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RESEARCH

Effectiveness of attractants and bait for Iberian wolf detection: captivity-based and free-ranging trials

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Abstract

Monitoring large carnivores requires substantial effort, which is why indirect methodologies such as camera trapping with attractants or baits are commonly employed. The Iberian wolf (*Canis lupus signatus*) is one of the top predators in the Iberian Peninsula, and monitoring its packs is essential to understand its distribution and mitigate conflicts arising from livestock predation. We performed a captivity-based study evaluating the effectiveness of five attractants (beef extract, cadaverine, Fatty Acid Scent (FAS), lynx urine and valerian extract) on wolf detection. To accomplish this objective, Jacobs selectivity index and generalized linear models were employed to assess the attractiveness and induced behaviour of each attractant. Subsequently, the three most effective attractants, combined or not with a bait, were tested in the field and analyzed using generalized linear mixed models. The five attractants tested elicited different behavioural responses in the wolves in captivity, including smelling, rubbing, rolling, marking and licking. Among the captive wolves, cadaverine, FAS and lynx urine emerged as the top three preferred attractants. In the field tests with these three attractants cadaverine remained the most preferred option. The inclusion of bait did not have any significant effect on the wolf's visitation rates. Our results show that employing species-specific attractants can significantly improve the efficiency of carnivore surveys conducted in the field. Specifically, cadaverine was the most effective attractant for wild Iberian wolves. Consequently, the careful selection of an appropriate attractant becomes crucial to attain the precise objectives of the study, such as camera trapping, bait deployment or DNA sampling.

Keywords Behaviour · *Canis lupus signatus* · Carnivores · Detection · Lures · Wildlife management

Introduction

Large carnivores are scarce and most of them are endangered, which makes necessary to monitor their populations for assessing their conservation status (Woodroffe et al. 2007; Persson et al. 2015). Therefore, it is critical to estimate their distribution (Jędrzejewski et al. 2018), abundance (Wilson and Delahay 2001) and population trends (Ripple et al. 2014) to design effective conservation strategies. However, monitoring large carnivores can be difficult and expensive, given their tendency to inhabit large spatial areas and their nocturnal and elusive habits (Alibhai et al. 2017). Consequently, multiple monitoring methods are utilized. The most used are sign surveys (Barea-Azcón et al. 2007), camera trapping (Kelly et al. 2008), hunter surveys (Ausband et al. 2014) and records of roadkills (Santos et al. 2011). Among these methods, camera trapping is a non-invasive and prevalent technique used to study and monitoring carnivores (Trolliet et al. 2014).

Some attractants such as baits and lures are used to attract the target species in wildlife studies (Bischof et al. 2014; Thorn et al. 2009) based on methods such as camera trapping or genetic sampling (Steyer et al. 2013; Holinda et al. 2020; Avrin et al. 2021). Attractants for carnivores can be classified in three groups based on their characteristics: (i) natural attractants, which are naturally occurring in the environment with communicative function as faeces, gland secretions or urine; (ii) baits, typically consisting of food or its derivates, which are intended to be consumed

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and attract animals through smell or taste; and (iii) lures, which are substances that are not naturally present in the environment and attract animals through smell, sound or sight (Schlexer 2008). The use of these attractants improves the detectability, or even the selectivity of the target species (Steyer et al. 2013; Ferreras et al. 2018; Tobajas et al. 2022), increasing the cost-effectiveness of the surveys, especially in areas of expansion with low abundances (Ferreras et al. 2017; Buyaskas et al. 2020). This is especially relevant in cases such as large carnivore surveys, where the large home ranges imply high sampling and economic efforts. Thus, the use of effective attractants can help researchers and managers to improve surveys in large carnivore species. However, it must be considered that the use of attractants also has limitations since it can alter the results of distribution, abundance and behaviour of the animals (Holinda et al. 2020).

Our study focused on the Iberian wolf (*Canis lupus signatus*), a subspecies of the grey wolf (*Canis lupus*) endemic to the Iberian Peninsula. Its distribution reached a minimum in the 1980s, but after that, it gradually reoccupied some of its previously lost territories (Torres and Fonseca 2016). Before 2021, some wolf management practices were legally allowed in Spain north of the Duero river, including hunting with quotas and lethal control measures to mitigate livestock damages. However, in 2021, the species was designated as fully protected in Spain (RD 139/2011). Similarly, the species has been fully protected in Portugal since 2016 (Ley 90/88). The primary conservation challenges facing the Iberian wolf are retaliatory killings resulting from livestock predation, which represents the main cause of persecution (Torres et al. 2015; Miller et al. 2016). Therefore, after the full legal protection of the Iberian wolf, European legislation mandates the monitoring of wolf packs in various regions to determine its conservation status. Wolves commonly establish their packs over vast territories, with pack home range size in the northwest region of the Iberian Peninsula estimated to be between 120 and 320 km^2 (López-Bao et al. 2018; Dennehy et al. 2021). The wolf is an elusive species; thus, the use of attractants might improve the already used monitoring techniques. The most used methods for assessing wolf presence include acoustic localization (Papin et al. 2018), camera trapping (Galaverni et al. 2012) and sign surveys (Barja and Rosellini 2008). Attractants are frequently employed to enhance the effectiveness and efficiency of these methods to estimate wolf abundances (Ausband et al. 2022), densities (López-Bao et al. 2018), parentage (Godinho et al. 2011), genetic viability (Ramirez et al. 2006) and productivity (Mech 1977).

