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## Hog badger (*Arctonyx collaris*) latrine use in relation to food abundance: evidence of the scarce factor paradox

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**Abstract.** Many carnivores use latrines, and investigations of latrine use have typically been concerned with territorial defense, often at the expense of fully evaluating other, not mutually exclusive, functions. In particular, the relationship between food abundance and latrine use patterns has been explored inadequately, where latrine location may be used to aid spatial memory, to stake a claim on access to temporally variable food resources, or to signal the local depletion of resources. Little is known about the hog badger (*Arctonyx collaris*), however the consensus is that they are solitary, but nonetheless deposit their feces in latrines, but without any group-territory defense function. This provides an ideal study system to investigate how temporal and spatial variation in latrine use strategy is associated with food resource availability throughout the year. We use generalized linear mixed models (GLMM) and an information-theoretic approach to test the hypothesis that seasonal latrine use patterns signal the resources most valued (i.e., the foraging book keeping hypothesis). We found that latrine use showed significant seasonal and habitat-related variations, where the number of feces per latrine reached seasonal maxima in early summer but was lowest in autumn, and was significantly higher in logged forest and selectively logged forest but lowest in farmland. The intensity of latrine use exhibited a significant negative relationship with environmental food abundance, and was related to dietary output (fecal contents). That is, hog badgers invested most in ‘marking’ those more limited resources, concurring with the scarce factor paradox, which asserts that the value of any commodity is a function of its rarity.

**Key words:** *Arctonyx collaris*; China; diet; foraging; latrine; mustelid; resource distribution and defense; scarce factor paradox; scent marking; subtropical forest.

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## INTRODUCTION

Most carnivore species make use of their intrinsically pungent feces for scent-marking, often deposited in localized defecation sites, or latrines (reviewed by Macdonald 1985, Hutchings and White 2000). Although we recognize that latrines can also serve other functions unrelated to scent-marking (reviewed by Buesching and Jordan, *in press*), here we will concentrate on their generally accepted function in olfactory communication (Macdonald 1985; Buesching and Jordan, *in press*). Latrine sites typically comprise several feces, are visited at regular intervals (Roper et al. 1993, Kilshaw et al. 2009), and—depending on the social organization of the species concerned—are often used by more than one individual (Buesching and Macdonald 2001). Investigations into latrine use are generally limited to territorial defense (Begg et al. 2003, Jordan et al. 2007, Kilshaw et al. 2009), often at the expense of fully evaluating other, not mutually exclusive functions.

Patterns of latrine use may signal the local depletion of resources (e.g., the passive range exclusion hypothesis; see Stewart et al. 1997), and/or have implications for disease transmission (Page et al. 1999, Riordan et al. 2011) and parasite avoidance (Hutchings et al. 2001, Ezenwa 2004); while at the ecosystem level, latrine use can relate to endozoochory seed dispersal (Zhou et al. 2008b, Capece et al. 2013, O’Farrill et al. 2013).

In particular, the relationship between environmental food abundance and latrine use patterns has been under-explored, and that is our focus here. Different latrines, in different locations, may aid spatial memory in order to optimize foraging efficiency (Garber 1989), to stake a claim on access to temporally variable and potentially limiting scarce food resources (especially by females raising young: Covich 1976, Mertl-Millhollen 2006, Espírito-Santo et al. 2007).

The hog badger (*Arctonyx collaris*) is a medium-sized monotypic carnivore species, which is distributed throughout sub-tropical East and Southeast Asia, including much of China, the eastern Indian Subcontinent, Indo-China and Sumatra (Helgen et al. 2008), and classified as “Near Threatened” by IUCN. Very little is known about hog badgers (Helgen et al. 2008), making it

imperative and helpful to better understand their socio-ecology, to inform conservation measures (Hutchings and White 2000). Their social system is not firmly established, although the consensus is that they are solitary, except for a brief period during the mating season, which, in northern China, occurs during a post-partum estrus in April–May (Zheng et al. 1988). Phylogenetically (see Bryant et al. 1993), it would seem plausible that they may have delayed implantation, as known in other mustelids (Thom et al. 2004). Although speculative, this would fit with superficial observations that both mating and cub rearing season seem to overlap (Zheng et al. 1988).

Although information on their individual territorial ranges is lacking, they nonetheless are known to deposit their feces in latrines, where camera trapping has revealed that these are used by several individuals (Y. C. Wang, *personal communication*; Zhou et al. *unpublished data*).

Their emerging social system is thus ecologically similar to that of low-density populations of the better known European badger, *Meles meles*, in southern Europe (Li et al. 2013), where latrines are used in a far less territorial way than in high-density, group-living populations in the south of England (e.g., Roper et al. 1986, 1993, Kilshaw et al. 2009). Under these less territorial circumstances, environmental factors (both biotic and abiotic, spatial and temporal) and variation in food availability have proven the key factors associated with European badger latrine use (Pigozzi 1990).

