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Contrafreeloading in maned wolves: Implications for their management and welfare

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ABSTRACT

Contrafreeloading occurs when animals spend time and effort to obtain food in the presence of freely available food. There are several interpretations for such an apparent contradiction to optimal foraging models, with an emphasis either on the need to gather and update information about the environment or on the value of performing species-typical responses. Evidence suggests that both gathering information about the environment and the expression of species-typical behaviour are important for the welfare of captive animals. The aim of the present study was to assess the existence of contrafreeloading in maned wolves (*Chrysocyon brachyurus*), in a situation where animals could get food directly from a "free" source and/or search and handle hidden food items, an alternative that requires more effort and is probably more similar to natural foraging conditions. Eight captive, pair-housed maned wolves were given weekly choice tests in which they could obtain food either by approaching the usual food tray in one section of the enclosure (Tray), and/or by searching for food at variable sites amongst the vegetation in the other section of the enclosure (Scattered). Results indicate that maned wolves spent more time in the Scattered than in the Tray section of the enclosure ($P = 0.02$) and that they obtained about half of the food from that section (48.54% ± SE 0.69). Our results, the first to demonstrate contrafreeloading in maned wolves, have implications for the husbandry and welfare of this endangered species.
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1. Introduction

Contrafreeloading occurs when an animal chooses to work for food in the presence of identical and easily obtainable food. After it was first described in rats by Jensen (1963), this apparently paradoxical effect has been demonstrated in several species (Bean et al., 1999; de Jonge et al., 2008; Inglis et al., 1997; Lindqvist et al., 2002; McGowan et al., 2010; Menzel, 1991; Reinhardt, 1994; Rozek and Milam, 2011). Inglis et al. (1997) have summarised the major explanations for contrafreeloading: (1) aspects of the earned food alternative become endowed with secondary rewarding value sufficient to maintain the costly performance; (2) neophobic tendencies cause withdrawal from free food offered in a familiar "working" context; (3) stimulus change associated with earned food increases its rewarding value; (4) working for food, especially if this means the performance of species-typical behaviour, may be reinforcing in its own right; (5) the Information Primacy Hypothesis states that contrafreeloading is adaptive in a natural environment, since it is advantageous for a wild animal to invest a certain amount of energy searching for possible future food sites. The energy spent in this activity would be compensated by the possibility of more efficient feeding intake in the long run.

Osborne (1977) proposed that feeding activity should only be considered contrafreeloading when the proportion of food that is difficult to obtain exceeds 50% of the

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total amount of food consumed during a session. There is however no reason to assume 50% as a point of discontinuity between preference and non-preference (Morgan, 1974). Inglis et al. (1997) suggested that, as optimal foraging and learning paradigms predict a total preference for the free food, any deviation from such an outcome should be explained using other theories. In the present study we shall consider contrafreeloading as any level of effort invested in obtaining a resource in the presence of this resource available in an easily accessible form (McGowan et al., 2010).

The few experimental studies of contrafreeloading in wildlife have focused on birds (Bean et al., 1999; Rozek and Milam, 2011), primates (Anderson and Chamove, 1984; Menzel, 1991; Reinhardt, 1994) and bears (McGowan et al., 2010). Some evidence of contrafreeloading has been reported in maned wolves, *Chrysocyon brachyurus* (Vasconcellos et al., 2009), but, until now, to our knowledge, no systematic study has been conducted to investigate this phenomenon in the species.

C. brachyurus is a poorly known South American species which may present behavioural problems in captivity: poor reproduction (Maia and Gouveia, 2002), pacing, and low levels of activity (Bestelmeyer, 1998). Maned wolves are solitary animals: male and female in the wild only remain together during the reproductive season (between March and May in the Southern hemisphere, Dietz, 1984). As opportunistic omnivores that feed on a wide variety of food types (fruits, insects, rodents, birds) and spend considerable time foraging in the wild (Queirolo and Motta-Junior, 2007; Rodrigues et al., 2007), these animals require an appropriate environment to perform their wide range of foraging behaviours. In many zoos, maned wolves are kept without sufficient stimulation, sometimes in barren enclosures, which may affect their welfare.