The effectiveness of various types of attractants for grey wolves has been evaluated, albeit with limited success as the number of visits is very low. Moreover, attractants have not been previously tested for Iberian wolves. Some of the most used wolf attractants are Long Distance Call, Government Call and Canine Call (O'Gorman Long Line Lures in Broadus, Montana), comprising a blend of skunk and musk scents (Ausband et al. 2011). However, these lures demonstrated low efficacy (Holinda et al. 2020). Two additional scent attractants tested were a lure derived from beaver (*Castor canadensis*), castoreum, and a lure derived from the anal scent gland of skunk (*Mephitis mephitis*) (Bischof et al. 2014). In the case of the Iberian wolves, several attractants have been assessed for their effectiveness, including Collarum Canine Bait (Wildlife Control Supplies, Connecticut), Fatty Acid Scent (FAS) (Roughton 1982), lynx urine, stone marten excrement, valerian solution and red fox (*Vulpes vulpes*) urine. Only the first three options were preferred by wolves (Monterroso et al. 2011), although it is worth noting that currently the Collarum Canine Bait cannot be imported to Europe. Captive testing allows to test attractants with the target species and to optimize the time they are available, as it ensures their presence (Monterroso et al. 2011).

The main objective of this study was to identify the most effective attractants (those generating more interest, more interactions and more time on it) for its application in the monitoring of Iberian wolves. To achieve this goal, various attractants were tested on captive Iberian wolves, and the most effective ones were further tested in the field with and without bait for wild Iberian wolves.

Captivity tests

Methods

The captivity tests were carried out in over a period of twenty days in February 2022 at Sendaviva zoological park located in Arguedas, province of Navarra, Northern Spain, where six wolves were kept in the same enclosure spanning approximately one hectare. We tested the following five attractants on the basis of previous studies with wolves and other carnivores: (1) a commercial concentrated beef extract (Bovril®; Roche 2008); (2) cadaverine, an own elaboration water solution of rotten fish (Avrin et al. 2021; Jiménez et al. 2023); (3) FAS containing a mixture of ten synthetic volatile fatty acids found in fermented egg (Roughton 1982; Monterroso et al. 2011; Tobajas et al. 2022) that is commonly used as a generalist carnivore attractant in North America (Roughton and Sweeny 1982); (4) lynx urine (obtained from captive specimens of Iberian lynx (*Lynx pardinus*), Monterroso et al. 2011; Tobajas et al. 2022); and (5) valerian-extract solution containing valeric acid found in urine and anal-sac secretions of coyote (*Canis latrans*) and red fox (Saunders and Harris 2000; Ferreras et al. 2018). The six Iberian wolves were adults (four females and two males) and they had access to the attractants 24 h a day, as they were in the same enclosure as the wolves, during the 20 days of experiment.

Six sampling points, five with a different attractant and one with water as a control, were strategically positioned within the enclosure, separated at least 3 m between them. In each sampling point, a drilled plastic tube (Ø = 0.01 m; depth = 0.08 m) containing a gauze soaked with 5 ml of the corresponding attractant was affixed vertically to a metal stake at a height of ~0.6 m above ground (Online Resource, Fig. S1). The tubes were weekly replenished with 5 ml of the same attractant. The behaviour of the animals was recorded with six no-glow camera traps (Spartan SR1-BK® HCO Outdoor Products, Norcross, Georgia, USA), positioned at a height of 0.8 m on a tree. The cameras were configured to record videos of 30 s duration and 1080p quality, with a 0 s trigger interval. Each camera aimed at a given sampling point. We coded the occurrence of different types of behaviour with each attractant: (1) smelling, the subject approached at a distance of 30 cm from the stake and smelled it with the nose at < 10 cm from the object); (2) rubbing, the subject rubbed its neck, head or snout against the stake with the attractant; (3) rolling, the subject approached at a distance of 30 cm from the stake, laid down and rolled on its back right next (< 10 cm) to the stake with the attractant; (4) licking, the subject licked the stake with the attractant; and (5) marking, the subject urinated on the stake with the attractant. Smelling could be related to curiosity (Monterroso et al. 2011). Rubbing and rolling are related to impregnating oneself with the scent, either for the purpose of smelling like prey or food for camouflage or for being more attractive to other individuals (Reiger 1979). Licking is related to appetite and marking for territory competition (Tebelmann and Gansloßer 2023). A given event could include different specific behaviours.

Statistical analyses

To systematically investigate, under controlled conditions, whether each attractant triggered varied types of interactions, behaviours, or total time interacting, we quantified the number of independent events per day wherein one or more behaviours occurred. For an event to be considered independent, a minimum interval of 20 min between successive occurrences was required. Each event was considered when an individual was at 30 cm or closer from the attractant and clearly interacted with it. A given event could include different specific behaviours: smelling, rubbing, rolling, marking or licking.

We calculated the number of total interactions as the sum of all specific behaviours that occurred at each event, and we calculated the time per event as the total sum of seconds that wolves spent on each attractant in any behaviour per event.

To determine the wolf preference for one attractant in detriment of the others we used the Ivlev selectivity index as modified by Jacobs (Jacobs 1974).

$$D = (r - p)/(r + p - 2rp)$$

where r is the observed proportion of events for each attractant and p is the expected proportional availability of each attractant (Lechowicz 1982; Monterroso et al. 2011). As we had 6 attractants and all had the same availability, p value was 1/6. The resulting D value of Jacobs selectivity index ranges from − 1 to + 1, according to the effectiveness of the attractant (Jacobs 1974). The standard error was calculated through bootstrapping with 500 resamples for each attractant, using the "bootstrap" package (Tibshirani and Leisch 2019) with the R software version 4.2.1 (R Core Team. R 2014) .