Our previous long-term surveys, observing seed dispersal mutualism (April 2004–June 2010; Zhou et al. 2013a), indicate that hog badger latrine placement in the environment is non-random. Furthermore, they exhibit dietary shifts in the sub-tropics, tracking the seasonal peaks of their main food items, such as earthworms, arthropod imagoes and fruit (Zheng et al. 1988; Zhou et al., *in press*). Unobstructed by group-territory marking behaviors, hog badgers thus provide an ideal study system to investigate how latrine use patterns relate to food resource availability throughout the year in seasonal, subtropical ecosystems (Zhou et al. 2008a, Almeida et al. 2012, Hanya et al. 2013). We take a eulerian approach to this investigation, by observing defecation patterns at latrines, rather

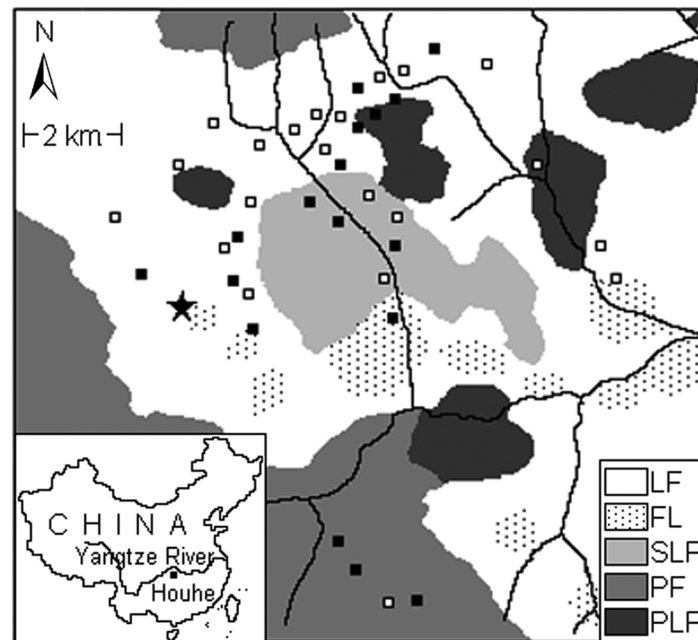


Fig. 1. Map of the study area in Houhe National Nature Reserve, China, illustrating five habitat types and 38 latrine sites (quadrats). PF, primary forest; SLF, selectively logged forest; LF, logged forest; PLF, plantation forest; FL, farmland. Solid black squares represent the 17 latrines used for our survey of environmental food abundance, and the asterisks indicate the position of a supplemental comparative point near farmland (not a true latrine, but a site where two feces were collected). Solid lines denote streams. The location of the Reserve within China is inset.

than tracking individual badgers in a lagrangian way (see Aarts et al. 2008) in part because tracking would only give us information on the presence of the individual in the vicinity of the latrine and not whether it contributed feces; and in part to establish a foundation for further work on this otherwise little-known species.

Here, we use information theoretic modeling (Burnham and Anderson 2002) to investigate: (1) whether latrine site use varies seasonally in different habitat types (Almeida et al. 2012); (2) whether latrine use relates to hog badger diet and responds to the environmental abundance of trophic resources (i.e., the foraging book keeping hypothesis; Henry 1977, Kruuk 1992, Remonti et al. 2011); and (3) whether any patterns in latrine use relate to the abundance or scarcity of key food types in accord with Leontief's scarce factor paradox (Valavanis-Vail 1954), which states that in commodity theory scarcity affects value (Lynn 1991, Patterson 1998).

## METHODS

### Study area

This study was carried out in Houhe National Nature Reserve (30°2'45"–8'40" N, 110°29'25"–40'45" E), located in Hubei Province, central China (Fig. 1). This reserve lies in the transitional belt between the middle and northern subtropical zones and is characterized by four distinct seasons, including a cold winter and a hot, humid summer. Mean annual temperature is 11.5°C, and mean annual precipitation is 1,814 mm. The study site was located in a mid-mountain alpine habitat zone, at an elevation ranging from 1000 m to 1800 m, with rugged dolomite and limestone geology. Based on human management, we categorized habitats within the reserve into primary (unlogged) forest (PF), selectively logged forest (SLF), logged forest (LF), plantation forest (PLF), and farmland (FL) (see Zhou et al. 2008a for details).

### Survey procedure

Informed by our earlier long-term surveys in Houhe National Nature Reserve, observing carnivore ecology and behavior (April 2004–June 2010; Zhou et al. 2008a, 2008b, 2013a), and by the advice of local previous trappers, we located and monitored latrines every two-weeks between February 2011 and April 2013 along 14 transects, with an average length of 2.49 km (0.78 SD; range 1.4–4.3 km; total transect length = 34.8 km) traversing the five habitat categories (Fig. 1). The terrain in our study site is extremely rugged. This has two-fold implications. Firstly, it made it impractical for us to generate linear cross-country transects, because these would likely have not been surveyable. Secondly, we know from our other survey work in this study area that a lot of terrain comprises very unsuitable habitat for hog badgers, which they do not appear to use (Zhou et al. 2013c). Consequently, to optimize ability to collect meaningful data on latrine use patterns, we positioned transects in areas used consistently by hog badgers, such as hill slopes, ditches, roads, trails, natural narrow paths and habitat patch edges (ecotones) (Zheng et al. 1988, Zhang et al. 2009). While this survey protocol was designed to enable us to collect more useful data than surveying random linear transects (we are confident to have included the majority (>95%) of hog badger latrines in these surveys), this selective sub-sampling should not influence the relative use of these latrines in relation to proximate food resources.

The position of latrines and any additional feces encountered opportunistically were recorded along each transect survey, following the methods of Zhou et al. (2008a). A site was considered a latrine only if it contained  $\geq 3$  scats combined across all visits, and was used  $\geq 3$  times over the duration of the study (Crowley et al. 2012). Unique latrine sites were delimited as sites at least 10 m apart.

In our previous long-term surveys, observing seed dispersal mutualism (April 2004–June 2010; Zhou et al. 2013a), we recovered no hog badger feces between December–February, corroborating that hog badgers undergo a period of winter torpor or (semi-) hibernation from November to March in central and northern China (Zheng et al. 1988). In addition, the potential for winter snow cover in this mountainous study site (see

Zhou et al. 2013a) would have impaired our ability to find scats reliably, and biased our results. Consequently, we defined sub-seasons with respect to the seasonal rhythm of hog badger biology, as well as seasonality in environmental food abundance: spring (March–April), early summer (May–June; where spring and early summer comprise the reported breeding season), summer (July–August), autumn (September–October), early winter (November–December), and winter (January–February).

