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Research article

Activity budget of zoo-housed Patagonian mara *Dolichotis patagonum* mates

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Abstract

Captive conditions differ widely from an animal's natural environment and risk making them prone to reduced behavioural flexibility and sometimes impaired reproduction. The Patagonian mara *Dolichotis patagonum*, a near threatened species, is a large rodent endemic to Argentina with a singular social organisation that combines monogamy with communal breeding. The aim of this study was to learn more about the activity budget and behavioural synchrony between mates of zoo-housed *D. patagonum* and thus contribute to research and conservation programmes at modern zoos worldwide. The study implicated 28 animals housed at Córdoba Zoo (Argentina) under natural photoperiod and temperature conditions. Behaviour was recorded once a week every hour from 0800–1800 for a 28-day period and the total offspring at the end of the spring-summer season were counted. The recorded activity budget was: resting (43%), feeding (25%) and alert (13%), the remaining categories accounting for less than 10%. Resting, feeding and alert were the only categories associated with hourly changes. There was 48% behavioural synchrony between mates (both sexes engaging in the same behaviour at the same time) and a total of 23 offspring were counted, corresponding to one litter each reproducing female. The similarity between the behavioural response of these zoo-housed individuals and available data on the behaviour of *D. patagonum* in the wild indicates that zoo-housed *D. patagonum* behavioural activities can be considered positive responses, providing useful information for the future development of reintroduction programmes.

Introduction

Animals housed in artificial habitats such as zoos face a wide range of environmental challenges including restricted movement and foraging opportunities, all of which are liable to affect behavioural repertoires (Morgan and Tromborg 2007). Breeding animals in captive conditions which differ substantially from their natural environment also risks making them prone to reduced behavioural flexibility and sometimes impaired reproduction (Mason et al. 2013). Accordingly, it is important to understand animal behaviour in zoos as a means to ensuring their welfare (Hosey 2005). In particular, observation of normal or naturalistic behavioural patterns provides insight into the animals' physical and psychological welfare, enabling an evaluation of the appropriateness and relevance of current husbandry and management regimes (Kleiman et al. 1986; Carlstead and Shepherdson 1994; McPhee an Carlstead 2010; Rose and Riley 2019).

The present study focuses on the Patagonian mara *Dolichotis patagonum;* a large rodent (8–12 kg) endemic to Argentina (Redford and Eisenberg 1992; Campos et al. 2001). *D. patagonum* is listed by the IUCN Red List of Threatened Species as Near-Threatened (IUCN 2020) and in Argentina as Vulnerable (Alonso Roldan et al. 2019), with a decreasing population trend as a consequence of habitat degradation and poaching. It is already locally extinct in some regions, such as Buenos Aires Province (Cabrera 1953) and the southwest of Córdoba (Rosacher 2009; Periago et al. 2015).

The most singular characteristic of *D. patagonum* is its reproductive system; monogamy, combined with communal breeding (Taber 1987). Monogamy is uncommon in mammals, with an estimated occurrence of only 3% (Carter et al. 1995) and only a few socially monogamous species have developed cooperative breeding (Lukas and Clutton-Brock 2012; Johnson and Young 2015). Dubost and Genest (1974) were the first to describe *D. patagonum* behaviour in semi-captivity (an area of 10 ha, largely consisting of open meadows). *D. patagonum* pairs are united by strong bonds, the male and female always remaining in close proximity, with the female adopting the role of passive leader, initiating most activities (resting, walking, grazing, moving toward communal burrows) and the male following suit. Members of a pair, therefore, do not behave independently of one another, reaching a behavioural synchrony of 57% for daylight activities in the wild (Taber 1987; Taber and MacDonald 1992).

No information could be sourced on the activity budget and behavioural synchrony of zoo-housed *D. patagonum* individuals. The aim of this study was to expand knowledge of this captive species' behavioural repertoire with a view to assisting in the development of breeding programmes at zoos and ultimately repopulating this species in the wild. Knowledge of animal behaviour can be a powerful management tool for modifying the trajectory of crisis scenarios and will allow the design of more effective mitigation strategies, such as the successful implementation of conservation translocations (Berger-Tal et al. 2011, Greggor et al. 2016).

