) than for nest boxes with odour of predator, but that the hazard ratios did not vary between control and non-risk odour nest boxes, and between nest boxes with olfactory information (Table 2, Fig. 2b). However, the proportional hazard assumption for the treatment "non-risk odour" was not satisfied (supremum tests, $P=0.02$), and hence this result should be carefully considered.

A Cox proportional hazard model on temporal next box occupation by rodents showed that the hazard function varied in relation with odour treatment and plot ID, but was not influenced by bird or rodent occupation before starting the experiment (Table 2). Specifically, control nest boxes were occupied faster by rodents than those exposed to odour of predator (Table 2, Fig. 2c). Although nest boxes treated with lemon tended to be occupied earlier than those treated with predator odour, and later than control next boxes, differences were not significant as the 95% CL included 1 (Table 2).

Discussion

Chemical cues play a fundamental role in the assessment of predation risk in mammals, as they can trigger fear and avoidance responses in prey (Apfelbach et al. 2005; Kavaliers et al. 2005; Ferrero et al. 2011; Sharp et al. 2015), which may result in cascading ecological effects on communities (Brinkerhoff et al. 2005; Sunyer et al. 2013). Settlement patterns in the community were influenced by the olfactory landscape in an unexpected way. We found clear signs of aversion toward nest boxes with olfactory information, because species settled in more numbers and earlier in non-odorous control nest boxes than in risky and than in non-risky odour-treated nest boxes. Moreover, both birds and rodents occupied control nest boxes earlier than those exposed to a risky odour treatment. However, although there was a trend that nest boxes treated with predator odour were occupied less frequently and later than those treated with lemon essence, the patterns did not reach statistical significance. Several mutually non-exclusive explanations about the found settlement patterns are possible.

First, it could be argued that birds and rodents related the presence of lemon odour in the nest boxes to researcher activity and, thus, perceived that as a predator threat. Also, it could be that lemon scent was perceived as a repellent by rodents and birds rather than as a predation threat. Indeed, essential oils extracted from citrus can prevent the movement of mites between plants, and are potentially usable as mite repellent in the commercial greenhouse industry (da Camara et al. 2015). Also, the use of fungicides based on a Citrus terpene formulation has proved to induce aversion to rice by Blackbirds *Agelaius phoeniceus* (Werner et al. 2008). The use of lemon essence as a non-harmful odorous control may have induced undesirable aversion effects to our experiment. Ideally, an optimal control odour for our experiment would have been an odour resembling the ferret odour but without providing any information that would affect the focal species in our community in a positive or negative way.

Alternatively, it could be that the odour of ferret was not perceived as a true predation risk by species in our community. Experimental work has shown that some rodent species possess a finely tuned sense of smell and that they can recognize levels of predation in a graded way based on odour cues (Taraborelli et al. 2008). Accordingly, they would disregard odour cues on ferrets when settling, because they recognized that ferrets are not a major predation threat in cavities. Also, we cannot discard the alternative possibility that rodents in our community were not able to recognize predation risk

Table 2 Results of Cox proportional hazards models testing nest-box occupation order in relation to odour treatment and previous occupation by birds and rodents as fixed terms, and ID plot as a random term

Fixed effects	*df*	Wald Chi square	*p*	Level	Coefficient	SE		Hazard ratio	Lower 95% CL	Higher 95% CL
All species (54 occupied, 127 censored)										
Treatment	**2**	**15.10**	**0.0002**	Control	1.55	0.42	Control versus non-risky odour	**2.70**	**1.20**	**6.06**
				Non-risky odour	0.56	0.47	Control versus risky odour	**4.73**	**2.07**	**10.80**
				Risky odour	0	–	Non-risky odour versus risky odour	1.75	0.69	4.45
Bird presence	10.65	2.56	0.11		− 0.62	0.39				
Rodent presence	10.68	0.19	0.50		− 0.15	0.35				
Random effects	Wald Chi square	*P*	REML estimate	SE						
Plot ID	18.42	0.12	0.39	0.27						
Birds (29 occupied, 152 censored)										
Treatment	2	4.16	0.08	Control	1.11	0.55	Control versus non-risky odour	1.49	0.55	4.01
				Non-risky odour	0.72	0.59	Control versus risky odour	**3.06**	**1.04**	**8.95**
				Risky odour	0	–	Non-risky odour versus risky odour	2.05	0.64	6.53
Bird presence	10.70	0.009	0.92		− 0.05	0.56				
Rodent presence	10.72	0.14	0.70		− 0.17	0.46				
Random effects	Wald Chi square	*P*	REML estimate	SE						
Plot ID	11.87	0.24	0.47	0.44						
Rodents (28 occupied, 153 censored)										
Treatment	**2**	**5.34**	**0.03**	Control	1.37	0.63	Control versus non-risky odour	2.69	0.75	9.66
				Non-risky odour	0.38	0.72	Control versus risky odour	**3.93**	**1.14**	**13.53**
				Risky odour	0	–	Non-risky odour versus risky odour	1.46	0.35	6.05
Bird presence	10.57	1.10	0.16		− 0.63	0.60				
Rodent presence	10.62	0.42	0.34		− 0.36	0.55				
Random effects	Wald Chi square	*P*	REML estimate	SE						
Plot ID	32.60	0.008	1.18	0.65						