### Diet analysis

Individual fecal samples were soaked in water and washed through three sieves of 1.5, 0.5, and 0.1 mm mesh size, using up to one liter of water, following the standard analytical procedures described by Kruuk and Parish (1981). We divided the items recovered from hog badgers feces to represent the six principle food categories consumed, reflecting foraging behavior; these categories being comparable to those used in European badger studies (Murdoch and Buyandelger 2010, Li et al. 2013): earthworms, insects, diplopods, invertebrate larvae, fruits and other minor items (i.e., mammals, birds, reptiles and fungi).

We then extrapolated the actual biomass of food items consumed from the average fresh mass of that food item (Zhou et al. 2008a), or by multiplying the dry mass of prey remains with a coefficient of digestibility—i.e., the correction factor (Jędrzejewska and Jędrzejewski 1998). Hog badgers prefer multi-seed fruit (Zhou et al., *in press*), and we therefore counted the mean number of seeds per fruit and the mean mass of fruits from parent plants for each fresh fruit specimen collected. For unidentified seeds, we used an estimate of average fruit mass. Data on the mean number of seeds per fruit and fruit mass were obtained from Zhou et al. (2013b). We assigned invertebrate prey species their average fresh weight from measurements of specimens in the field. Consumed biomass of vertebrate prey and fungi were calculated by using correction factors provided by Martin et al. (1995) and Revilla and Palomares (2002) for European badger diet.

### Key food resource abundance

The environmental abundance of these food



categories (except for ‘other’) was quantified for 17 of the 38 latrine sites identified, as well as at an additional farmland site. At each of these 18 sampling points (Fig. 1), we used the formalin extraction method (Raw 1959, Callaham and Hendrix 1997) to measure earthworm and invertebrate larvae abundance; however, because formalin sampling for earthworms is toxic and kills soil microbiota, we sought to minimize our environmental impact by only sampling at every second latrine. To do this, we laid out duplicate  $0.5 \times 0.5$  m quadrates over which we poured four liters of 5% formalin solution, and collected specimens surfacing over 20 minutes. In addition, we dug through the sample plot to a depth of 20 cm in order to count all individuals killed by formalin. All specimens collected were weighed and measured. Because earthworms in the study region are available throughout the year (Zhang et al. 2010), we undertook sampling once in each sub-season.

For other prey types, we sampled duplicate 50-m length transects (1 m width) within ca. 50 m of each of the 18 sampling sites, following the methods of Revilla and Palomares (2002). Insects and diplopods were counted, collected, inspected, weighed and measured. In total, 36 (18 duplicates) arthropod-transects were sampled once in each of the six sub-seasons. Because hog badgers are entirely cursorial feeders, we used the number and weight of ripe fruits on the ground along these same arthropod-transects to represent fruit availability.

#### Statistical procedure

We used R language for statistical computing (version 3.0.1; R Development Core Team 2013) for all analyses. Due to over-dispersion in the data set, a negative binomial model was used to analyze variation in fecal deposition at latrine sites over time and across habitats. We used a likelihood ratio test, confirming that this negative binomial distribution was preferable to Poisson (see *Results*). We included the explanatory variables sub-season, year and habitat, and applied a Tukey’s hsd multiple comparison test ( $\alpha = 0.05$ ) for post hoc comparisons.

To analyze the effects of environmental food abundance on latrine use patterns, we used a generalized linear mixed model (GLMM, the “lme4” package), resolving upon a Poisson

distribution, with a logarithmic link function. The abundance of the different food categories was included as explanatory variables (fixed effects). To control for repeated observations from the same latrine, we used ‘latrine’ as a random factor (Schielzeth and Forstmeier 2009). Data were  $\ln(x + 1)$  transformed. The variance inflation factor (VIF) was used to assess each variable for excessive multi-collinearity. In VIF values exceeded 10, we would have excluded the variable involved from the analysis (Chatterjee and Hadi 2012), however, in this study none of the model variables had excessive multi-collinearity.

We used the Akaike Information Criterion corrected for small sample sizes ( $AIC_c$ ) to identify the most parsimonious explanatory models, where models with  $AIC_c$  differences of less than two had substantial support (Burnham and Anderson 2002). We used beta-coefficients and z-statistics ( $P < 0.05$ ) to assess the relative influence of the parameters included within the most-parsimonious explanatory models.

Because we estimated environmental food abundance, we were able to evaluate food selection by comparing these data with ingested biomasses inferred from fecal contents. Food selection was analyzed with a GLM procedure, using the log-likelihood ratio test with a type III hypothesis (ANOVA Type III function in the ‘car’ package), with binomial distribution (ingested biomass versus abundance) and logit link function. We evaluated the simple effects of the continuous variables as well as their interactions with the two categorical ones (i.e., season and habitat). We used log-likelihood ratio tests using chi-square to test whether these models were significantly different (Moya-Laraño and Wise 2007). We then applied the Bonferroni step-down correction (Holm 1979), to adjust the outputs generated with this procedure. To control for repeated observations from the same latrine, we initially tested for random effects (i.e., latrine as a random factor), fitting the general linear mixed models with the lme4 package in R statistical software. To standardize the two biomass measures used for our explanatory variables (i.e., kg/latrine of ingested biomass and kg/100 m<sup>2</sup> for food availability), we adjusted them to present the *percentage* of each prey per latrine or per 100 m<sup>2</sup>, respectively.