Foraging performance may be seen as not necessary under captive conditions, since animals are, in such a context, reliably provided with acceptable amounts of food. Several studies have however reported that animals retain, in captivity, a strong motivation to explore the environment (Everitt et al., 2001; Inglis, 2000; Panksepp, 1998; Spruijt et al., 2001) and that a lack of opportunity to explore may have negative emotional consequences and may generate abnormal behaviour (Clubb and Mason, 2003). It has been repeatedly shown that well-being is enhanced by providing animals with appropriate challenges (Meehan and Mench, 2007; Morgan and Tromborg, 2007) and options (Carlstead, 1996; Markowitz and Aday, 1998; Owen et al., 2005; Ross, 2006; Van de Weerd et al., 2006), by providing foraging opportunities.

The value of foraging for maned wolves may be assessed by giving the animals some control over their environment and observing their choices in contexts in which two or more alternative resource are available. In preference tests, the resource that the animal chooses more often, consumes in a greater quantity, or spends more time with is said to be preferred (Fraser and Matthews, 1997; Galhardo et al., 2009; Kirkden and Pajor, 2006).

The aim of our experiment was to assess the existence of contrafreeloading in maned wolves by investigating their foraging performance in a context where two forms of feeding were available: (a) eating from familiar trays (easily accessible food), or (b) searching for food in the midst of vegetation (more costly and unpredictable food). Intake from the costly alternative and/or time spent at the costly site would indicate the existence of contrafreeloading. Considering that the possible choices reflect the "point of view" of the animals (Dawkins, 1990), results might indicate the type of food presentation that is best for the welfare of captive maned wolves.

2. Materials and methods

2.1. Animals and feeding

We observed eight (four males – M1–M4; four females – F1–F4, Table 1) maned wolves, two from the São Bernardo do Campo Zoo and six from the Associação Mata Ciliar, both in São Paulo, Brazil. All animals had been housed as mixed-sex pairs for at least 1 year before the experiment and had free access to both indoor quarters and outdoor exhibit for 24 h per day.

Wolves were fed once a day, in the morning. Meals – offered in trays, one for each individual – consisted of fruits (apple, banana, papaya) and meat (beef heart or chicken necks). The amount of food offered per pair was about 2400 g in the Associação Mata Ciliar and about 7000 g in São Bernardo do Campo Zoo. In order to comply with the institutions' husbandry protocol and to prevent from introducing a confounding variable, these amounts were maintained during the experimental procedures.

Two of the animals had previously been given environmental enrichment through food scattering 3 years before the beginning of the experiment (M1/F1), whilst the other six were experimentally naïve when the experiment started.

This study complies with the policy of the Guidelines for Ethical Treatment of Animals in Applied Animal Behaviour and Welfare Research (ISAE, 2002).

2.2. Experimental enclosure

The experiment was performed in the animals' exhibition enclosures, which contained grass and trees, and varied in size from 85 to 490 m^2 (Table 1). These enclosures comprised a Starting compartment, a Choice area, a Scattered and a Tray sections (Fig. 1). Scattered and Tray

Table 1
Characteristics of the study animals.

Animal	Weight (kg)	Date of birth in the zoo (B) or capture (C)	Institution	Enclosure size (m^2)
M1	22.2	B 1994	SBCZ	490
F1	20.5	B 1999	SBCZ	490
M2	25.0	C 1998	AMC	454
F2	26.5	C 1998	AMC	454
M3	26.0	B 2005	AMC	85
F3	26.5	B 2005	AMC	85
M4	27.0	B 2002	AMC	99
F4	25.5	B 2002	AMC	99

SBCZ, São Bernardo do Campo Zoo; AMC, Associação Mata Ciliar.

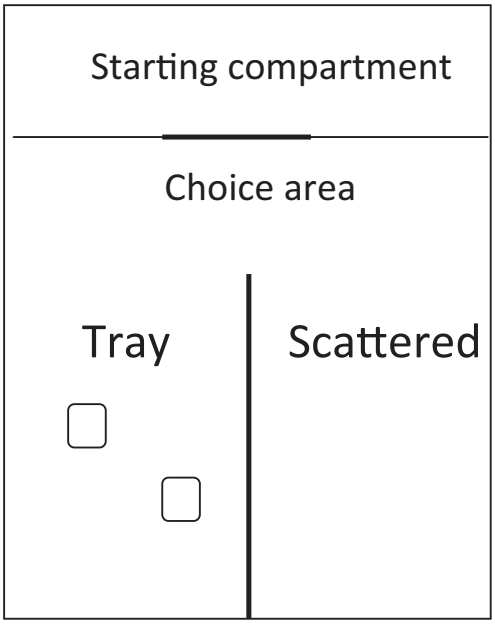

Fig. 1. Experimental set-up: Starting compartment, Choice area, Tray and Scattered sections of the enclosure during experimental tests.

sections were equal halves of the enclosure and were separated by a mesh partition.