We performed generalized linear models (GLMs) to assess the preference for any of the six treatments used in this study (beef extract, cadaverine, control, FAS, lynx urine and valerian extract) according to the number of events, total number of interactions and total time spent interacting with each attractant. We fitted two GLMs with a Poisson distribution and log link, considering two response variables: the number of events and the total number of interactions (hereafter "total interactions"). Also, we fitted a third GLM with a normal distribution and log link, using the log-transformed total time (referred to as "total time") to satisfy assumptions of normality. In each model, the attractant was included as a factor.

When the coefficients of certain parameters of the GLMs resulted significant, we conducted post hoc Tukey's tests for assessing the differences between pairs of attractants for each response variable, using the "postHoc" package in R (Labouriau 2020).

Field tests

Study area

Field experiments were conducted in Sierra de la Demanda (La Rioja province, Northern Spain, 42.12480°N, 2.98557°W) (Fig. 1), located in the southwestern region of the northwestern Iberian mountain range. These mountains encompass a series of valleys characterized by gently sloping hillsides and narrow valley bottoms, interspersed by hills (Lasanta et al. 2022). The climate is Mediterranean with some Atlantic influence in the western valleys (Cuadrat and Vicente-Serrano 2008). The altitude exceeds 2000 m.a.s.l, with an average annual temperature of 11 °C and an average annual precipitation of 1203 mm (Cuadrat and Vicente-Serrano

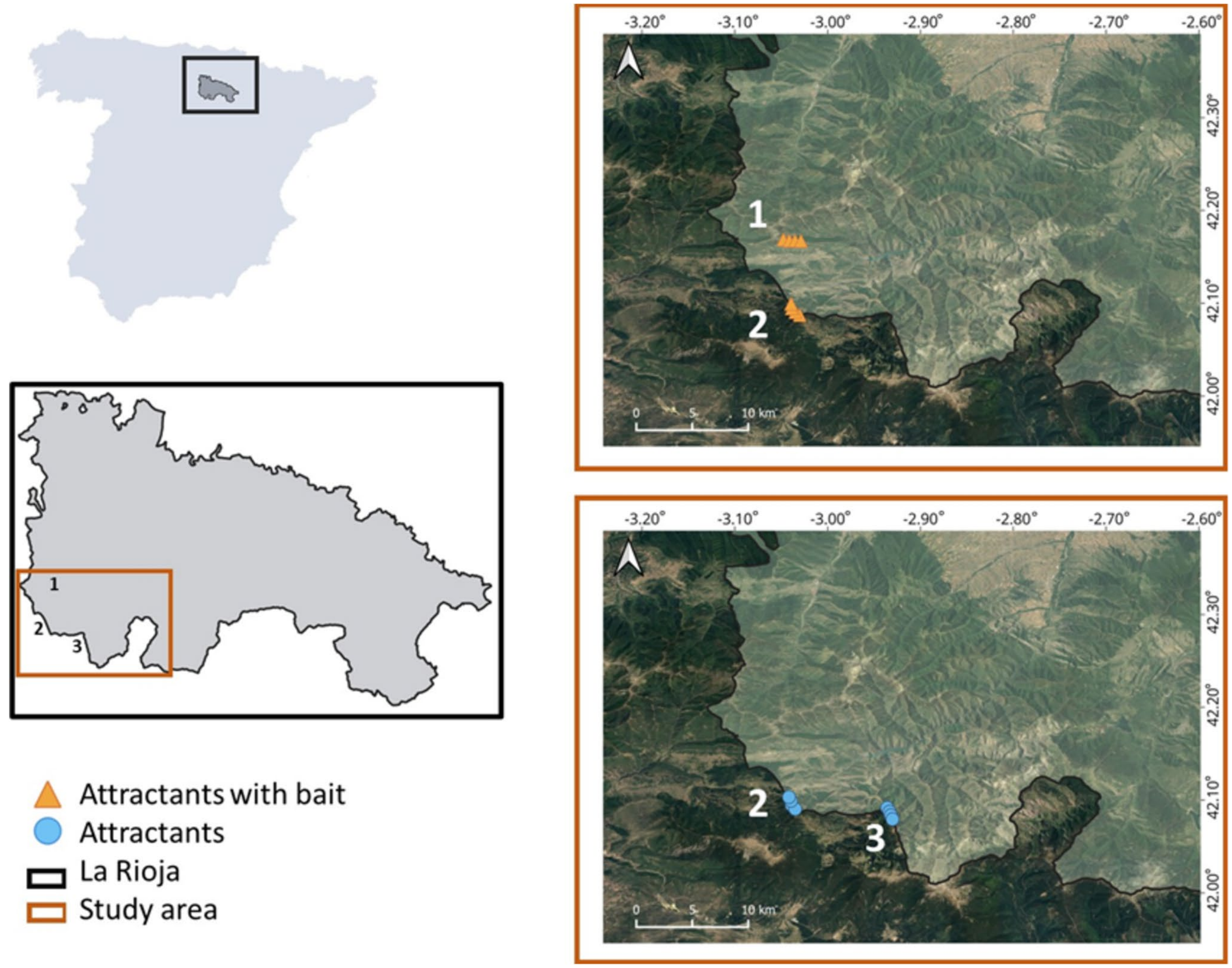

Fig. 1 Study area of field tests showing the location of the sampling zones in the ranges of three different wolf packs (numbers) in Sierra de la Demanda, La Rioja province, Spain (from 17/06/2022 to 06/12/2022)

2008). The vegetation in the area predominantly consists of forests, primarily composed of oak species (*Quercus pyrenaica* and *Q. faginea*), beech (*Fagus sylvatica*) and Scots pine (*Pinus sylvestris*). Shrubs such as *Calluna vulgaris*, *Cytisus scoparius* and *Genista scorpius* are also present (Fernández-Aldana 2015). The animal community in this region comprises extensive livestock and various wild ungulates such as red deer (*Cervus elaphus*), wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*). Carnivore species include red foxes, stone martens (*Martes foina*), Eurasian badgers (*Meles meles*), Eurasian otters (*Lutra lutra*) and Iberian wolves. The recolonization of this area by the Iberian wolves occurred over the past few decades.