Materials and methods

Subject, pair selection and housing conditions

This study implicated 14 *D. patagonum* pairs (28 adults: 14 males: 6.85±0.48 kg and 14 females: 7.45±0.83 kg mean body weight±SD) in spring 2017 (17 October–14 November) at Córdoba Zoo (31°12.32'S, 64°16.84'W; Córdoba, Argentina). The present study was developed within the *D. patagonum* distribution area (28–50°S; Redford and Eisenberg 1992; Alonso Roldan et al. 2019; Campos et al. 2001).

Based on the report of Genest and Dubost (1974), the 14 *D. patagonum* pairs were selected between May and July 2017 from a larger zoo population that had been marked the previous month (April) with listed collars. In August 2017 the selected animals were individually captured and immediately transported to the 800 m^2 study enclosure, a 5-min walk away. Transportation to the study enclosure was undertaken by zookeepers and researchers, each animal being carried individually in a small wooden box.

Once in the study enclosure, the group of mates gathered at a single warren. Since the core area of wild mate activity is concentrated around the warren, with no evidence of alternative areas of activity on a microhabitat scale (Alonso and Baldi 2016), it is important to note that they behaved similarly in the enclosure, where alternative areas were available.

Housing conditions in the enclosure imitated the natural Patagonian landscape of *D. patagonum*, with an abundance of bare soil and logs on the ground as shelter. Animals were exposed to natural photoperiodic (light: 0450–2110; dark: 2115–0445) and temperature conditions. Zookeepers supplied food twice a day, between 1200–1300 (balanced rabbit feed (GEPSA FEEDS) and 1700–1800 (alfalfa), on the bare soil of the enclosure. Water was provided ad libitum. Zookeepers also performed daily cleaning routines between 0900–1100, collecting faeces and food remains from the day before.

Behavioural data collection

An instantaneous sampling method proposed by Altmann (1974) was used to register animal behaviour (Martin and Bateson 2013) every hour, starting at 0800 and ending at 1800, totalling 11 sample points. This sampling procedure was repeated once a week during a 28-day period.

Table 1. Ethogram of adult zoo-housed mara *Dolichotis patagonum*. Behavioural categories were based on the ethogram developed by Taber (1987).

Behaviour	Definition
Resting	Lying on the ground in a sphinx or lateral position, with eyes closed or open.
Feeding	Variable positions, ingesting food.
Alert	Sitting with head erect and actively looking around.
Locomotion	Using all four limbs at different rhythms, either walking, trotting or running, with head erect.
Exploration	Variable position, moving with head bent towards the ground, sniffing
Other	Grooming, lactation, sexual interactions and digging at den mouth.

Using binoculars, the same observer (JB) recorded individual behaviours from outside the enclosure. Applying a scan rule, the observer began recording the behaviour of each individual in a pair, continuing to the next pair in a random order until completing the whole group. Since it could take up to 30 min to record all the animals, a one-hour sample point was chosen in order to leave sufficient time to prepare for the next scan.

The data collected allowed the characterisation of pair behavioural synchrony by analysing the data of male behaviour with respect to that detected for females. Thus, for instance, when the female was resting, the behaviour of the male was simultaneously recorded, resulting in the following activity combinations: resting-resting, resting-locomotion, resting-alert, resting-feeding, resting-exploration and resting-other, respectively.

The behavioural categories described in Table 1 are based on the ethogram developed by Taber (1987) with an additional category for the exploration behaviour frequently observed at Córdoba Zoo during preliminary ad-libitum observations. Records of behaviour were considered as a binary variable, assigning a value of 1 to the behaviour displayed and 0 to the remaining behaviours.

As a basic measure of reproductive activity, the total number of offspring were counted at the end of the spring-summer season (21 March 2018) and it was verified that all females produced offspring during the recorded season.