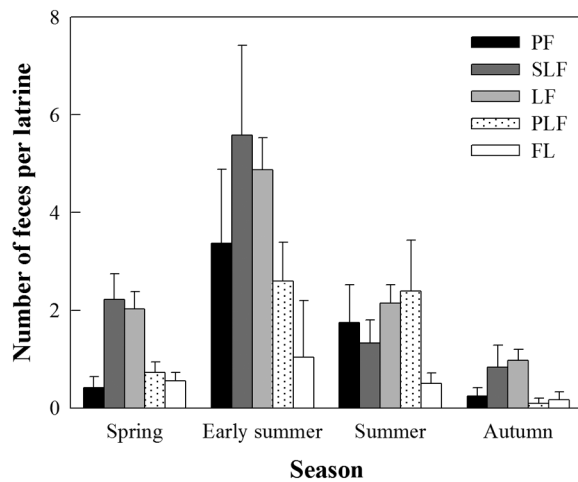


Fig. 2. Number of hog badger (*Arctonyx collaris*) feces (mean  $\pm$  SE) found at each of the 38 latrines per season, across five habitat types, in Houhe National Nature Reserve, China. PF, primary forest; SLF, selectively logged forest; LF, logged forest; PLF, plantation forest; FL, farmland.

## RESULTS

The 38 latrines we located contributed a total of 701 feces between February 2011 and April 2013. An additional 34 feces were found incidentally, as single deposits, during surveys. Latrines each contained between 3 and 54 feces ( $18.45 \pm 12.84$  feces/latrine; mean  $\pm$  SD). For the analysis of spatial and temporal variation in feces counts, the negative binomial regression model performed better than the Poisson regression model ( $G^2 = 269.03$ ,  $P < 0.001$ ). The main effects of season and habitat were significant (season:  $X^2 = 71.396$ ,  $P < 0.001$ ; habitat:  $X^2 = 26.004$ ,  $P < 0.001$ ). In all habitats, the number of feces per latrine reached seasonal maxima in early summer (Tukey's hsd,  $P < 0.009$ ; Fig. 2), and was significantly higher than in autumn ( $P < 0.001$ ). Number of feces per latrine was significantly higher in SLF and LF, and lowest in FL ( $P < 0.008$  in both cases). No significant interaction effects were detected between season and habitat ( $X^2 = 17.702$ ,  $P = 0.125$ ).

### Effects of food abundance on latrine use

The three models we used to examine the effects of food abundance on latrine use had nearly equal AIC<sub>c</sub> support (Table 1). The first-

ranked model (earthworms + fruits) was most parsimonious ( $w_i = 0.458$ ), and included variables that contributed repeatedly in the top eight models, although variables (invertebrate larvae and insects) from the second- and third-ranked models also had the potential to effect the influence of food abundance on latrine use patterns. From AIC<sub>c</sub> models, however, relative importance ( $w_+$ ) and model-averaged variable estimates indicated that earthworms and fruits were the only two influential variables; latrines were used most frequently when earthworms and fruit were least abundant in the environment (Table 2).

### Food selection and fecal output

Despite earthworms being the principal food item selected, with a year-round mean of 45% of ingested biomass, our measures of the contribution this category made to feces, relative to simultaneous seasonal abundance in the environment, showed a tendency for earthworms to be under-utilized in the hog badgers' diet (across all seasons;  $X^2 = 12.587$ ,  $P = 0.027$ ; Table 3 and Fig. 3). By contrast, the opposite was true of insect consumption, with high contributions to feces occurred even when environmental abundance was low; i.e., a significant preference was apparent ( $X^2 = 11.865$ ,  $P = 0.037$ ; Table 3 and Fig. 3). This insect consumption did not, however, influence latrine use. In autumn, hog badger diet was comprised predominantly by fruit (73%; Fig. 3), although this consumption was proportionate to high environmental abundance, with no evidence of selection preference ( $X^2 = 1.278$ ,  $P = 0.734$ ). No seasonal selection preference for diplopods or invertebrate larvae was apparent ( $X^2 = 4.039$ ,  $P = 0.401$  and  $X^2 = 6.465$ ,  $P = 0.167$ ), and we observed no selection preferences across habitat types ( $X^2 = 1.433$ – $4279$ ,  $P = 0.370$ – $0.838$ ).

## DISCUSSION

Fecal marking behavior varies with social system (Buesching and Macdonald 2001) and/or ecological conditions (Remonti et al. 2011, Almeida et al. 2012), such as with seasonality in food resources (Pigozzi 1990). Nevertheless, the function of fecal marking and latrine use is generally assumed to be linked, primarily, to territorial defense (Begg et al. 2003, Jordan et al.

Table 1. Summary of AICc model selection statistics for candidate models relating food abundance with hog badger (*Arctonyx collaris*) feces counts in Houhe National Nature Reserve, China.

Model parameters	Rank	AICc	$\Delta$ AICc	$w_i$
Earthworms, fruits	1	154.55	0.00	0.46
Earthworms, fruits, invertebrate larvae	2	156.11	1.56	0.21
Earthworms, fruits, insects	3	156.33	1.78	0.19
Earthworms, fruits, diplopods	4	156.86	2.31	0.14

2007).

Even for high-density European badger populations, more subtle functions of scent-marking, beyond simple territorial defense (Roper et al. 1986, 1993), have been proposed, such as Passive Range Exclusion (Stewart et al. 1997) and Individual Advertisement (Buesching and Macdonald 2001), and there is evidence of coordination in latrine use between group members (Kilshaw et al. 2009). These different or subsidiary functions are, however, often obscured, or overwhelmed, in studies focused tightly on group defense functions.