2.3. Procedures

Sixteen 30-min videotaped sessions were conducted, with a left-right alternation of sections, so that Scattered (food scattered amongst the vegetation) and Tray (food divided into two trays) sections were alternately situated at the left on half of the sessions, and at the right on the other half. The sessions were performed once a week so that data from each session might be considered independent from the others.

All trials were run between 8:00 and 10:00 h, the regular feeding time in both institutions. Before the start of each experimental session, the usual daily portion of food was divided into two equal amounts: one half was equally divided into two trays (the same trays used to feed the animals during regular husbandry), and placed in the Tray section; the other portion was distributed in the Scattered section. In this section, each piece of food (8–20 per session) was placed randomly at a different location: hidden amongst the grass, inside tree trunks, under stones, or in holes in the ground, to make their location as unpredictable as possible.

The animals were tested in pairs (Sherwin, 2003; Lindqvist et al., 2002, 2006). The wolves, kept indoors before the beginning of the session, were released (1) simultaneously (pairs M1/F1, M3/F3 and M4/F4) or (2) with the male released some seconds before the female (pair F2/M2) due to enclosure characteristics. When released, animals could see both sections from the starting compartment (trays were visible in the Tray section; no food was visible in the Scattered section). Animals were free to move from one section to another during the test. After the end of the trial, the animals were taken to the indoor quarters and both sections were carefully scrutinised and scanned in order to retrieve every remaining piece of food.

All trials were videotaped with a camera placed outside of the enclosure. Videos were coded by continuous sampling, using the program Solomon Coder Beta (version 11.06.20 ELTE TTK Department of Ethology H-117 Budapest, Hungary). Reliability was tested on a random subsample (20%) of recordings (average Cohen Kappa: 0.96).

Variables assessed were: (1) The section each individual chose at the beginning of the session. (2) The time spent in each area (Choice area, Tray section, Scattered section). The entrance of one animal in a certain area was determined based on the wolves' distinct position: the two forepaws into the area. When in the starting compartment, animals were out of reach of the camera: their location was coded as "out of view". (3) The number of shifts from one section to another. (4) The intake of both animals in each section. This was calculated by subtracting from the food provided, the weigh that remained in the section at the end of the session.

2.4. Data treatment and analysis

As male × female differences in time spent in the Scattered section were not detected (General Linear Model, time in the scattered section as the response variable and sex as the explaining variable), we decided to analyse time and intake data at the pair level. Paired *t* tests were used to compare initial choices, food intake and time spent in each of the sections. Taking the pair as a random factor, the General Linear Model was used to compare the intake and the time spent in the Scattered section amongst pairs, and to test for changes in these variables throughout the experiment (a possible expression of learning or habituation effects).

In order to examine the possible influence each animal might have on the choices of the other one in each pair, we recorded: (1) the number of times animals chose the same section at the very beginning of a session and (2) the proportion of set time (i.e., the time spent in areas where food could be found) they were observed sharing one of the sections during a session.

All data were tested for normality with a *Kolmogorov–Smirnov* test. Statistical tests (with $P < 0.05$ as level of significance) were performed with Minitab Statistical Software (version 13.20, copyright© 2000 Minitab Inc.).

3. Results

3.1. Investigation and manipulation

Immediately upon admittance to the experimental enclosure, wolves ran to the food sites and explored the section they entered running and using paws and muzzles. The animals in a pair were never seen eating together from the same tray or from any of the patches in the Scattered section. Shifts between sections were common during the

Table 2
Mean number of shifts between the sections (Tray and Scattered) and proportion of set time spent sharing a section with another individual during the choice tests.

Animal	Number of shifts between sections mean ± SE	Mean percent of set time sharing a section with another individual mean ± SE
M1	8.44 ± 0.74	26.50 ± 4.14
F1	16.06 ± 1.36	16.88 ± 2.20
M2	12.63 ± 0.81	27.91 ± 3.17
F2	34.44 ± 5.20	11.20 ± 1.63
M3	34.69 ± 3.76	36.60 ± 2.47
F3	33.31 ± 3.27	47.50 ± 2.33
M4	16.81 ± 2.32	45.90 ± 2.83
F4	27.50 ± 4.31	32.98 ± 3.60

sessions (Table 2), no matter which section the animals had started eating in.