Data analysis

To analyse behavioural data, mixed general linear models (MGLM) were applied to the percentage of behaviours over the hours analysed. First, hours and individuals were considered as fixed factors and sex and day of sampling as random factors, and then sex as a fixed factor and individual and day of sampling as a random factor. A binomial error distribution was assumed and a logistic link function used, since the recorded behaviour corresponded to a binary variable. Fisher´s posteriori test was applied when the statistical analysis showed a p-value ≤0.05.

In order to assess behavioural synchrony, the X^2 test was used to check whether pair members were behaving independently of one another, following the statistical approach of Taber (1987) to analyse this variable. All analyses were performed using InfoStat (Di Rienzo et al. 2020). Results are expressed as mean±standard error.

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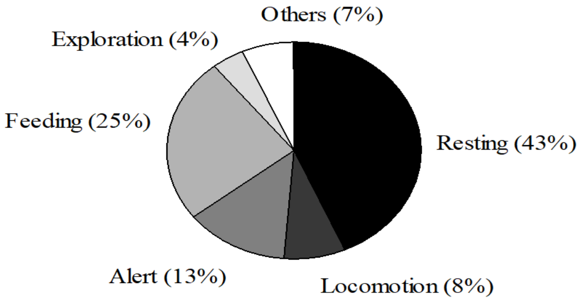

Figure 1. Activity budget in zoo-housed adult mara *Dolichotis patagonum* (n=28, 14 males and 14 females). Behaviour was recorded every hour from 0800–1800, once a week, during a 28-day period of spring (11 sample points*28 individuals*4 weeks: 1232 total records).

Results

Figure 1 shows the activity budget of zoo-housed *D. patagonum*. The highest number of records corresponds to resting behaviour, followed by feeding and alert; the remaining categories correspond to less than 10% of total behaviours.

The statistical analysis showed highly significant differences over the hours for resting (P<0.0001; X^2=64.94), feeding (P<0.0001; X^2=106.01) and alert (P<0.0001; X^2=49.68; Figure 2). No significant differences were detected among individuals or between sexes of *D. patagonum*.

As shown in Table 2, 48.05% (centre diagonal, n=283/589 records) of behavioural synchrony between mates was detected, that is, occasions when males and females were observed engaging in the same behaviour at the same time. The synchrony for each category was: 62% (n=173/279) for resting, 54% (n=23/43) for locomotion, 29% (n=15/51) for alert, 42% (n=59/142) for feeding, and 25% (n=6/24) for exploration. The other category was the exception, showing the highest combination with resting. Table 2, furthermore, shows that the percentage in each category was similar for both sexes, for example female resting 47.4% (n=279/589) and male resting 44.3% (n=261/589).

The X^2 test showed that the observed records differed significantly (P<0.0001; X^2=266.66) from the results expected if the animals had engaged in different behaviours from their mate (Table 3).

Finally, a total of 23 offspring were counted at the end of the spring-summer season. Each mother had between one and two offspring.

Discussion

The activity budget of zoo-housed *D. patagonum* was evaluated based on changes in behaviour over daylight hours and behavioural synchrony between pair members was detected. It was found that individuals spent almost half their time resting in the enclosure, followed by a quarter of their time feeding, and a small amount of their time alert, in movement or engaged in other behaviour. Resting, feeding and alert were associated with hourly changes. Pair members did not behave independently of one another during a high proportion of their time (48%). As stated

