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Vegetarian vs. Carnivore Feeding Enrichment in a Pack of Captive Iberian Wolves (*Canis lupus signatus*): Towards Individual and Species-Typical Needs

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The aim of this study was to compare two different types of feeding enrichment (vegetarian vs. carnivore) through the daily activity patterns, space use, and inter-individual distances in a captive Iberian wolf (*Canis lupus signatus*) pack housed at the Barcelona Zoo. Multifocal sampling methods were used for data collection and instantaneous scans were made at 15-min intervals during sessions of varying duration. The enrichment sessions were carried out once a day, three days per week—Monday, Wednesday, and Friday—repeating the delivered schedule of items every two weeks. Thus, both feeding phases included six different enrichment sessions; the vegetarian phase included chopped fruit—apples inside a burlap sack, scattered bananas, peaches, frozen pears, and oranges, along with kiwis inside a frozen water block; the carnivore phase included animal products—beef raw lean meat inside a burlap sack or inside a frozen water block, horse leg, live carp, frozen rabbit skin, and live grasshoppers. There were individual differences in the responses to both feeding enrichments. Only the carnivore enrichment provoked statistically significant differences in exploration, locomotion, inactivity, and out of visual range. Only the indeterminate zone showed changes during both enrichment phases. The inter-individual distance between Iberian wolves was significantly lower during both feeding enrichment phases—especially during the carnivore as compared to the vegetarian phase—than during the baseline phase. Enrichment items designed more according to the natural history of these animals seem to have a greater capacity to improve the wolf welfare. Future studies on this species are necessary to improve husbandry techniques, welfare, and conservation programs.

Keywords: animal welfare, daily activity patterns, environmental enrichment evaluation, Iberian wolf, inter-individual distance, space use

The Iberian wolf (*Canis lupus signatus*, Linnaeus 1758, Canidae, Carnivora) is an endemic subspecies of the gray wolf, which inhabits the forests and plains of northern Portugal and north-western Spain. Wolves are social animals, and they live in a hierarchical pack: a dominant alpha breeding pair, accompanied by the pups of the year, and young wolves from previous litters that cooperate in hunting and caring for the young. Their survival and success as predators depend on their organization in packs—from 5 to 10 members—that occupy territories from 100 to 500 km^2. The 2012-2014 census by Ministerio de Agricultura, Alimentación y Medio Ambiente from Spain, estimated the total Iberian population to be 297 packs, which is more than the 2007 census estimation of 250 packs (Blanco & Cortés, 2002; Grande del Brío, 2000; Sáez de Buruaga, 2018). In 2018, the International Union for Conservation of Nature's (IUCN) Red List Species categorized the Iberian wolf as Least Concern (LC), whereas the Red Book of Vertebrates in Spain categorized this species as Vulnerable (VU) (Iglesias et al., 2017).

The Iberian wolf is an opportunistic carnivore predator. The diet composition of this species is 35% wild-born herbivores (wild boars, deer, roe deer, fallow deer, and mouflons), 24% domestic ungulates (goats, horses, cows, and sheep), 14% rabbits and hares, 9% wood mice, 7% carrion, 5% reptiles and birds, 4% insects, grains, and wild fruits (blueberries, strawberries, blackberries, and figs), and 2% other carnivores (foxes and dogs) (Rodríguez de la Fuente, 1978).

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In terms of animal welfare, Iberian wolves are exceedingly difficult to maintain properly in captivity for different reasons: hierarchical social pack management, enclosure with an appropriate size to allow territorial patrolling as well as diet composition considering wolves' predatory nature. Captive Iberian wolves could be potentially used in reintroduction programs for the conservation of the species; however, it is necessary to not only fulfill their physical and psychological necessities as a species but to also consider the individual temperaments (Maple & Perdue, 2015). The concept that animals possess individual temperament is gaining traction among the scientific community (Watters & Powell, 2012). This has occurred slowly and it is most often only informally considered, thus, it is necessary to develop techniques that reliably assess animal temperament and provide measures that can easily be used in population planning models in order to improve animal welfare, conservation programs, and zoo guest experiences (Watters & Powell, 2012).

One of the techniques used to improve animal welfare is environmental enrichment through the potentiation of species-typical behavior taking into consideration the life-history of the species and the individual preferences (Young, 2003). Thus, feeding enrichment in canids tries to alleviate the restriction of a wide-range of behavior such as hunting, foraging, and territorial patrolling (Clubb & Mason, 2007). This kind of enrichment is designed to provide animals with an opportunity to use natural foraging strategies to obtain food in captivity (Shepherdson et al., 1993).

There is only one article so far that tests the use of enrichment on captive Iberian wolves, which determined the effect of the death of the dominant male in a captive pack of wolves on the daily activity patterns and space use (Soriano et al., 2006a). A wide range of enrichment strategies needs to be investigated in order to assess which are the most effective for providing more stimulating enrichment.