3.2. First choice

There was no significant difference between number of initial choices to the Scattered or Tray section ($t = -0.89$, df = 7, $P = 0.402$). Most wolves tended to repeat the side (left or right), in several sections, a possible indication of a laterality bias.

In most of the sessions, an animal's first choice was to enter a different section from the one the other member of the pair entered into. M2/F2, M3/F3 and M4/F4 entered into different sections in 13 out of 16 sessions; M1/F1 in 7 out of 16 sessions.

3.3. Time spent

Animals spent part of each session either in the choice or in the non-visible (Starting compartment) area, they were thus not engaged in active foraging during all the available time. Proportion of time spent by pairs either in the Scattered or in the Tray section was: M1/F1: 47.96% ± 2.72; M2/F2: 47.94% ± 2.74, M3/F3: 64.56% ± 3.77; M4/F4: 72.74% ± 4.51.

All animals spent more than 50% of the mean set time in the Scattered section than in the Tray section (Fig. 2). Mean time spent by each pair in the Scattered section was greater

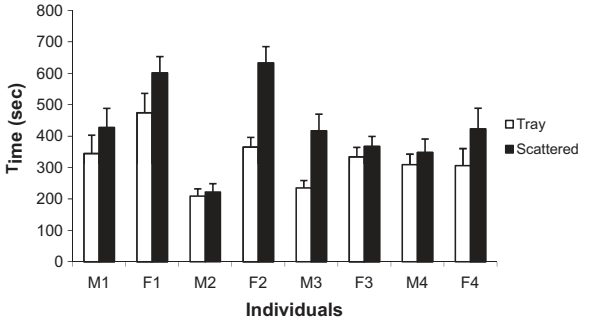

Fig. 2. Mean time (+SE) spent in each test section (Tray and Scattered) by each maned wolf during the choice tests.

than time spent in the Tray section (Paired t-test, $t = 4.29$, df = 3, $P = 0.02$).

All animals spent more time foraging alone in any section than sharing it with the partner (Table 2). Although agonistic behaviours (growls) were rare, we sometimes observed the approach of one animal being followed by the partner shifting to the other section. The animal who first approached one item, was the one who ate it.

Time spent in the Scattered section did not differ amongst pairs (GLM, $F = 1.99$, df = 3, $P = 0.125$), nor was there an effect of sex on this variable (GLM, $F = 3.57$, df = 1, $P = 0.108$). No significant changes in time spent in the Scattered section were evidenced throughout the months of the experiment (GLM $F = 0.52$, df = 3, $P = 0.669$).

3.4. Food intake

There were no significant differences in intake between Scattered and Tray sections (t-test, $t = 2.29$, df = 3, $P = 0.106$, Fig. 3). There were also no differences in the proportion of intake in the Scattered section between pairs (GLM, $F = 0.51$, df = 3, $P = 0.674$), nor throughout the months (GLM, $t = 1.51$, df = 3, $P = 0.222$). In 80% of the sessions, there were leftovers of food, in both sections.

4. Discussion

Our results show that maned wolves, when confronted with a situation in which both an easy (Tray section) and a more costly (Scattered section) alternative of getting food are available, spend more time in the Scattered section and eat an equivalent amount of food in both sections. This outcome strongly supports the conclusion that contrafreeloading exists in maned wolves.

Results may be examined taking as a departure Inglis' set of major explanations for contrafreeloading. Explanations 1 (secondary rewarding value of the costly performance) and 2 (neophobic tendencies towards the "free" alternative) are clearly not valid in our context, as animals were not trained and were more familiar to tray feeding than to searching for food; therefore could not shift to the costly alternative because of any neophobia towards food offered in a very familiar way. Explanation 3 (stimulus change) does not seem plausible either, as contrafreeloading performance remained well after the first (novel) trials; it actually persisted till the end of the experiment.