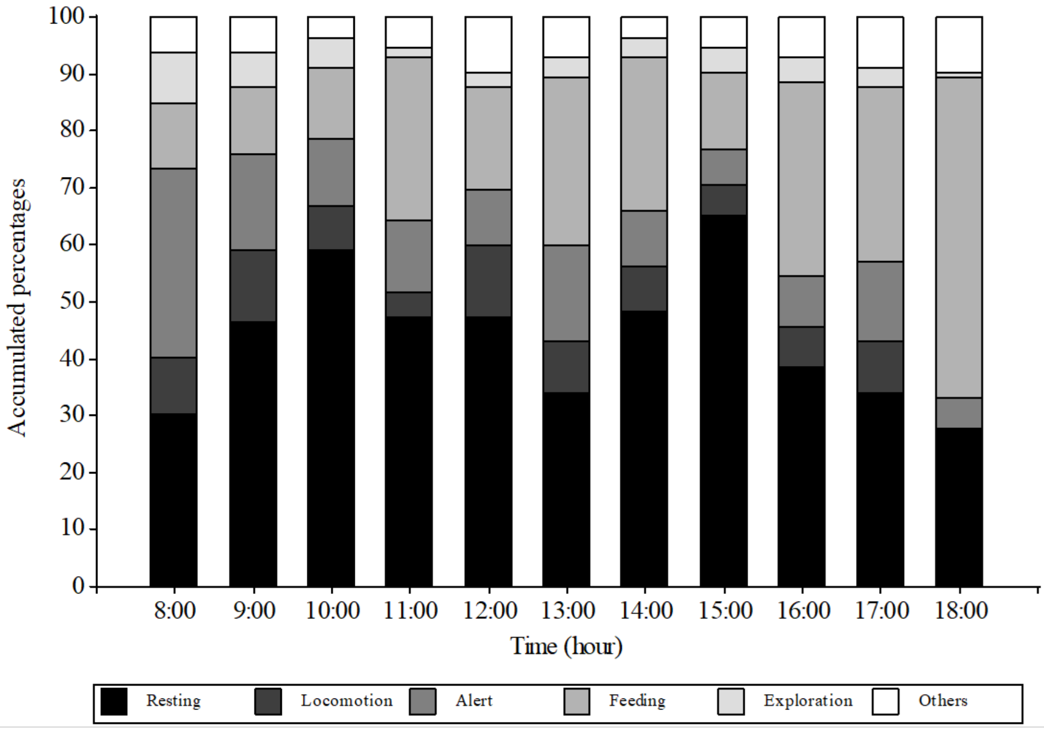

Figure 2. Variation in hourly behavioural records of zoo-housed adult mara *Dolichotis patagonum*. Fisher´s posteriori test indicated the following hourly differences: for resting: 10, 15>9, 11, 12>8, 13, 16, 17, 18; for feeding: 18>11, 13, 16, 17> the remaining hours; and for alert at 0800, the highest number of records. Food was supplied at 1200–1300 and 1700–1800.

Table 2. Combined records of behavioural categories of pairs of zoo-housed mara *Dolichotis patagonum* and percentage for each category by sex.

	Female behaviour							
	Resting	Locomotion	Alert	Feeding	Exploration	Other	Total	%
Resting	173	10	10	43	5	20	261	44.3
Locomotion	6	23	1	8	3	4	45	7.6
Alert	39	4	15	22	6	6	92	15.6
Feeding	40	2	14	59	3	10	128	21.7
Exploration	9	2	2	4	6	3	26	4.4
Other	12	2	9	6	1	7	37	6.3
Total	279	43	51	142	24	50	589	
%	47.4	7.3	8.7	24.1	4.1	8.5		

by McPhee and Carlstead (2010), behavioural data of this nature will be useful for ex-situ and in-situ conservation efforts relating to this mammal species. Indeed, these authors pointed out that the presence of normal activities and species-specific behaviours similar to those observed in the wild are a potential indicator of an optimal environment in captivity and of animal good health and wellbeing.