Reference category for the treatment effect was set to “risky odour”

Hazard ratio represents the change in odds of occupation of a nest box treated with a given treatment A divided by the odd of occupation of a nest box treated with a different treatment B. A hazard ratio > 1 indicates that nest boxes treated with a given treatment A are more likely to be occupied at any time than nest boxes treated with treatment B. Significant terms (i.e., $P < 0.05$) and hazard ratios (i.e., 95% confidence interval for the hazard ratio is above 1) are highlighted in bold. Non-significant effects were removed one by one starting with the less significant (i.e., high *P* value)

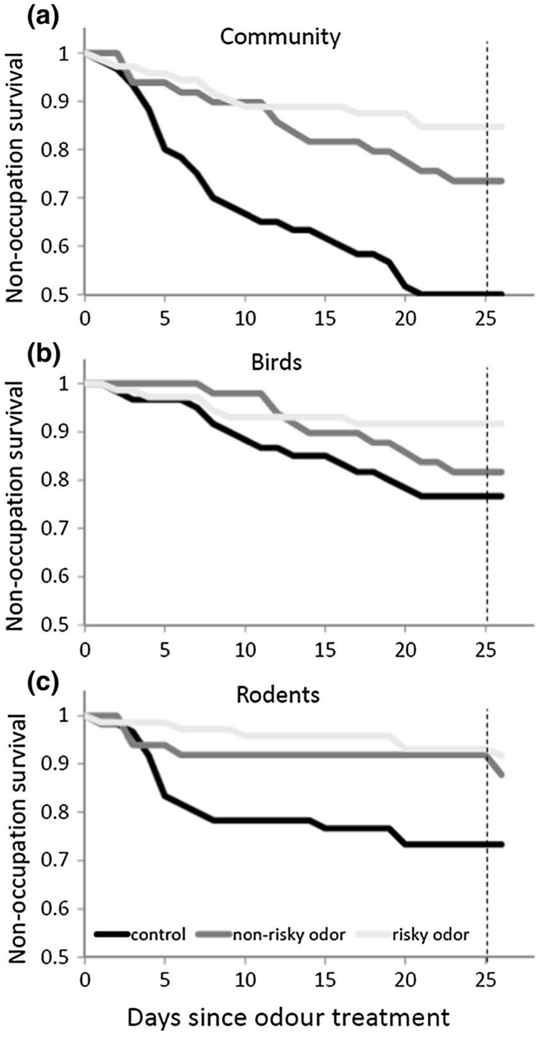

Fig. 2 Kaplan-Meier survival curves generated by Cox proportional hazard models predicting hazard of nest-box occupation by all cavity-dependent species in the community (**a**), birds (**b**) and rodents (**c**). Lines represent predicted probability of a nest box remaining unoccupied for varying levels of odour treatment. The dashed vertical line indicates the end of the experiment. Survival estimates are calculated without accounting for the random effect of plot ID

based on mammal odour cues, because they are very rarely exposed to mammalian predation in cavities. Previous studies have found that house mice *Mus domesticus* showed little discrimination between traps bearing faecal odours of the predators and traps bearing conspecific odours or no odour in areas without mammalian predators, whereas in areas with mammalian predators, mice avoided traps with smell of predators (Dickman 1992). This possibility, however, seems unlikely given that previous studies have consistently shown that ferret scent is recognized as a predation threat by birds (Amo et al. 2008, 2011) and that the found pattern of aversion in relation to odour cues for rodents paralleled that for birds. Future research on the use of olfactory cues on predation risk for habitat selection could focus on discriminating among these possibilities.