Is looking for hidden food reinforcing in its own right? Supporters of explanation 4 argue that natural activities would be more likely to generate contrafreeloading than artificial, reward-linked responses. In support of this hypothesis, Young and Lawrence (2003) did not find contrafreeloading in domestic pigs using a pressing apparatus (as the costly alternative) whilst de Jonge et al. (2008) reported contrafreeloading in the same species, offering a task in which food was hidden in straw, a situation that elicits more natural behaviour in pigs. Parrots, when presented with "earned food" in pieces that were larger than the food items they normally consume in the wild did not contrafreeload: they prefer items that more closely resemble native wild foods, such as palm fruits (Rozek and Milam, 2011). It is possible to think that, in our experimental

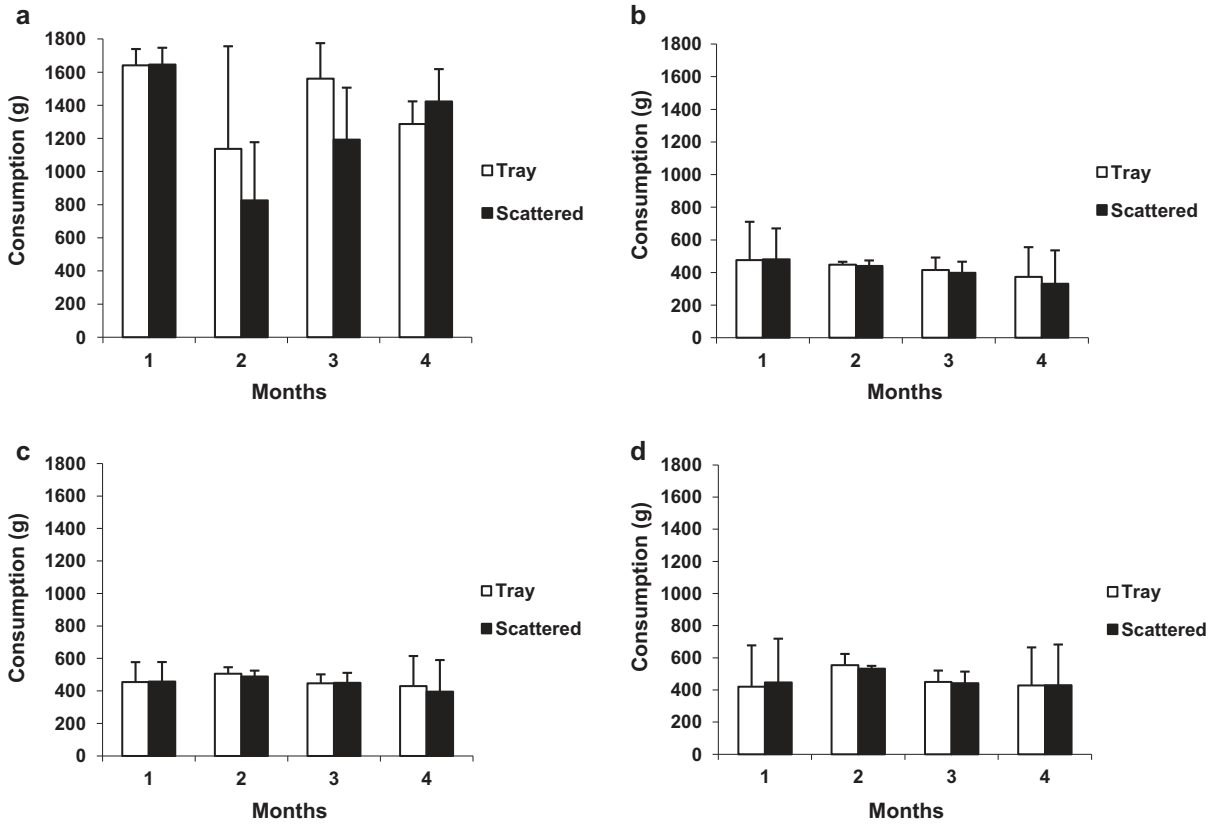

Fig. 3. Average individual food intake (+SE) per month per each pair ((a) M1/F1; (b) M2/F2; (c) M3/F3; (d) M4/F4) in each test section (Tray and Scattered), during the choice tests.

setup, the activities of looking for food placed in different, somewhat unpredictable sites, sometimes requiring active handling performance may be analogous, in captivity, to foraging of maned wolves in the wild; at least, much more than eating from a fully provisioned tray.

Glickman and Sroges (1966), studying exploratory behaviours of birds reported that animals whose natural habit is feeding on a diet that requires extensive search and manipulation (e.g. fruits, insects, reptiles) tend to show sustained investigatory activity, whereas those who feed on readily available food (e.g. leaves) do not. Because maned wolves in the wild feed on a diet that is about 50% fruits and 50% insects, birds, and small mammals (Queirolo and Motta-Junior, 2007), it is expected that they be highly explorative, tending to search and probe from different sources, since these foraging behaviours are essential for their survival. The frequent alternation between the trays and the hidden food spots observed in this study suggests that they used the trays as one of multiple patches of food.