Methods

Field experiments were conducted from June to December 2022. We simultaneously tested those attractants most frequently selected by wolves in captivity (see results). In a first phase over a period of 125 days from June to October 2022, we placed in four sampling points a sheep leg bait combined with the three selected attractants and one with water as a control. The objective of incorporating bait was to assess whether it could attract wolves more effectively than attractants alone, in a synergistic effect. Moreover, we aimed to investigate whether the utilization of attractants could optimize the consumption of bait by Iberian wolves, with a view towards its potential application in studies involving conditioned food aversion (Tobajas et al. 2020). The sampling points were in the forest with a minimum separation distance of 500 m between them and at least 40 m away from the trails. We employed two sampling zones separated 9 km as spatial replicates (blocks) (Fig. 1), corresponding to the ranges of two identified wolf packs. At each sampling point, 5 ml of the assigned attractant (or water as control) was spilled onto a stone close to a sheep leg bait that was secured to a tree using a piece of string. A camera trap with the same configuration and distance as described in the captivity tests (see above) was placed in front of each sampling point. The attractants were restocked (5 ml) every 10 days, and the treatments (attractant or control) were rotated within a block every 30 days to account for any potential positional effect. Therefore, all attractants were tested in each sampling point. The bait was covered with rocks or logs to prevent other animals such as foxes or martens with less strength from taking it. The bait was replaced with a fresh bait every 10 days and the old bait was removed.

In the second phase, we tested the three attractants and control without bait. We employed two spatial replicates (blocks) separated by 8 km, corresponding to the ranges of two identified wolf packs. One of these areas was common to the first phase for attractants with bait while the other was a new one (Fig. 1). We used the same methodology as in the first phase, the same cameras and configuration. The camera traps were attached to a tree in front of another tree with the attractant. The treatment positions were rotated and restocked with 5 ml of attractant (or water for control) every 7 days (Online Resource, Fig. S1). Therefore, all attractants were in the four sampling points. The test was conducted for 28 days, from November to December 2022.

Statistical analyses

For each attractant, a relative abundance/activity index (RAI) was calculated as the number of positive days divided by the total camera sampling effort (total days), multiplied by 100 (Azlan and Sharma 2006). A day was considered positive for a given treatment when wolves were detected at least once from midnight to midnight. The sampling unit was the day in each sampling point in the study area ($n=8$). The sampling effort was determined by summing the number of days each camera was operational during the study. We used the RAI as a descriptive measure of the frequency of wolf visits to each attractant relative to the available time (Sollmann et al. 2013).

Then, we used Generalized Linear Mixed Models (GLMMs) with binomial distribution and logit link using "lme4" package (Bates et al. 2015) to relate the use of bait and attractant to wolf presence in each day. The response variable was the daily wolf presence, codified as present (1) or absent (0), with treatment (cadaverine, control, FAS and lynx urine), bait (present or absent) and their interaction as fixed effects, and the sampling point nested within the sampling zone as random effect. To determine the best explanatory models, we compared the models using the Akaike Information Criterion (AIC), following an information theoretical approach (Burnham and Anderson 2004). Delta AIC (ΔAIC) values were calculated to determine the strength of evidence of each model. This approach allows the most parsimonious model (lowest AIC) to be identified and ranks the remaining models. We considered models with $\Delta AIC < 2$ to have similar support (Burnham and Anderson 2004). We evaluated the GLMM model performance using the AIC comparison with the null model. Finally, we performed pairwise comparisons between attractants using Tukey's test with "postHoc" package (Labouriau 2020). Also, we calculated the daily encounter probability with the antilogit function from logit (ψ) of the selected GLMM, where Ψ is the probability of wolf detection in the camera.

Results

Captivity tests

Cadaverine exhibited the highest number of wolf events ($n=39$) among the attractants tested in captivity, followed by lynx urine ($n=30$) and FAS ($n=22$). Valerian and beef extract had the lowest numbers of events among the attractants, with only 10 and 12 observed events, respectively. Control elicited the fewest events overall ($n=8$). The most frequently observed behaviour was smelling ($n=121$), followed by rubbing ($n=47$), rolling ($n=43$) and marking ($n=7$). Licking behaviour ($n=6$) was only observed in response to the food taste attractants, beef extract and FAS. In control, only smelling behaviour was observed (Fig. 2).

The attractants that elicited the longest durations of wolf interaction were cadaverine (3107 s), FAS (1546 s) and lynx urine (1037 s) (Online Resource, Table S1). Beef extract was the attractant which elicited the shorter interaction time (306 s), preceded by valerian (416 s) (Online Resource, Table S1). Control was the treatment with the shortest interaction time (124 s; Online Resource, Table S1).

The three attractants that were chosen above their availability, based on Jacobs index (D), were cadaverine ($D=+0.40$), lynx urine ($D=+0.24$) and FAS ($D=+0.05$) (Fig. 3). The remaining two attractants and the control treatment were used below their availability: beef extract ($D = -0.28$) and valerian ($D = -0.37$) (Fig. 3), as well as the control treatment ($D = -0.47$).