By investigating latrine use in a badger species that does not form social groups (i.e., the hog badger), and does not engage in the defense of a group-territory (Johnson et al. 2002), we were able to observe latrine use in relation to the environmental abundance and seasonality of the food types consumed. Although our study design relied on removal of all recorded feces for dietary analysis, any consequential affect on marking behavior would be limited by the fixed volume of feces available within the local hog badger population. Furthermore, any such affects should remain constant throughout the study period and thus have no influence on seasonal or environmental marking patterns. That is, despite our interference with their latrines, we were still able to observe a clear pattern of resource marking.

Specifically, we found evidence that hog badgers mark latrines in relation to food resources, in support of the book keeping hypothesis (Kruuk 1992, Remonti et al. 2011). In particular, their latrine use was inversely related to seasonal variation in environmental food abundance; that is, although they consumed predominantly earthworms and fruits (by season), latrines were used most frequently when earthworm and fruit were least abundant in the environment. Furthermore, despite earthworms comprising 43% of their annual diet, hog badgers did not exploit this resource to its full environmental capacity, rather they selected preferentially for insects. Similarly, they did not fully exploit the abundance of fruits in the environment in autumn, where hog badgers forage not only as insectivores but also play a significant role as fruit consumers and seed dispersers in the study area (Zhou et al. 2008b). They also tended to deposit more feces in latrines in habitat types characterized by poorer food abundance.

This behavior concurs with Leontief's scarce factor paradox (Valavanis-Vail 1954), which states that in commodity theory scarcity affects value (Lynn 1991, Patterson 1998). Similar patterns have been reported for European badgers in central Italy, where latrines were more active in years when the autumnal availability of fruit (i.e., their most important food resource in that study area) was low (Pigozzi 1990). Further

Table 2. Relative influence ( $w_+$ ) and model-averaged estimates for AICc selected model variables relating the effect of food-type abundance on hog badger (*Arctonyx collaris*) feces counts, in Houhe National Nature Reserve, China.

Variable	$w_+$	Coefficient	SE	95% CI	$P$
Intercept		1.312	0.279	0.752–1.860	<0.001
Earthworms	1.00	–0.317	0.088	–0.492–0.146	<0.001
Fruits	1.00	–0.716	0.252	–1.210–0.221	0.005
Invertebrate larvae	0.25	0.167	0.190	–0.207–0.540	0.382
Insects	0.22	0.551	0.744	–0.907–2.009	0.459



Table 3. Significant differences between the utilization and environmental abundance of the principal food categories consumed by hog badgers (*Arctonyx collaris*) at 95% confidence interval, after binomial regression, in Houhe National Nature Reserve, China.

Food items	Season	Ingested biomass	Availability	Z	P
Earthworms (%)	Spring	44.92 ± 5.666	74.39 ± 5.66	-2.994	0.003
	Early summer	62.86 ± 3.77	70.72 ± 6.12	-2.274	0.006
	Summer	52.38 ± 4.89	77.11 ± 4.88	-3.104	0.002
	Autumn	16.09 ± 5.84	58.56 ± 7.54	-3.253	0.001
Insects (%)	Spring	20.42 ± 4.06	5.04 ± 2.59	2.280	0.023
	Early summer	31.14 ± 3.87	1.17 ± 0.54	2.701	0.007
	Summer	34.62 ± 3.68	3.87 ± 1.44	2.745	0.006

Notes: Only significant tests after Bonferroni step-down correction are shown. Results are presented means ± SE.

evidence that hog badgers were marking most when resources were most precious was apparent in the trade-off between energy expended to acquire food and its reciprocal energetic value (Weiner 1992). In spring and early summer, when they fed mostly on ‘expensive’ food items requiring comparatively high energy expenditure to acquire (such as earthworms, which needed to be unearthed), latrines were used more actively than in the autumn, when badgers consumed ‘cheap’ foods (i.e., comparatively low energy expenditure during acquisition), such as fallen

fruit, which could simply be picked up from the ground (Zhou et al., *in press*).

Hog badgers are generalists, with the majority of their food types distributed randomly throughout their habitat (i.e., earthworms, fruits, insects, etc.: Zheng et al. 1988; Zhou et al. *in press*). Thus, in times of food super-abundance (e.g., autumn), it would likely prove unnecessary and uneconomical (Carpenter 1987) for an individual to signal a right of access to these resources, to ensure its food security requirements (*sensu* Carr and Macdonald 1986) were

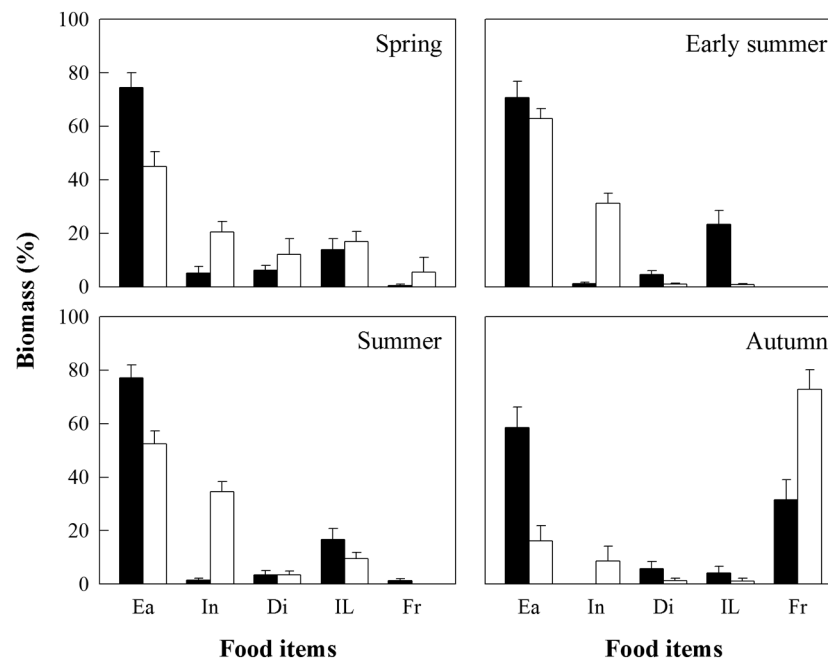


Fig. 3. Biomass (percentage; mean ± SE) of Ea, earthworms; In, insects; Di, diplopods; IL, invertebrate larvae; Fr, fruits available (black) and consumed (white) in the diet of hog badgers (*Arctonyx collaris*) for all seasons in Houhe National Nature Reserve, China.