In canids, environmental enrichment has been studied from different perspectives. Two studies investigated the effect of feeding enrichment on the behavior of Coyotes (*C. latrans*), where the food was delivered at random times and locations (Gilbert-Norton et al., 2009), and Bush dogs (*Speothos venaticus*), where the food was hidden in woodpiles and other appropriate places (Ings et al., 1997). Another study on wolves (*C. lupus*) investigated the preferences of these animals for training or environmental enrichment (tires and Boomer Balls®) (Dorey et al., 2015). There is also a study that evaluated the effect of five enrichment treatments (Boomer Balls®, various scents, a sandpit with hidden food, a blood trail leading to rawhide items/pig's ears, and all the foraging items simultaneously) on the behavior of captive African painted dogs (*Lycaon pictus*; Price, 2010).

Most studies on canids have also studied the effectiveness of different environmental enrichments by associating stress indicators (cortisol levels) with expressed behaviors such as an olfactory enrichment (fecal odor cues from natural competitors and natural/unnatural prey species) in African painted dogs (Rafacz & Santymire, 2014; Rafacz et al., 2016), the effects of zoo visitors in Mexican wolves (*C. lupus baileyi*; Pifarré et al., 2012), and different enrichment treatments in maned wolves (*Chrysocyon brachyurus*): (a) food hiding and Boomer Ball® (Cummings et al., 2007), (b) foraging for interspecific and intraspecific items (Coelho et al., 2012, 2016), and (c) food scattering, edible toy, and a combination of both (Vasconcellos et al., 2009).

The aim of this study was to compare two different types of feeding enrichment treatments (vegetarian vs. carnivore) through the daily activity patterns, space use, and inter-individual distances in a captive Iberian wolf pack in order to determine their effects on individual and species-typical characteristics. It would be expected that the carnivore enrichment would provoke more changes in the tested variables than the vegetarian enrichment. This is due to the fact that the Iberian wolves' diet is approximately 96% of animal origin with more species-typical behaviors related to predation than to harvest.

Method

Subjects and Housing

The study subjects were three captive Iberian wolves housed at the Barcelona Zoo (Table 1).

Table 1

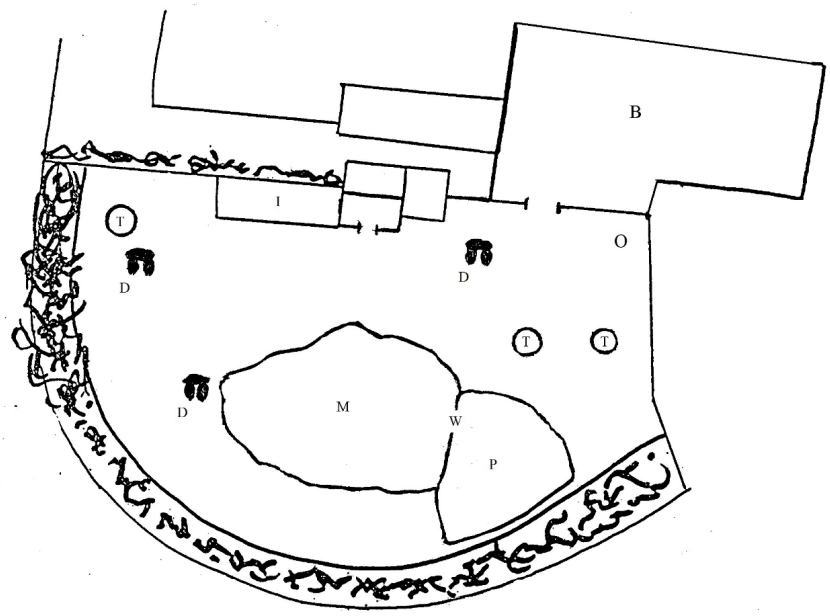
Demographic Data for Iberian Wolves

Age class and sex	Birth date	Born	Rearing condition	Arrival date at zoo
Adult female	May 1996	In captivity	Parent	October 1996
Male	May 1995	In captivity	Hand	January 1999
Young female	May 1999	In captivity	Parent	May 1999

During the observations, the Iberian wolves were housed in a 940 m^2 naturalized outdoor enclosure surrounded by a metallic fence with vegetation (see Figure 1). The outdoor enclosure contains typical Mediterranean vegetation, three dolmens made of three big stones, a waterfall that feeds into a pond, and different enrichment devices such as metallic boxes, an L-shaped metallic structure for hiding food, and a mechanical rabbit for chasing. In the middle of the outdoor enclosure there is a mound measuring 2 m in height and 5 m in length. The indoor enclosure contains three cement cages out of sight from the public (7 m^2 each) and the breeding enclosure (300 m^2) which is a prolongation of the outdoor enclosure separated by a metallic fence and a door (Soriano et al., 2006a, 2021a).

Figure 1

Diagram of the Iberian wolves' Enclosure



Note. B = breeding enclosure; D = dolmen; I = indoor enclosure; M = mound; O = outdoor enclosure; P = pond; T = tree; W = waterfall.