Cadaverine ($Z=4.08$; $p<0.001$), FAS ($Z=2.45$; $p=0.014$) and lynx urine ($Z=3.19$; $p=0.001$) were the most preferred attractants according to generalized linear models (GLMs) for number of events. Beef extract and valerian extract did not show significant differences in the number of

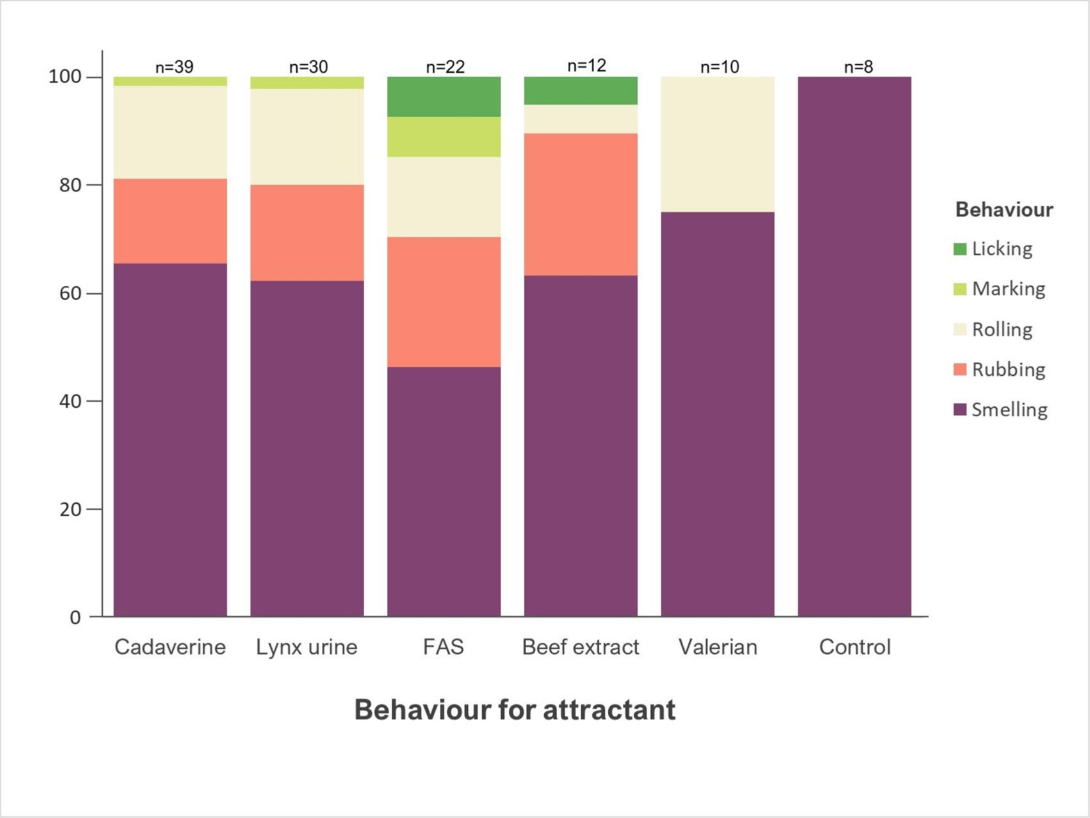

Fig. 2 Percentage of events corresponding to each behaviour in each attractant: smelling, rubbing, rolling, marking and licking, and the total number of events (n) observed in each attractant, during the captivity test by wolves in Sendaviva zoological park, province of Navarra, Spain (from 04/02/2022 to 23/02/2022)

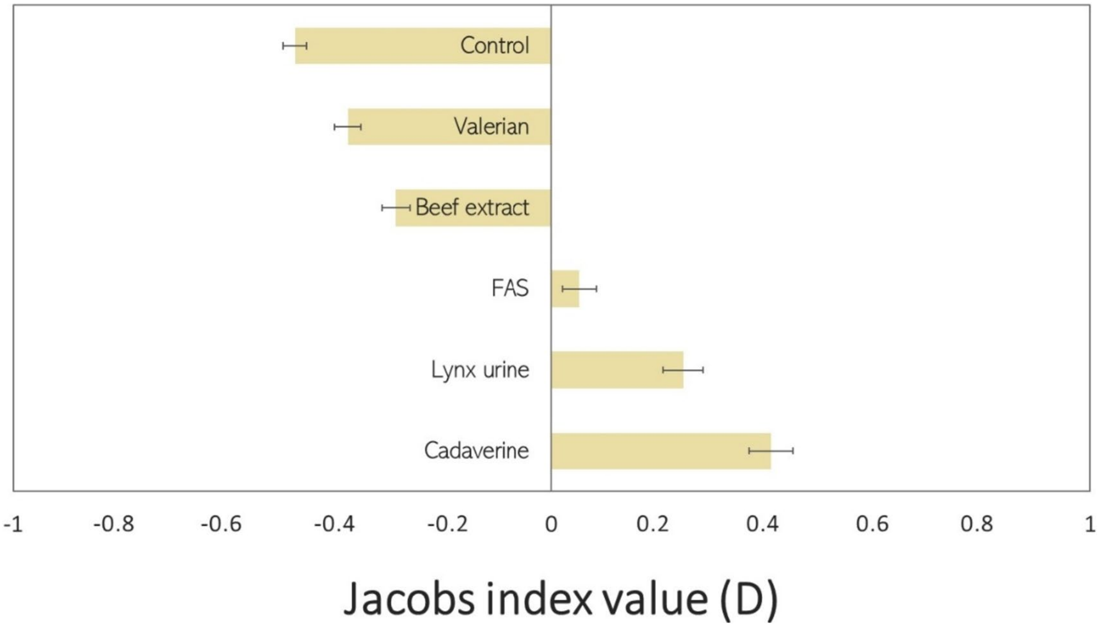

Fig. 3 Mean Jacobs selectivity index value (*D*) and standard error for each of the tested attractants during the captivity tests with wolves in Sendaviva zoological park, province of Navarra, Spain (from 04/02/2022 to 23/02/2022)