met, or to mark the depletion of these resource (Stewart et al. 2001). This also concurs with the tenets of the resource dispersion hypothesis (Macdonald 1983) where the dispersion of scarce food patches, occurring at the most food-stressed time of the year (i.e., the most limiting factor; Rosalino et al. 2005), would be predicted to determine the spatial extent and carrying capacity of an individual's range.

In line with this, the spring and early summer peak in latrine use we observed could be due at least in part to the need for lactating mothers to sequester access to resources to ensure sufficient food security to raise their offspring (Buesching and Macdonald 2004, Goltsman et al. 2005). This peak could also be bolstered by individuals advertising their reproductive condition during the spring mating season (Buesching and Macdonald 2001, 2004).

Understanding of the role latrine marking plays in hog badger society also has epidemiological implications. Hog badger removal operations to manage rabies (Hu et al. 2012) would seem likely to disturb patterns of latrine use and social contacts, potentially causing perturbation effects similar to those reported in other species (Prentice et al. 2014), and resonating with lessons from bovine tuberculosis management in European badgers (e.g., Tuytens et al. 2000, Riordan et al. 2011). Habitat management, such forestry operations, influence hog badger latrine use, with latrines being used most in logged and selectively-logged forest and least in farmland; this too has implications for disease epidemiology (White et al. 1993, Delahay et al. 2007).

In conclusion, we provide evidence that hog badger latrine marking behavior concurred with the scarce factor paradox (Valavanis-Vail 1954), where latrine use related inversely to the environmental abundance of the key food resources they consumed (Lynn 1991, Patterson 1998); scarcity driving perceived value. We reiterate that, because almost nothing is known about hog badger ecology, our conclusions must be considered against an almost blank context.

Having taken this initial step to elucidate hog badger socio-biology, individual tracking seems warranted to advance understanding further. While we are entirely open to the possibility that future data may refute, or modify our interpretation, we think this paradigm will prove

resilient, and generalizable, based on knowledge of other similar species. Our future studies will aim to link current findings with marginal value theorem and Oaten's stochastic model of optimal foraging (Green 1980), by matching foraging preferences directly to food availability.

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## LITERATURE CITED

- Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* 31:140–160.
- Almeida, D., R. Barrientos, R. Merino-Aguirre, and D. G. Angeler. 2012. The role of prey abundance and flow regulation in the marking behaviour of Eurasian otters in a Mediterranean catchment. *Animal Behaviour* 84:1475–1482.
- Begg, C. M., K. S. Begg, J. T. Du Toit, and M. B. L. Mills. 2003. Scent-marking behaviour of the honey badger, *Mellivora capensis* (Mustelidae), in the southern Kalahari. *Animal Behaviour* 66:917–929.
- Bryant, H. N., A. P. Russell, and W. D. Fitch. 1993. Phylogenetic relationships within the extant Mustelidae (Carnivora): appraisal of the cladistic status of the Simpsonian subfamilies. *Zoological Journal of the Linnean Society* 108:301–334.
- Buesching, C. D., and N. R. Jordan. *In press*. The function of small carnivore latrines: case studies and a research framework for hypothesis-testing. *In* E. Do Lin San, editor. *Small carnivores in space and time*. Wiley, Oxford, UK.
- Buesching, C. D., and D. W. Macdonald. 2001. Scent-marking behaviour of the European badger (*Meles meles*): resource defence or individual advertisement? Pages 321–327 *in* A. Marchlewska-Koj, J. L. Lepri, and D. Müller-Schwarze, editors. *Chemical signals in vertebrates 9*. Kluwer Academic/Plenum, New York, New York, USA.
- Buesching, C. D., and D. W. Macdonald. 2004.