According to the most recent reviews (Campos et al. 2001; Kessler et al. 2009; Alonso Roldan et al. 2019), little new information has been reported on the activity budget of *D. patagonum*. Comparing the present findings on the zoo-housed *D. patagonum* activity budget with those relating to wild conspecifics (Taber 1987), differences were found only in the amount of time spent resting and feeding, the remainder of the activity budget being similar within the reported ranges (locomotion 4–11% for data collected in the wild vs locomotion 8% for data collected in Córdoba Zoo). The prsent data on the proportional amounts of time spent on resting vs feeding at Córdoba Zoo are in agreement with reports of similar patterns for other zoo mammals that also tend to rest more and feed less in captivity than in the wild (e.g. Höhn et al. 2000; Melfiv and Feistner 2002; Kerridge 2005). Less time spent on feeding and more time spent on resting behaviour would appear to be the trend in zoos: part of the time formerly spent in the wild on moving and feeding is replaced in captivity by resting (Melfiv and Feistner 2002). At Córdoba Zoo, differences in the proportion of time spent resting vs feeding could be due in large part to the stability of the twice daily food supply, a lack of grazing opportunities and the absence of predation, combined with other zoo-related factors such as the size and complexity of the enclosure.

Generally speaking, time and energy in the wild are limited resources that animals have to allocate between different behaviours. There is a trade-off between allocation of time and energy to feeding activities (that guarantee growth and reproduction) and vigilance (that reduces mortality) (Pulliam and Caraco 1984; Karasov 1992).

Among large ungulates, a better-studied taxon than *D. patagonum*, the proportion of time spent on feeding during foraging is also high (80–90%/hour for grazers and 65–85%/hour for browsers). Approximately 5–15% of foraging time is diverted to wards being alert or other non-foraging actions, leaving 7–20% of time spent on moving (Owen-Smith et al. 2010). *D. patagonum* resembles ungulates, such small deer and antelope, when walking or running, and as a herbivore, spends a high proportion of its time feeding (46%; Campos et al. 2001). From an energetic point of view, feeding could be considered to constitute elastic behaviour: food resources vary through the year and changes in foraging decisions may in the long term have minimal impact on lifetime fitness.

As mentioned above, data collected at Córdoba Zoo on locomotion and alertness were within similar ranges to that reported for wild *D. patagonum*. It would appear that the restricted movement associated with artificial habitats (Morgan and Tromborg 2011) does not affect the level of locomotion in the studied zoo-housed *D. patagonum*. This could be due to the appropriateness of the current husbandry and management regime (Rose and Riley 2019) applied in Córdoba Zoo. The similarity between the alert behaviour of zoo-housed *D. patagonum* and corresponding data recorded in the wild could indicate that zoo environment stimuli resemble stimuli in the wild. For example, fear caused by human presence and/or general noise (Quadros et al. 2014; Queiroz and Young 2018) in the zoo environment could evoke the same type of stress response as that brought on by fear of wild animals, leading in the wild to predator avoidance behaviour and/or routine scanning (vigilance) of the surroundings (Rushen 2000). From an energetic point of view, the alert state could be considered a fixed behaviour in the wild, because reducing time spent on vigilance means failing to avoid a predator and possibly dying or drastically decreasing future fitness (Lima and Dill 1990). Compared to *D. patagonum* in the wild, individuals at Córdoba Zoo allocated more time to resting than feeding (elastic behaviours) but spent a similar amount of time on vigilance/alertness (fixed behaviour).

Analysis of the present data on a temporal scale showed variations in the display of the different behavioural categories of zoo-housed *D. patagonum* over daylight hours (0800–1800, representing approximately 62% of the light phase). Veissier et al. (1993) suggests that changes in the circadian patterns of activity and rest (of calves) could indicate how well animals are adapted to their environments. The value for feeding behaviour was highest at 1800, followed by intermediate values between 1100 and 1700 and lowest earlier in the morning, likely reflecting the routine food supply timetable 1200–1300 and 1700–1800). Genest and Dubost (1974) reported that *D. patagonum* in semi-captivity with natural pastures showed two foraging peaks, the highest being observed in the afternoon, which is similar to the present finding

Table 3. The X^2 test of the assumption that mara *D. patagonum* males and females engage in different behaviours independently of their mate's behaviour. Deviations from expectation under independence are shown as "+" and "-" values, indicating whether the observed value was greater or smaller than the derived expected value.