Table 1 Results of generalized linear models for number of events, total number of interactions and total time by wolves in captivity test in Sendaviva zoological park, province of Navarra, Spain (from 04/02/2022 to 23/02/2022). The relationships between attractant and the response variables are shown. The estimates of the coefficients for each parameter (the intercept includes control), their standard errors (SE), *Z* value and *p* value are shown. Bold font shows attractants with *p*-value < 0.05

Response variable	Model	Parameter	Estimate ± SE	*Z* value	*p* value
Number of events	Attractant	Intercept	−0.91 ± 0.35	−2.59	0.009
		Beef extract	0.35 ± 0.45	0.78	0.434
		Cadaverine	**1.58 ± 0.38**	**4.08**	**< 0.001**
		FAS[a]	**1.01 ± 0.41**	**2.45**	**0.014**
		Lynx urine	**1.27 ± 0.39**	**3.19**	**0.001**
		Valerian	0.22 ± 0.47	0.47	0.63
Total interactions	Attractant	Intercept	−0.91 ± 0.35	−2.59	0.009
		Beef extract	0.81 ± 0.42	1.93	0.052
		Cadaverine	**2.30 ± 0.37**	**6.21**	**< 0.001**
		FAS[a]	**1.96 ± 0.37**	**5.20**	**< 0.001**
		Lynx urine	**1.72 ± 0.38**	**4.50**	**< 0.001**
		Valerian	0.48 ± 0.48	1.08	0.27
Total time	Attractant	Intercept	1.11 ± 0.19	5.59	< 0.001
		Beef extract	0.34 ± 0.27	1.25	0.21
		Cadaverine	**0.79 ± 0.24**	**3.27**	**0.001**
		FAS[a]	**0.64 ± 0.25**	**2.55**	**0.013**
		Lynx urine	**0.55 ± 0.23**	**2.35**	**0.021**
		Valerian	0.37 ± 0.27	1.36	0.17

[a] Fatty Acid Scent

events compared to the intercept, which includes the control treatment (Table 1). Post hoc tests showed that cadaverine ($p < 0.001$) and lynx urine ($p < 0.016$) significantly elicited a greater number of events than the control (Online Resource, Table S2).

The selected GLM for the number of interactions revealed that cadaverine ($Z = 6.21$; $p < 0.001$), FAS ($Z = 5.20$; $p < 0.001$) and lynx urine ($Z = 4.50$; $p < 0.001$) significantly increased the number of interactions (Table 1). Post hoc tests showed that cadaverine ($p < 0.001$), lynx urine ($p < 0.001$) and FAS ($p < 0.001$) significantly elicited more interactions than the control (Online Resource, Table S2).

Three attractants were found to increase the total time based on significant coefficients in GLMs (Table 1): cadaverine ($Z = 3.27$; $p = 0.001$), FAS ($Z = 2.55$; $p = 0.013$) and lynx urine ($Z = 2.35$; $p = 0.021$). Post hoc tests indicated that only cadaverine ($p = 0.013$) significantly elicited more total time compared to the control (Online Resource, Table S2).

Field tests

The three most preferred attractants in captivity tests according to Jacobs index (cadaverine, lynx urine and FAS, Fig. 3) were used for the field tests (Online Resource, Table S3). Cadaverine showed the highest relative activity index (RAI) in field tests, regardless of the presence of bait (RAI with bait = 2.07; RAI without bait = 5.36) (Fig. 4). Non-baited cameras with FAS and lynx urine had the same RAI (RAI = 1.79), but baited cameras with lynx urine were more frequently visited (RAI = 2.00) than cameras with FAS (RAI = 1.79) (Fig. 4). Control with bait (RAI = 0.83) was slightly more visited than baited FAS (RAI = 0.8) (Fig. 4). Control without bait had no visits (RAI = 0.00). Cadaverine was also the attractant with the longest wolf interactions (Online Resource, Table S4). Results by wolf packs are shown in Table S4 (Online Resource, Table S4).

The best supported GLMM for the daily wolf detection included the attractant as fixed explicative variable and the sampling point nested within the sampling area as random factors (Table 2; Online Resource, Table S5). The GLMMs that included bait and the interaction between bait and attractant had a higher AIC and therefore lower support (Table 2).

The selected model showed a good performance, according to the difference AIC (= 9.98) with the null model (Table 2). According to the selected model (Table 3), only cadaverine had a significant effect on wolf detection (2.85 ± 1.05 - Estimate ± SE, $Z = 2.7$; $p = 0.006$). The post hoc tests indicate that cadaverine significantly increased the wolf detection compared to control ($Z = 2.70$; $p = 0.03$), whereas the effect of FAS and lynx urine did not significantly differ from the control (Online Resource, Table S6). Cadaverine ($\psi = 0.025$), FAS ($\psi = 0.005$) and lynx urine ($\psi = 0.008$) produced higher daily detection probability than control ($\psi = 0.001$) (Table 3).