Daily Management

The management protocol allowed the Iberian wolves to go into their indoor enclosures voluntarily for the duration of the evening and the morning, which varied with the season (from 5:00 p.m. to 9:00 a.m. in November and December; from 6:00 p.m. to 9:00 a.m. in March and October; and from 7:00 p.m. to 9:00 a.m. from April to September).

The Iberian wolves' diet was seasonally unvaried and delivered twice daily. In the morning, each wolf ate 1 kg of raw horse meat in the outdoor enclosure and in the evening each wolf ate 1 kg of raw horse meat with bone in the indoor enclosure. All aspects of animal husbandry that have been described were the same for all phases of the study.

During the vegetarian enrichment phase (VP) and the carnivore enrichment phase (CP), the application of enrichment sessions was once per day for three days per week—Monday, Wednesday and Friday—repeating the delivered schedule of items every two weeks. The keeper threw the enrichment items from the visitor's viewing area around 11:00 a.m. The enrichment devices or their residues were removed the following morning when the keeper cleaned the wolve's enclosures (8:00 a.m.).

During the VP, the six different enrichment sessions included 500 g of vegetarian products –mainly chopped fruits- per subject. The chronology of the sessions was as follows: burlap sack containing apples, scattered bananas, peaches, oranges, frozen pears, and a 5 L bucket with 3 L of frozen water and kiwis (see Figure 2A). During the CP, the six enrichment items included mainly animal products which were chronologically delivered per subject: burlap sack containing 500 g of raw beef lean meat, a piece of 1 kg of horse leg, one live carp, one frozen rabbit skin (see Figure 2B), 15 live grasshoppers, and a 5 L bucket with 3 L of frozen water and 500 g of raw beef lean meat (see Figure 2C).

Figure 2

The Three Iberian Wolves with Different Enrichment Items

Note. A = young female exploring scattered fruit; B = male biting frozen raw meat; C = adult female transporting rabbit frozen skin.

Procedure

Fourteen different trained observers in wolf behaviors conducted the registers. These observers were students from psychology and biology. They participated in a study about Iberian wolves' welfare in captivity through observing daily activity patterns and space use in different conditions. The observers spent four sessions per month to achieve inter-observer reliability testing, in which they were required to demonstrate an average agreement with another experienced observer higher than 85% (Lehner, 1998).

The baseline phase (BP) was conducted from the 17th of April to the 25th of June 2000 to document the wolves' daily activity patterns, their space use, and the inter-individual distance before the delivery of enrichment devices. The VP was conducted from the 26th of June to the 3rd of September 2000, and the CP from the 4th of September to 12th of November 2000.

Multifocal sampling methods were used for data collection given that there were several wolves to be observed—all-animal sampling—and more specifically, at the same time. Instantaneous scans were made at 15-min intervals for 7.5 hr sessions in November, 8.5 hr sessions in October, and 10 hr sessions from April to September (Altmann, 1974). The three phases consisted of 30 observation sessions, three per week (Monday, Wednesday, and Friday) that were balanced for the daily periods to obtain the daily activity period.

The variables recorded for the three Iberian wolves at each observational session were: (a) the phase of study (BP, VP, or CP); (b) the period of day (morning, midday, and afternoon); (c) the daily activity patterns (behavioral categories were defined as comprehensive and mutually exclusive; see Table 2) (Lehner, 1998); (d) the space use, by graphing the whole enclosure as the outdoor enclosure (divided into seven similarly sized zones (Zones 1-6 and mound)), the indoor and the breeding enclosures, and an undetermined zone—when the animal location was unknown—(see Figure 3); and (e) the inter-individual distance (ID) is measured in meters and it is defined as the space that separates two animals. It was calculated by using the distance formula between two points from the Pythagorean Theorem in an enclosure plan (1:10) and assumed that animals were in the barycenter of each zone. The Cartesian values of each zone were calculated through the enclosure plan (Barlow, 2016; Soriano et al., 2021a).