	Female behaviour					
	Resting	Locomotion	Alert	Feeding	Exploration	Other
Resting	49.37	-15.32	-4.58	-20.63	-3.32	-5.53
Locomotion	-9.05	19.71	-2.72	-7.34	0.1	-0.7
Alert	-12.6	-2.9	7.03	2.92	-0.25	5.8
Feeding	-19.92	-2.85	-0.18	28.14	-2.27	-2.92
Exploration	-5.63	1.17	2.25	-2.22	4.94	-0.51
Other	-2.16	0.18	-1.81	-0.87	0.79	3.86

of peak feeding at 1800 under the different conditions of a food supply routine and lack of access to grazing. This peak of feeding activity therefore appears to be independent of whether the animals are in semi-captivity or in a zoo enclosure and may reflect an endogenous feeding pattern. In terms of alert behaviour, the highest value exhibited by zoo-housed *D. patagonum* was at 0800, the time that zoo-staff commence their working day (involving activities such as the cleaning of enclosures, food distribution, internal transit of vehicles etc.), which likely affected animal behaviour. Further studies are nevertheless required in order to fully understand single-factor effects on responses of *D. patagonum* housed at zoos.

The significant differences detected in the present study in terms of resting behaviour could correspond to adjustments to the behavioural repertoire: animals were alert at 0800 and then rested increasingly as of 1000, the amount of time spent on resting then decreasing again as feeding increased. A similar variation pattern was observed for behaviour throughout the afternoon.

The behavioural characterisation of pairs showed 48% of synchrony between mates. Taber (1987) found 57% of behavioural synchrony in the wild. Despite this almost 10% difference, the present findings still show that mates exhibit equivalent behaviour almost half the time, that is, that they do not behave independently of one another. Mating systems in animals usually entail a high degree of plasticity (Crook and Gartlan 1966) and captivity offers a number of opportunities for polygyny to develop (Wilson 1975). Nevertheless, *D. patagonum* bred in Córdoba Zoo continued to exhibit a similar degree of behavioural synchrony between mates, despite opportunities in the zoo for males to increase their reproductive success by monopolising several females.

Finally, zoo-housed *D. patagonum* mates produced one or two pups during the study. Although in the wild the average litter size ranges from 1–3 (Campos et al. 2001), pairs reproduce all year round, whereas in the present study offspring production was only monitored during spring-summer.

The collection and evaluation of data show how, where and when animals exert choice over what they do is considered a possible way of improving husbandry outcomes of species bred in zoos (Rose and Riley 2019). This study of the daily time-allotment choices of *D. patagonum* individuals at Cordoba Zoo shows how this species responded to its captive environment. The reported findings constitute useful normative data for the ex-situ management of conservation programs.

Conclusion

The present paper describes the activity budget of zoo-housed *D. patagonum* mates. It was found that resting was the main inactive behaviour and feeding the main active behaviour. These two categories, together with alertness, showed temporal variation during the sampling period, presumably due to zoo challenges such as the absence of predation, routine food administration and the presence of human activity.

Zoo-housed *D. patagonum* mates exhibited behavioural synchrony, that is, pair members did not behave independently of one another, the synchrony being necessary for preservation of the pair. Additionally, zoo-housed *D. patagonum* showed reactivity of alertness, a vital behaviour for survival, and all pairs produced offspring during the studied season.

The similarity between the behavioural response of these zoo-housed individuals and available data on the behaviour of *D. patagonum* in the wild, indicates that zoo-housed *D. patagonum* behavioural activities can be considered positive responses, providing useful information for the future development of reintroduction programs.

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Ethical Approval
All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. We carried out this study in accordance with the CONICET Ethics Committee (Resolution 1047 Annex II, 2005) and the Argentinean National Law of Animal Protection (Nº 14346) and received the approval of the Bioethics and Laboratory Animal Commission in accordance with the Annex to the Regulations for the 'Care and Use of Laboratory Animals' (IIBYT, institution of CONICET- FCEFyN-UNC).

Conflict of interest
The authors declare that they have no conflict of interest.

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