Discussion

In the captive trials, three attractants (cadaverine, lynx urine and FAS) resulted more selected by wolves than the control. Subsequently, these attractants were chosen to be

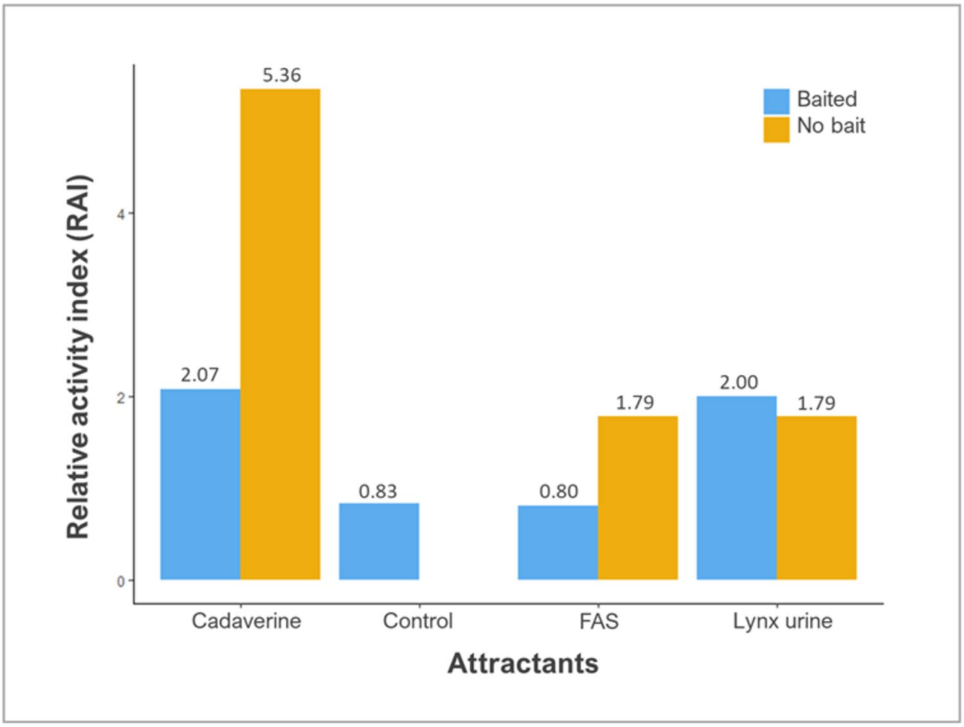

Fig. 4 Relative activity index ((positive days/available days) × 100) of attractants with and without bait in field tests in Sierra de la Demanda, La Rioja, Spain (from 17/06/2022 to 06/12/2022)

Table 2 Generalized linear mixed models for daily detection probability of wolf in field tests in Sierra de la Demanda, La Rioja, Spain (from 17/06/2022 to 06/12/2022). Wolf detection was the response variable and attractant, bait and their interaction were factors. Sampling point was included in the models as a random effect, nested within sampling area. The AIC and ΔAIC values are shown. The selected model according to AIC is shown in bold

Model	AIC[a]	ΔAIC[b]
Attractant + sampling point/sampling area	**185.02**	**0.00**
Attractant + bait + sampling point/sampling area	187.11	2.09
Attractant + bait + attractant*bait + sampling point /sampling area	190.35	5.33
Sampling point/sampling area	195.00	9.98
Bait + sampling point/sampling area	196.71	11.69

[a] Akaike information criterion

[b] Delta Akaike information criterion

tested in the field. The results of the field tests revealed that cadaverine was the most effective attractant for the wolves, significantly increasing their daily visits. Notably, the use of bait had no positive effect on attracting wolves. Unfortunately, we were not able to identify individuals in the tests as including them in the analyses would allow to detect possible individual bias or preference.

Table 3 Results of the selected generalized linear mixed model for the daily detection probability of wolf (logit-transformed) in field tests in Sierra de la Demanda, La Rioja, Spain (from 17/06/2022 to 06/12/2022). Sampling point nested within sampling area was included in the model as a random effect. The estimate of the coefficient for each parameter (the intercept includes control), their standard error (SE), *Z* values and *p* values are shown. The attractants with significant effect are shown in bold

Model	Parameter	Estimate ± SE	Z value	*p* value
Attractant + sampling point/sampling area	Intercept	−6.50 ± 1.15	−5.64	< 0.001
	Cadaverine	**2.85 ± 1.05**	**2.7**	**0.006**
	FAS[a]	1.39 ± 1.16	1.19	0.23
	Lynx urine	1.73 ± 1.19	1.45	0.14

[a] Fatty Acid Scent

Captivity vs. field tests

By testing the attractants in captivity prior to field testing, we were able to optimize the study and only evaluate those attractants that were likely most preferred also by wild wolves in their natural environment (Fig. 4). The conditions in captivity are more controlled, and the presence of wolves is guaranteed, allowing preliminary tests to be performed in a short time. However, the short distance between lures due to the small size of the enclosure in the captivity experiment may be a limitation. The tests in captivity allowed us to discard ineffective attractants, to which wolves devoted little time and did not perform any specific behaviour. During captivity tests, we observed various behaviours towards the attractants, including smelling, rubbing, rolling, marking and licking (Fig. 2). In contrast, we obtained scarce information on the behaviour of free-ranging wolves which could not be compared with that of captive wolves. However, based on the literature, one would expect a greater distrust of wolves in the wild due to greater neophobia (Calisi and Bentley 2009).

Effective attractants

Cadaverine proved to be the most effective attractant, both in captivity and in the field (Tables 1 and 3, Online Resource, Figs. S2 and S3). In the field test, it elicited the highest number of events (Fig. 4). Being a food-related attractant, its odour could be associated by wolves with food acquisition (Izquierdo et al. 2018; Avrin et al. 2021). On the other hand, lynx urine was effective, both in captivity and in the field. It is a natural attractant that can be found in the environment. Although these large carnivores do not currently coexist in the wild in the Iberian Peninsula, they have historically coexisted. In other parts of Europe, the grey wolf and the Eurasian lynx (*Lynx lynx*) coexist with no evidence of competition (Schmidt et al. 2009). However, an exploitative competition between wolves and cougars (*Puma concolor*) has been reported in Yellowstone, where wolves are coursing predators and cougars are ambush predators (Bartnick et al. 2013). The effectiveness of lynx urine to attract wolves may be due to the curiosity about the presence of another top predator (Monterroso et al. 2011) or to territory defence, as in captivity wolves also marked the stakes containing this attractant (Fig. 2). FAS was also effective, both in captivity (Fig. 3) and in the field (Fig. 4). Our data show that FAS, a food-related attractant, was licked by the wolves (Fig. 2). Other authors recommend this attractant for canids and specifically for wolves (Roughton 1982; Monterroso et al. 2011).