Table 2

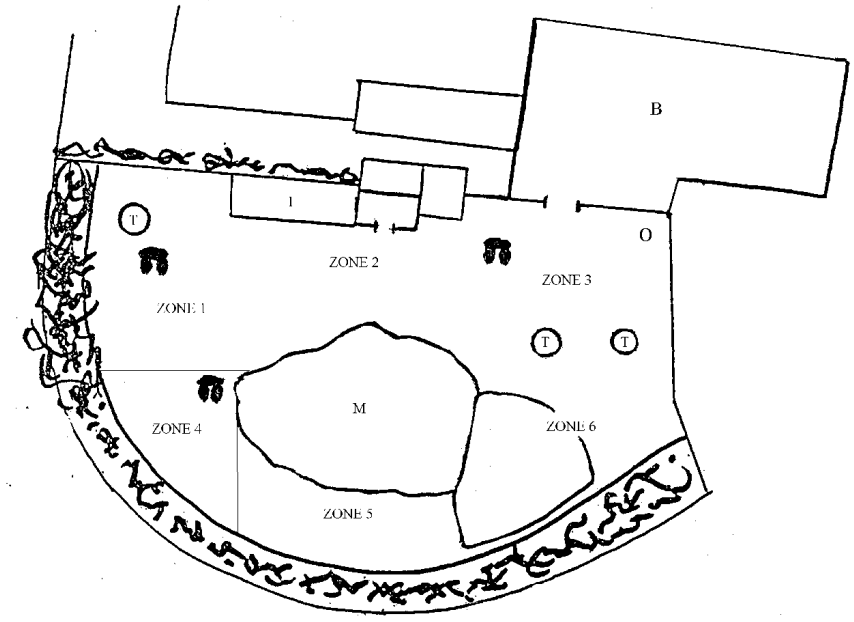
The Definitions of the Iberian Wolves' Daily Activity Patterns

ACTIVITY: means any behavior not classified as inactive, which includes:	
Exploration	The wolf sniffs the air, the substrate, the food or the objects. It also includes when the wolf is alert with the head up and the eyes open.
Locomotion	The wolf moves around the enclosure without exploration.
Scent marking	The wolf defecates or urinates using different leg postures. It also includes substrate scratching after urination or defecation and rubbing against odors.
Feeding	The wolf consumes food items; this also includes drinking and nibbling on herbs.
Solitary play	It mainly involves the wolf's movements; vigorous, rigorous, exaggerated like jumping or running. This also includes den preparation.
Maintenance	The wolf self-grooms and scratches with the mouth and/or the paws. It also includes when the animal shakes.
Manipulation	The wolf claws at, swipes at, nibbles at, picks up the food and the non-food items with the mouth and/or the paws.
Human interaction	The wolf sits up while orienting to humans. The wolf tries to communicate with humans in different forms (e.g., following the same path as the humans).
Social interaction	This includes affiliation, play, howling or agonistic behavior.
INACTIVITY: the wolf rests seated or lain with relaxed musculature.	
OUT OF VISUAL RANGE: the wolf or its' behavior is not observable because the Iberian wolves' enclosure design allowed wolves to hide (i.e., behind the mound or the dolmen or inside the indoor or the breeding enclosures).	

Note. The daily activity patterns were classified into three macro categories

Figure 3

The Iberian Wolves' Enclosure Showing the Division of the Area



Note. B = breeding enclosure; I = indoor enclosure; M = mound; O = outdoor enclosure.

Data Analyses

All data analyses were performed using the Statistical Package for Social Sciences (SPSS Inc., Chicago, IL 60606, USA) Version 23.0 for Windows. A $p = .05$ rejection criterion was applied to all tests. The Shapiro-Wilk values failed the normality. Therefore, we continued to run non parametric statistics (Sokal & Rohlf, 1995).

Friedman's test determined if the behavioral and spatial categories differed significantly among the study phases. The Wilcoxon signed-rank test revealed what type of environmental enrichment showed statistically significant differences in two-by-two comparisons (Soriano et al., 2021b).

In order to analyze the effect of the two different enrichment programs on a homogeneous space use, a Modified spread-of-participation index (SPI) for observed frequencies was used. A value of 1 indicated minimum use of the enclosure, and a value of 0 indicated that the use of space was totally homogeneous (Plowman, 2003; Rose & Robert, 2013). Moreover, in order to evaluate statistically significant differences in ID between dyads and study phases, the Wilcoxon signed-rank test was calculated.

Results

Effect of Enrichment on the Daily Activity Patterns

Table 3 shows how the two types of enrichment—vegetarian and carnivore—provoked significant differences in exploration, locomotion, inactivity, and out of visual range for the three Iberian wolves. Moreover, the comparison between BP and VP showed no significant differences for the daily activity patterns. When comparing BP and CP, we observed a significant increase in exploration and locomotion and a decrease in inactivity and out of visual range during CP for the three subjects. Concerning the comparison between VP and CP, we also observed a significant increase in exploration and locomotion and a decrease in out of visual range for the three Iberian wolves during the CP (Table 3 and Figure 4).