Finally, it could be argued that, provided lemon was an appropriate control, our experiment had low power to report differences in settlement patterns between odour treatments. Indeed, although not significantly different, risky odour-treated nest boxes were less occupied at the end of the experiment than those treated with lemon essence, and examination of hazard ratios showed that nest boxes treated with lemon were more likely occupied at any time than those treated with ferret odour. Only 11 (15.27%) out of 72 nest boxes treated with ferret odour were occupied at the end of experiment as compared to 13 (26.5%) out of 49 nest boxes treated with lemon (Fig. 1). Considering that our odour manipulation induced a small effect size (non-risky treated versus risky treated, effect size = 0.1123), and our sample size (i.e., $N = 121$ nest boxes), the power of our test was low (power 0.23). With that sample size, our experiment yielded a maximum detectable effect size of 0.27 for a high power of 0.8 (see Cohen 2013).

Our results cannot be explained by differences in habitat characteristics among plots, as these were matched by proximity before the randomization of treatments (see methods), and because we took into account environmental variability by including plot ID as a random intercept in the analyses. Moreover, we restricted our analyses to the time that treatments were applied, which increases the chance that odour signals were detected by prospecting animals. Finally, the number of available nest boxes per plot did not differ between treatments (see methods) and there were empty nest boxes in plots under all treatments during the time we assessed settlement (Fig. 1), which diminishes the possibility that differences in competition for nest boxes could account for the found patterns. Therefore, our findings provide empirical support for the view that odour cues may have ecological consequences altering composition and phenology in a Mediterranean cavity community composed of rodents and non-excavator hole-nesting birds.

Our study has some obvious weaknesses worth mentioning that may affect the strength of our conclusions. First, we cannot make an analysis based on single species due to the low number of individuals of each species (see Table 1 Appendix, Supplementary material). Different species may differ in their olfactory capabilities and in their assessment of predation risk based on ferret and lemon odour cues, so that some species may show zero response and thus decrease the overall effect size. Also, late breeders may avoid settling in plots not because of the odour per se but due to the absence of a cue species informing on habitat quality (Parejo et al. 2005; Seppanen et al. 2007). However, this possibility is unlikely because we disregarded occupied nest boxes after the end of the experiment, which reduced the possibility to copy the rejection of nest boxes by late breeders. In addition, the possible role of competition is minimized in our study, because we restricted our analyses to the time that treatments were applied and censored those nest boxes with signs of occupation at the start of the experiment. This ensures that mammals and birds had a surplus of available nest boxes. Moreover, we have corrected our analyses by the presence of birds and rodents in the plots before starting the experiment, and found that the number of used nest boxes before applying odours to plots did not differ between treatments, which precludes a possible influence of social cues on reported settlement patterns.

In conclusion, our study has shown that odour cues perceived at the time of choosing breeding territories may have effects on habitat settlement decisions in a Mediterranean cavity-dependent community composed of rodents and non-excavator hole-nesting birds. A large body of empirical work has previously demonstrated proactive responses to nest predators based on visual and acoustic cues informing on predator presence or density (Eggers et al. 2006; Fontaine and Martin 2006; Peluc et al. 2008; Monkkonen et al. 2009; Emmering and Schmidt 2011; Parejo and Aviles 2011; Parejo et al. 2018). Our findings reinforce the importance of olfactory cues in shaping this cavity-dependent community through the process of habitat selection. Our experiment, however, cannot pinpoint the exact mechanism promoting aversion to odour cues due to the difficulties in finding an appropriate non-risky odour control stimulus that works at the community level.

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Author contribution statement JMA and DP conceived, designed and coordinated the study. MEG participated in data analysis and in the design of the study and collected field data together with JMA and DP. JMA carried out the statistical analyses and drafted the manuscript. All authors gave final approval for publication.

Data availability All data used are included in dryad https://doi.org/10.5061/dryad.22rq4mm.

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