- Variations in scent-marking behaviour of European badgers *Meles meles* in the vicinity of their setts. *Acta Theriologica* 49:235–246.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Callaham, M. A., and P. F. Hendrix. 1997. Relative abundance and seasonal activity of earthworms (Lumbricidae and Megascolecidae) as determined by hand-sorting and formalin extraction in forest soils on the southern Appalachian Piedmont. *Soil Biology & Biochemistry* 29:317–321.
- Capece, P. I., E. Aliaga-Rossel, and P. A. Jansen. 2013. Viability of small seeds found in feces of the Central American tapir on Barro Colorado Island, Panama. *Integrative Zoology* 8:57–62.
- Carpenter, F. L. 1987. Introduction to the symposium: territoriality: conceptual advances in field and theoretical studies. *American Zoologist* 27:223–228.
- Carr, G. M., and D. W. Macdonald. 1986. The sociality of solitary foragers: a model based on resource dispersion. *Animal Behaviour* 34:1540–1549.
- Chatterjee, S., and A. S. Hadi. 2012. Regression analysis by example. Fifth edition. John Wiley & Sons, New York, New York, USA.
- Covich, A. P. 1976. Analyzing shapes of foraging areas: some ecological and economic theories. *Annual Review of Ecology and Systematics* 7:235–257.
- Crowley, S., C. J. Johnson, and D. Hodder. 2012. Spatial and behavioral scales of habitat selection and activity by river otters at latrine sites. *Journal of Mammalogy* 93:170–182.
- Delahay, R. J., A. I. Ward, N. Walker, B. Long, and C. L. Cheeseman. 2007. Distribution of badger latrines in a high-density population: habitat selection and implications for the transmission of bovine tuberculosis to cattle. *Journal of Zoology* 272:311–320.
- Espírito-Santo, C., L. M. Rosalino, and M. Santos-Reis. 2007. Factors affecting the placement of common genet latrine sites in a mediterranean landscape in Portugal. *Journal of Mammalogy* 88:201–207.
- Ezenwa, V. O. 2004. Selective defecation and selective foraging: Antiparasite behavior in wild ungulates? *Ethology* 110:851–862.
- Garber, P. A. 1989. Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. *American Journal of Primatology* 19:203–216.
- Goltsman, M., E. P. Kruchenkova, S. Sergeev, P. J. Johnson, and D. W. Macdonald. 2005. Effects of food availability on dispersal and cub sex ratio in the Mednyi Arctic fox. *Behavioral Ecology and Sociobiology* 59:198–206.
- Green, R. F. 1980. Bayesian birds: A simple example of Oaten's stochastic model of optimal foraging. *Theoretical Population Biology* 18:244–256.
- Hanya, G., Y. Tsuji, and C. C. Grueter. 2013. Fruiting and flushing phenology in Asian tropical and temperate forests: implications for primate ecology. *Primates* 54:101–110.
- Helgen, K. M., N. T. L. Lim, and L. E. Helgen. 2008. The hog-badger is not an edentate: systematics and evolution of the genus *Arctonyx* (Mammalia: Mustelidae). *Zoological Journal of the Linnean Society* 154:353–385.
- Henry, J. D. 1977. The use of urine marking in the scavenging behavior of the red fox (*Vulpes vulpes*). *Behaviour* 61:82–106.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.
- Hu, R. L., S. F. Zhang, and Y. Liu. 2012. Suggestions on rabies prophylaxis and control in China. *Chinese Journal of Zoonoses* 28:487–491.
- Hutchings, M. R., I. Kyriazakis, and I. J. Gordon. 2001. Herbivore physiological state affects foraging trade-off decisions between nutrient intake and parasite avoidance. *Ecology* 82:1138–1150.
- Hutchings, M. R., and P. C. L. White. 2000. Mustelid scent-marking in managed ecosystems: implications for population management. *Mammal Review* 30:157–169.
- Jędrzejewska, B., and W. Jędrzejewski. 1998. Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. Springer, Berlin, Germany.
- Johnson, D. D. P., W. Jetz, and D. W. Macdonald. 2002. Environmental correlates of badger social spacing across Europe. *Journal of Biogeography* 29:411–425.
- Jordan, N. R., M. I. Cherry, and M. B. Manser. 2007. Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Animal Behaviour* 73:613–622.
- Kilshaw, K., C. Newman, C. Buesching, J. Bunyan, and D. Macdonald. 2009. Coordinated latrine use by European badgers, *Meles Meles*: potential consequences for territory defense. *Journal of Mammalogy* 90:1188–1198.
- Kruuk, H. 1992. Scent marking by otters (*Lutra lutra*): signaling the use of resources. *Behavioral Ecology* 3:133–140.
- Kruuk, H., and T. Parish. 1981. Feeding specialization of the European badger *Meles meles* in Scotland. *Journal of Animal Ecology* 50:773–788.
- Li, F., Z. Luo, C. Li, C. Li, and Z. Jiang. 2013. Biogeographical patterns of the diet of Palearctic badger: Is badger an earthworm specialist predator? *Chinese Science Bulletin* 58:2255–2261.
- Lynn, M. 1991. Scarcity effects on value: A quantitative review of the commodity theory literature. *Psychology & Marketing* 8:43–57.
- Macdonald, D. W. 1983. The ecology of carnivore social behaviour. *Nature* 301:379–384.