Table 3

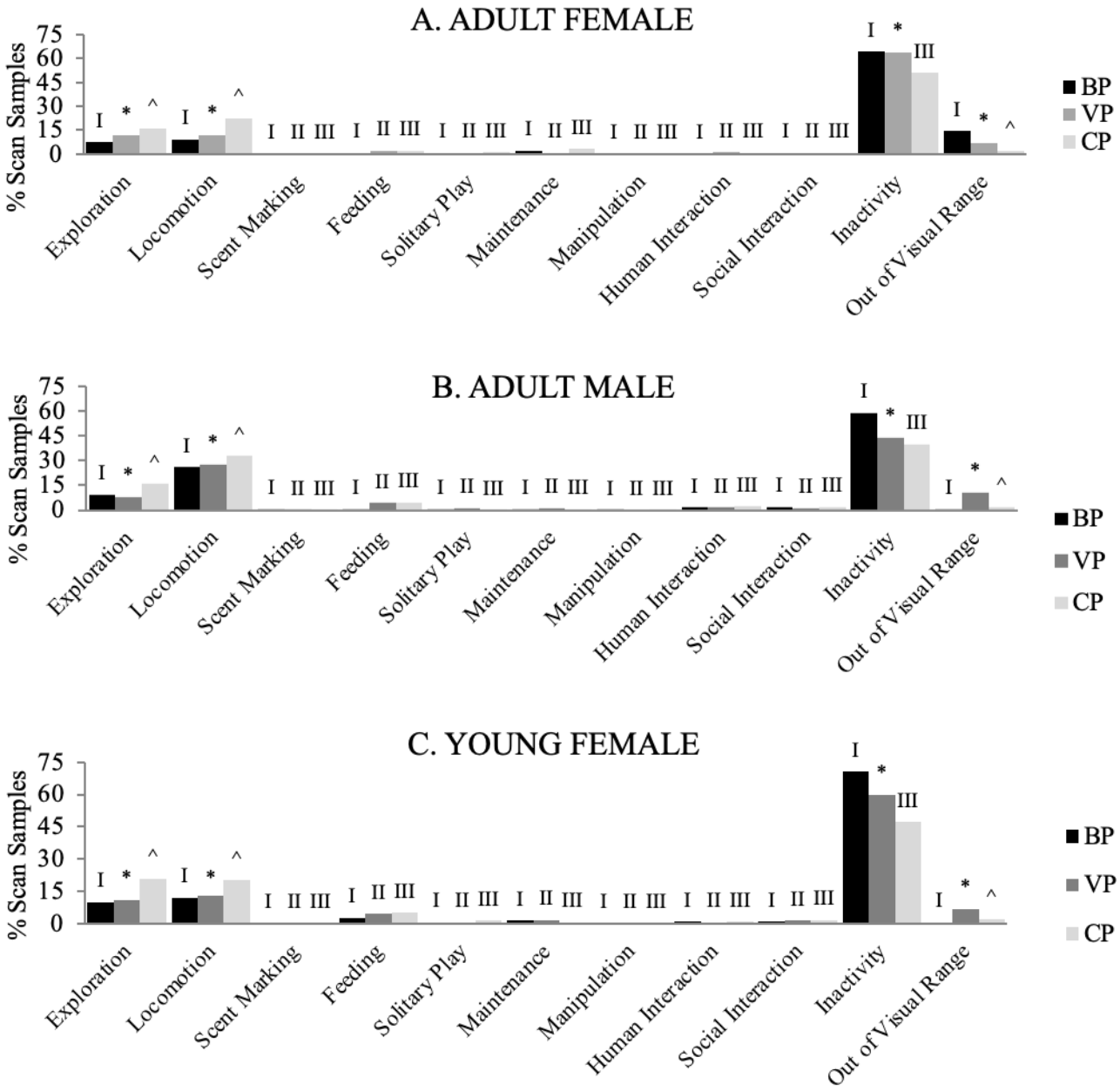
Friedman's Test and the Wilcoxon Signed-Rank Test for the Daily Activity Patterns

			Wilcoxon signed-rank test					
			BP vs VP		BP vs CP		VP vs CP	
	F(2)	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*
Exploration	-2.54	0.02*	-0.53	0.60	-1.60	0.11	-7.53	0.04*
Locomotion	6.00	0.04*	-1.60	0.11	-9.34	0.04*	-7.43	0.04*
Scent marking	0.28	0.87	-1.00	0.32	-0,45	0.65	0.00	1.00
Feeding	0.54	0.73	-1.60	0.11	-1.60	0.04	-1.60	0.11
Solitary play	0.52	0.73	0.45	0.66	0.53	0.60	0.00	1.00
Maintenance	0.52	0.76	0.00	1.00	0.45	0.66	0.00	1.00
Manipulation	0.67	0.72	0.00	1.00	-1.00	0.32	0.58	0.56
Human interaction	2.67	0.26	-0.82	0.41	-1.60	0.11	-0.53	0.59
Social interaction	0.67	0.72	-0.53	0.59	-1.60	0.11	-1.63	0.10
Inactivity	-2.35	0.02*	-1.60	0.11	18.05	0.02*	-1.60	0.11
Out of visual range	0.23	0.03*	-0.54	0.59	-8.77	0.02*	-7.53	0.04*

Note. Statistically significant differences *$p < 0.05$

Figure 4

Percentage of Scan Samples for the Daily Activity for the Three Study Phases in Each Iberian Wolf



Note. Statistical significance is set at $p < 0.05$. BP = baseline phase; VP = vegetarian phase; CP = carnivore phase. BP vs. VP (statistical non-significance: I); BP vs. CP (statistical significance: *; statistical non-significance: II); VP vs. CP (statistical significance: ^; statistical non-significance: III).