Animals may search for food sources not only because of the food, but also in order to possibly gain information about their environment, such as profitability estimates about these sources (Inglis et al., 1997). Therefore, information about the food which is difficult to access may be also motivating. According to this view (explanation 5), contrafreeloading may have been selected and maintained evolutionarily because it enhances survival in the long term, by providing animals with information about profitable feeding sites, food distribution, and abundance and territory qualities.

Our results fit nicely into explanation 5. We have the exploratory performance, with occasional shifts from one section to the other, which all wolves displayed in the experimental setup. They however do not allow us to distinguish clearly between this explanation and explanation 4, possibly because they seem to approach contrafreeloading from different perspectives. Whilst explanation (4) deals with the proximate causes of behaviour (i.e. the sensory input provided by the performance of behaviour may trigger and/or increase probability of behavioural occurrence), referring to internal states (that are puzzling to test, especially in animals), explanation (5) refers to the ultimate causes (costs and benefits which may have promoted selection and maintenance of behaviour). However, these two explanations regard contrafreeloading as a choice for one situation that seems positive, and preferable from the animals' "point of view", which has implications for welfare.

The greater consumption of pair M1/F1 cannot be attributed to the animals' sizes (Table 1). One can hypothesise that these animals were more active than the other pairs. However, our data do not allow us to speculate about this possibility.

The lateral bias observed in the wolves' first choice (most animals tended to start eating always in the same side of the enclosure as soon as they were released) may have been caused by different stimuli (visual, auditory, olfactory), not always obvious to humans, between the two enclosure sides that might have influenced the animals differently. For example, it is possible that the stimuli from different neighbouring animals on each side of the enclosure have affected the wolves' first choice. Another possible cause for this bias could be a social influence of one animal on another. As maned wolves are solitary animals and the experiment was conducted out of the mating season, we could expect them to be quite reserved and, to some extent, avoid contact with each other and forage on their own. Our data seem to support this expectation: animals in the same enclosure usually chose different sections to start feeding in and all animals spent more time foraging alone than sharing the section with the partner. These data point to the possibility of a certain level (although not absolute) of avoidance between the members of a pair. Should this avoidance be absolute, and one could expect the animals to spend the whole sessions separated. As a consequence, on the pair level, we would not have found contrafreeloading since only one animal would be able to spend more time in the Scattered section (the other one would be in a different section), which is not what we observed. When we examine all these results, we observe whatever the influence one animal has upon its companion, this did not prevent all animals from spending more than half of their observed time in the Scattered section.

The limitations of this study were similar to the ones faced by other studies which worked with wild species (Forthman et al., 1992; Jones and Pillay, 2004; Lindqvist et al., 2002; McGowan et al., 2010; Parker et al., 2006; Shepherdson et al., 1993; Weidenmayer, 1998), especially if endangered. These studies worked with the number of animals available to generate relevant data on less well-known species. Even with these constraints, we have shown a measurable effect of contrafreeloading, which suggests the strength of the contrafreeloading effect may surpass all the possible confounding noise discussed above. The investigation of the contrafreeloading would profit from further studies, with more wild animals, especially if designed to distinguish between the possible explanations for the phenomenon.

Maned wolves paid a price to perform foraging behaviour, which is here represented as extra energy and time to access food sources and consume the same amount of food they could do with no effort in the Tray section. The considerable proportion of contrafreeloading observed in these animals may be taken as an indication of the importance of foraging for the study animals. These results support the findings of other studies (Meehan and Mench, 2007; Morgan and Tromborg, 2007; Ross, 2006; Van de Weerd et al., 2006) that observed a positive effect of the provision of choices and appropriate challenges over the welfare of the animals and point to the importance of providing opportunities for the performance of foraging behaviours for this species.

In conclusion, maned wolves performed a considerable proportion of contrafreeloading and showed interest in demanding food. This tendency to spend extra time foraging indicates the value of foraging activities for these animals; therefore, the lack of opportunities for this performance is likely to decrease the welfare in captive specimens. We recommend the promotion of foraging opportunities in order to improve welfare of captive maned wolves.

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