- Macdonald, D. W. 1985. The carnivores: order Carnivora. Pages 619–722 in R. Brown and D. W. Macdonald, editors. *Social odours in mammals*. Clarendon Press, Oxford, UK.
- Martin, R., A. Rodriguez, and M. Delibes. 1995. Local feeding specialization by badgers (*Meles meles*) in a Mediterranean environment. *Oecologia* 101:45–50.
- Mertl-Millhollen, A. S. 2006. Scent marking as resource defense by female *Lemur catta*. *American Journal of Primatology* 68:605–621.
- Moya-Laraño, J., and D. H. Wise. 2007. Two simple strategies of analysis to increase the power of experiments with multiple response variables. *Basic and Applied Ecology* 8:398–410.
- Murdoch, J. D., and S. Buyandelger. 2010. An account of badger diet in an arid steppe region of Mongolia. *Journal of Arid Environments* 74:1348–1350.
- O’Farrill, G., M. Galetti, and A. Campos-Arceiz. 2013. Frugivory and seed dispersal by tapirs: an insight on their ecological role. *Integrative Zoology* 8:4–17.
- Page, L. K., R. K. Swihart, and K. R. Kazacos. 1999. Implications of raccoon latrines in the epizootiology of Baylisascariasis. *Journal of Wildlife Diseases* 35:474–480.
- Patterson, M. 1998. Commensuration and theories of value in ecological economics. *Ecological Economics* 25:105–125.
- Pigozzi, G. 1990. Latrine use and the function of territoriality in the European badger, *Meles meles*, in a Mediterranean coastal habitat. *Animal Behaviour* 39:1000–1002.
- Prentice, J. C., G. Marion, P. C. L. White, R. S. Davidson, and M. R. Hutchings. 2014. Demographic processes drive increases in wildlife disease following population reduction. *PLoS ONE* 9:e86563.
- Raw, F. 1959. Estimating earthworm populations by using formalin. *Nature* 184:1661–1662.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Remonti, L., A. Balestrieri, G. Smirolfo, and C. Prigioni. 2011. Scent marking of key food sources in the Eurasian otter. *Annales Zoologici Fennici* 48:287–294.
- Revilla, E., and F. Palomares. 2002. Does local feeding specialization exist in Eurasian badgers? *Canadian Journal of Zoology* 80:83–93.
- Riordan, P., R. J. Delahay, C. Cheeseman, P. J. Johnson, and D. W. Macdonald. 2011. Culling-induced changes in badger (*Meles meles*) behaviour, social organisation and the epidemiology of bovine tuberculosis. *PLoS ONE* 6:e28904.
- Roper, T. J., L. Conradt, J. Butler, S. Christian, J. Ostler, and T. Schmid. 1993. Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland latrine use. *Behaviour* 127:289–307.
- Roper, T. J., D. J. Shepherdson, and J. M. Davies. 1986. Scent marking with feces and anal secretion in the European badger (*Meles meles*): Seasonal and spatial characteristics of latrine use in relation to territoriality. *Behaviour* 97:94–117.
- Rosalino, L. M., D. W. Macdonald, and M. Santos-Reis. 2005. Resource dispersion and badger population density in Mediterranean woodlands: Is food, water or geology the limiting factor? *Oikos* 110:441–452.
- Schielzeth, H., and W. Forstmeier. 2009. Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology* 20:416–420.
- Stewart, P. D., C. Anderson, and D. W. Macdonald. 1997. A mechanism for passive range exclusion: Evidence from the European badger (*Meles meles*). *Journal of Theoretical Biology* 184:279–289.
- Stewart, P. D., D. W. Macdonald, C. Newman, and C. L. Cheeseman. 2001. Boundary faeces and matched advertisement in the European badger (*Meles meles*): a potential role in range exclusion. *Journal of Zoology* 255:191–198.
- Thom, M. D., D. D. Johnson, and D. W. Macdonald. 2004. The evolution and maintenance of delayed implantation in the Mustelidae (Mammalia: Carnivora). *Evolution* 58:175–183.
- Tuytens, F. A. M., R. J. Delahay, D. W. MacDonald, C. L. Cheeseman, B. Long, and C. A. Donnelly. 2000. Spatial perturbation caused by a badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). *Journal of Animal Ecology* 69:815–828.
- Valavanis-Vail, S. 1954. Leontief’s scarce factor paradox. *Journal of Political Economy* 62:523–528.
- Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. *Trends in Ecology & Evolution* 7:384–388.
- White, P. C., J. A. Brown, and S. Harris. 1993. Badgers (*Meles meles*), cattle and bovine tuberculosis (*Mycobacterium bovis*): a hypothesis to explain the influence of habitat on the risk of disease transmission in southwest England. *Proceedings of the Royal Society B* 253:277–284.
- Zhang, L., Y. P. Wang, Y. B. Zhou, C. Newman, Y. Kaneko, D. W. Macdonald, P. P. Jiang, and P. Ding. 2010. Ranging and activity patterns of the group-living ferret badger *Melogale moschata* in central China. *Journal of Mammalogy* 91:101–108.
- Zhang, L., Y. B. Zhou, C. Newman, Y. Kaneko, D. W. Macdonald, P. P. Jiang, and P. Ding. 2009. Niche overlap and sett-site resource partitioning for two sympatric species of badger. *Ethology Ecology & Evolution* 21:89–100.
- Zheng, S., G. Li, S. Song, Y. Han, and Z. Ma. 1988.

- Study on the ecology of sand badger. *Acta Theriologica Sinica* 8:65–72.
- Zhou, Y., C. Newman, C. Jin, Z. Xie, and D. W. Macdonald. 2013a. Anomalous, extreme weather disrupts obligate seed dispersal mutualism: Snow in a subtropical forest ecosystem. *Global Change Biology* 19:2867–2877.
- Zhou, Y., C. Newman, Z. Xie, and D. W. Macdonald. 2013b. Peduncles elicit large-mammal endozoochory in a dry-fruited plant. *Annals of Botany* 112:85–93.
- Zhou, Y., C. D. Buesching, C. Newman, Y. Kaneko, Z. Xie, and D. W. Macdonald. 2013c. Balancing the benefits of ecotourism and development: The effects of visitor trail-use on mammals in a Protected Area in rapidly developing China. *Biological Conservation* 165:18–24.
- Zhou, Y., W. Chen, Y. Kaneko, C. Newman, Z. Liao, X. Zhu, C. D. Buesching, Z. Xie, and D. W. Macdonald. *In press*. Seasonal dietary shifts and food resource exploitation by the hog badger (*Arctonyx collaris*) in a Chinese subtropical forest. *European Journal of Wildlife Research*. doi: 10.1007/s10344-014-0881-5
- Zhou, Y., J. Zhang, E. Slade, L. Zhang, F. Palomares, J. Chen, X. Wang, and S. Zhang. 2008a. Dietary shifts in relation to fruit availability among masked palm civets (*Paguma larvata*) in central China. *Journal of Mammalogy* 89:435–447.
- Zhou, Y., L. Zhang, Y. Kaneko, C. Newman, and X. Wang. 2008b. Frugivory and seed dispersal by a small carnivore, the Chinese ferret-badger, *Melogale moschata*, in a fragmented subtropical forest of central China. *Forest Ecology and Management* 255:1595–1603.