Effect of Enrichment on the Space Use

Table 4 shows how only the use of the indeterminate zone showed significant differences between the three study phases. Thus, concerning the comparison of BP with VP, we observed a statistically significant increase in the use of the indeterminate zone. However, for the comparison between BP and CP as well as between VP and CP, we observed a statistically significant decrease of the use of the indeterminate zone (Table 4 and Figure 5).

Table 4

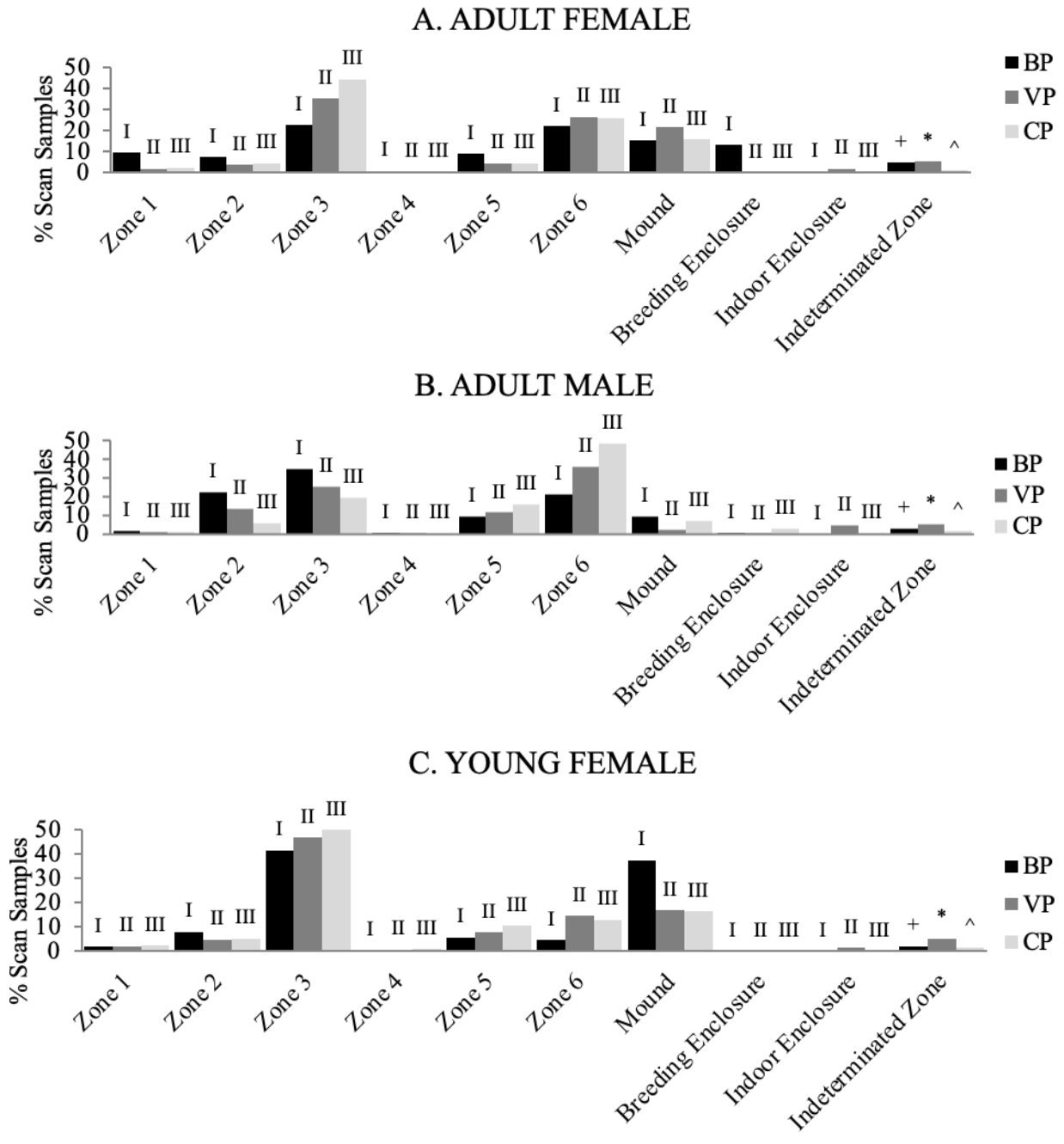
Friedman's Test and the Wilcoxon Signed-Rank Test for the Space Use