In captivity tests, the wolves exhibited various behaviours such as smelling, rubbing, rolling, marking and licking over the attractants (Fig. 2). Smelling is a research behaviour resulting from the curiosity generated by attractants, lures and baits (Monterroso et al. 2011). In fact, wolves displayed this behaviour in all events with all attractants (Fig. 2). Unlike in the captivity tests, wolves did not rub, lick, or mark in the field tests, likely because they were wary of the camera or new odours. However, an exception was observed with cadaverine, which caused the wolves to rub against the tree containing this attractant (Online Resource, Figs. S2 and S3), a common behaviour in canids and other carnivores (Fox 1971). It has been suggested that this behaviour serves as an odour camouflage, enabling carnivores to conceal their own body odour (Reiger 1979). Furthermore, this allows them to approach potential prey closely without being detected. Additionally, social behaviours may also contribute to this phenomenon as a way of attracting other individuals with this new scent, thus increasing social investigation (Drea et al. 2002).

Other studies suggest that valerian extract is a suitable attractant for some Iberian mesocarnivores, including red fox, common genet (*Genetta genetta*), Eurasian badger, stone marten and Egyptian mongoose (*Herpestes ichneumon*) (Ferreras et al. 2018; Grajera et al. 2021). However, our data suggest that valerian extract was ineffective in attracting wolves (Fig. 2; Table 1). Beef extract caused wolves to lick the tube with the attractant in the captivity tests (Fig. 3), possibly due to their food-related odour (Roche 2008). Nevertheless, this attractant was the second least effective among all those tested for wolves in captivity (Fig. 2; Table 1). Therefore, due to the low results obtained in captivity, valerian extract and beef extract were not employed in the field tests and not recommended for wolf monitoring.

Utility of attractants

The attractants tested in this study induced different behaviours in wolves, which can serve different purposes depending on the study objectives. Attractants that induce smelling behaviour (all tested) can be used for studies aiming to detect wolf presence, such as those based on camera trapping (Bischof et al. 2014). Attractants that induced rubbing and rolling behaviour (cadaverine, FAS and lynx urine) can be used in DNA sampling studies, because they facilitate hair or dermal sample collection (Steyer et al. 2013) (Online Resource, Table S1). In our study, cadaverine, FAS and lynx urine stood out as positive inducers for all these behaviours (Online Resource, Table S1). The rubbing behaviour elicited by cadaverine has recently proved as highly useful in spatially explicit capture-recapture models to estimate wolf density (Jiménez et al. 2023). Attractants that elicited more licking events (FAS and beef extract) would be recommended for bait administration, such as vaccination programs (Knobel et al. 2002, Gräßer et al. 2019), or for non-invasive collection of biological samples such as saliva (Lobo et al. 2015). However, attractants have some limitations which should be considered depending on the study objective (Holinda et al. 2020).

Combination of bait and attractant

Contrary to our expectations, using bait did not improve the attractants effectiveness since they were effective regardless of the presence of bait (Fig. 4; Table 2). Even though, some events were obtained using only bait without any attractant (Fig. 4). Our results suggest that attractants can be more effective than bait for wolves, in contrast with the results of studies with other carnivore species (Ferreras et al. 2018). However, in this study, attractants with bait were used at the end of the breeding period, when pups begin to emerge from the dens (Rio-Maior et al. 2018), while attractants without bait were tested when pups already travelled with the packs, possibly leading to more interactions with attractants. Regardless of the presence of bait, cadaverine was the most effective attractant (Fig. 4; Table 3).

Management implications

Our study provides evidence of the usefulness of attractants in monitoring studies involving large carnivores (Mills et al. 2019; Holinda et al. 2020). Cadaverine, lynx urine and FAS, increased the number of encounters of the target species, with potential applications to diverse objectives such as live captures (Gerber et al. 2012), bait administration (Delahay et al. 2000; Knobel et al. 2002; Tobajas et al. 2020), abundance estimation (Jiménez et al. 2023) or non-invasive collection of biological samples (Lobo et al. 2015). Among the observed behaviours of wolves towards the used attractants, smelling, rubbing and rolling were predominant, while marking and licking were rarely observed. Our results suggest that using cadaverine as an attractant in non-invasive sampling would increase detection probability of Iberian wolves. Other attractants such as valerian extract used for mesocarnivores in the Iberian Peninsula were not effective for the Iberian wolf (Monterroso et al. 2011). This knowledge can serve as a valuable tool in studies where enhancing wolf detection can improve the cost-effectiveness of monitoring methods, such as hair sampling studies (Torres et al. 2017).

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Author contributions Designed the methodology and aims of the study: LDR, JAZ, RM, PF and JT. Collected the data: LDR and JAZ. Analyzed the data: LDR, RM, PF and JT. Writing of the manuscript: LDR, JAZ, RM, PF and JT. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The data will be provided upon reasonable request to the corresponding author.

Declarations

Ethical approval The tests with captive and free-ranging wolves followed the current guidelines for the ethical use of animals in research and were approved by the Animal Experiment Committee of Castilla-La Mancha University (PR-2023-10), and were authorized by the Government of La Rioja, where the field tests were carried out.

Competing interests The authors declare no competing interests.

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