			Wilcoxon signed-rank test					
			BP vs VP		BP vs CP		VP vs CP	
	F(2)	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*
Zone 1	2.00	0.37	-0.82	0.41	-0.53	0.59	-1.60	0.11
Zone 2	4.67	0.10	-1.60	0.11	-1.60	0.11	-1.60	0.11
Zone 3	5.64	0.06	-0.53	0.59	-0.53	0.59	-0.53	0.59
Zone 4	2.00	0.37	0.00	1.00	-0.45	0.65	-0.58	0.56
Zone 5	0.67	0.72	0.00	1.00	-1.07	0.28	-1.34	0.18
Zone 6	4.67	1.00	-1.60	0.11	-1.60	0.11	0.00	1.00
Mound	0.67	0.72	-1.07	0.28	-1.07	0.28	-0.53	0.59
Breeding enclosure	2.00	0.37	-1.34	0.18	0.45	0.65	-1.00	0.32
Indoor enclosure	5.64	0.06	-1.60	0.11	-1.34	0.18	-1.60	0.11
Indeterminate zone	5.62	0.04*	-0.60	0.04*	-0.60	0.04*	-0.60	0.04*

Note. Statistically significant differences *$p < 0.05$

Figure 5

Percentage of Scan Samples for the Space Use for the Three Study Phases in Each Iberian Wolf



Note. Statistical significance is set at $p < 0.05$. BP = baseline phase; VP = vegetarian phase; CP = carnivore phase. BP vs. VP (statistical significance: +; statistical non-significance: I); BP vs. CP (statistical significance: *; statistical non-significance: II); VP vs. CP (statistical significance: ^; statistical non-significance: III).

Table 5 shows SPI values for the three study phases for the three Iberian wolves. The adult female showed more homogeneity of space use during the two enrichment phases than during the BP while the male and the young female used the space homogeneously during all study phases.

Table 5

The Iberian Wolves' SPI Values for the Three Study Phases

	BP	**VP**	**CP**
Adult female	0.77	0.11	0.11
Adult male	0.09	0.13	0.10
Young female	0.10	0.09	0.09

Effect of Enrichment on Inter-individual Distance

Table 6 shows statistically significant differences for the three Iberian wolves' ID in the comparison between the three study phases. Thus, the three Iberian wolves were closest from each other during CP and farthest apart during BP (Figure 6).

Table 6

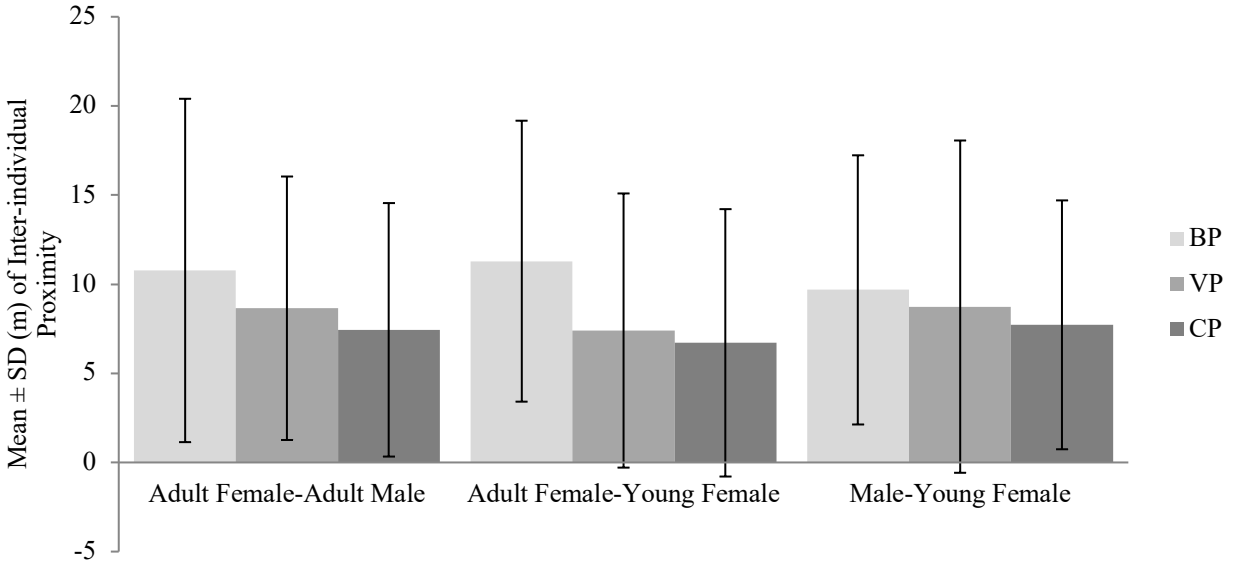
Wilcoxon Signed-Rank Test for the Inter-Individual Proximity in Each Dyad

	BP vs VP		BP vs CP		VP vs CP	
	Z	*p*	*Z*	*p*	*Z*	*p*
Adult female-Adult male	-28.18	< 0.001**	-26.42	< 0.001**	-26.04	< 0.001**
Adult female-Young female	-28.22	< 0.001**	-26.12	< 0.001**	-19.66	< 0.001**
Male-Young female	-28.29	< 0.001**	-27,68	< 0.001**	-26.14	< 0.001**

Note. Statistically significant differences $^{**}p < 0.001$

Figure 6

Mean ± SD Inter-individual Proximity (m) in each Study Phase for the Iberian Wolves' Dyads



Discussion

The CP had more effects on the daily activity patterns and proximity than the VP. This could be due to the wolf's diet being mainly composed of animal products rather than of vegetarian ones. The CP provoked an increase in exploration and locomotion and a decrease in inactivity for the three wolves. In comparison with other publications about feeding enrichment, we found similar results to: (a) an increase of exploration in spectacled bears (Fischbacher & Schmid, 1999); (b) an increase of activity in three species of bears (Forthman et al., 1992); (c) an increase in both exploration and activity in Western lowland gorillas (*Gorilla gorilla gorilla*; Ryan et al., 2012); and (d) an increase in locomotion in Moloch gibbon (*Hylobates moloch*; Wells & Irwin, 2009) and white-fronted lemurs (*Eulemur fulvus albifrons*; Sommerfeld et al., 2006).

Both out of visual range and the indeterminate zones are two categories with the same meaning: animals were out of visual ranges. In any case, in terms of animal welfare, the visibility of these animals is an important adaptation indicator. Visibility is often a problem in modern zoos in terms of visitor expectancies and animal welfare. The CP provoked an increase in the visibility of the animals while the VP provoked a decrease. This means that, in this case, the feeding enrichment is an effective and natural method for increasing and decreasing visibility, with both their advantages and disadvantages. Renner and Lussier (2002) also tested the increase and the decrease of visibility in Spectacled bears (*Tremarctos ornatus*). The increase of visibility makes the animals more visible for zoo users (e.g., keepers, vets, observers, visitors) as suggested by the results observed during feeding enrichment in African elephants (*Loxodonta africana*; Stoinski et al., 2000), three different species of bears (Altman, 1999), and large felids (Bashaw et al., 2003). The decrease of visibility is also possible during enrichment because it seems to allow the animals to choose more comfortable places for them to sleep, feed or groom. These comfortable places are usually more hidden and with fewer stress factors such as human presence, conspecifics, or weather conditions (temperature, humidity, and wind).

In terms of the use of space, the enrichment provoked an individually different use of the available space within the enclosure. However, one of the aims of environmental enrichment programs is to achieve a more homogenous use of space (Ross et al., 2009). Only the homogeneity of the Iberian wolf adult female during both enrichment phases was greater than during BP as the results found in a study for small cats (Shepherdson et al., 1993). The male and young female's homogeneity were similar for the three study phases.

Proximity is a welfare indicator of the relationship among subjects of the same or different species living in the same enclosure (Maple & Perdue, 2015; Soriano et al., 2021a). One of the aims of environmental enrichment is to promote social relationships among the animals. In this case, the wolves' inter-individual distance was greatest during the carnivore intervention than during the vegetarian one and the baseline. Proximity also increased in orangutans (*Pongo pygmaeus*) during a computer-assisted enrichment (Tarou et al., 2004).

The three Iberian wolves responded individually to the enrichment in a manner similar to what was observed in maned wolves (Vasconcellos et al., 2009), bottlenose dolphins (*Tursiops truncatus*; Eskelinen et al., 2015), different species of bears (Forthman et al., 1992; Soriano et al., 2006b, 2016) and squirrel monkeys (*Saimiri sciureus*; Izzo et al., 2011). Our results determined how the daily activity patterns, the space use, and the inter-individual distance in these wolves provide important information about the individual temperament of each animal. We would expect that the individual variation for these variables should be a complex function of: (a) daily internal cycles; (b) seasonal shifts in external stimuli from the physical environment (e.g., temperature, light, prey activity, human activity); (c) variation in the internal state of individuals (e.g., nutritional condition and reproductive phase); and (d) individual experience including expectations of the actions of companions (Mech & Boitani, 2003).

In conclusion, the enrichment items designed more according to the individual temperament and to the animal natural history have a greater capacity to improve the wolf welfare. This is comparable with the results observed in other enrichment publications where natural items had more effects than artificial ones (e.g., sticks were more attractive than nylon balls for Rhesus macaques (*Macaca mulatta*; Line & Morgan, 1991), and Asian small-clawed otters (*Aonyx cinereal*) made the most captures of live crickets and the least for gelatin capsules (Foster-Turley & Markowitz, 1982).

The wolf is a large and diverse specie of commonly kept and popular in zoos. Their large range of social, behavioural, and dietary requirements makes it challenging to form generalized suggestions for husbandry and management. The subjects of this study benefit from the provision of species-specific environmental enrichment and increases to the complexity of their enclosures. Further consideration of exhibit design and quality space, and the suitability of mixed species enclosure (where realistic) should be a priority. Overall, research outputs from species specific behavioral ecology study should be applied to all aspects of wolf management plans including enclosures, training, population management, and nutrition (Hunt, 2023).

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