Seasonal body mass changes and feed intake in spectacled bears (Tremarctos ornatus) at Zurich Zoological Garden

Gerstner, Kerstin ; Liesegang, Annette ; Hatt, Jean-Michel ; Clauss, Marcus ; Galeffi, Cordula

Research article

Seasonal body mass changes and feed intake in spectacled bears (*Tremarctos ornatus*) at Zurich Zoological Garden

Kerstin Gerstner[1], Annette Liesegang[1], Jean-Michel Hatt[2], Marcus Clauss[2*] and Cordula Galeffi[3]

[1]Institute for Animal Nutrition
[2]Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 270, 8057 Zurich, Switzerland
[3]Zurich Zoological Garden, Zurich, Switzerland
*Correspondence: Marcus Clauss; mclauss@vetclinic.uzh.ch

Abstract

Many animals display seasonal patterns of behaviour and metabolism that can also be observed in captivity. During an obesity-control programme for spectacled bears (*Tremarctos ornatus*) at Zurich Zoological Garden, a seasonal fluctuation in body mass was observed once ideal body mass had been reached. The aim of this study was to determine whether the metabolism of one male and three female animals was affected by seasonality according to their seasonal breeding behaviour, using data on pelleted food intake (from computer controlled feeders) and body mass (from regular weighing). The pelleted diet in the feeder boxes was provided in addition to a daily ration containing vegetables, fruits, pellets for environmental enrichment and fish. This daily ration was adjusted, within prescribed limits, by the animal keepers depending on the previous day's consumption. Formulas developed for domestic dogs were used to estimate the metabolisable energy (ME) content of the diet and maintenance requirement of the bears depending on their individual body mass. Energy requirements for minimum walked distances between the feeders was calculated as well as energy requirement for fat accretion or energy gained from body fat by body mass loss. Body mass showed a seasonal fluctuation with maxima in spring and minima in autumn, in contrast to the pattern typically observed in animals from the temperate zone; in the male, the body mass maximum occurred later than in the females. Feed intake from feeder boxes peaked in autumn, coinciding with the beginning of body mass gain in the females. These patterns cannot be explained as seasonal adaptations to climatic changes in the zoo environment, but match the natural breeding season of spectacled bears in their natural habitat, suggesting genetically fixed photoperiodic cues. The data indicate that body mass fluctuation within a range considered ideal for the species mostly corresponded to the amount of additional food, which was adjusted – within limits – by the keepers on a daily basis. Such individual adjustment, preventing the risk of obesity in bears, is a good example of the skill required in animal husbandry where not just a single fixed target but a seasonally fluctuating requirement must be met.

Introduction

Living organisms respond to changes in their environment. In the wild, most animals are subjected to seasonal changes in their habitat. Various aspects of their behaviour and physiology have adapted to these changes, mainly focused on tuning their energetically most demanding activity – reproduction – to the times of optimal resource availability, and on surviving extreme times of minimum resource availability in their habitat (Sadleir 1969). Because such seasonal changes have a high predictability, animals have evolved to depend on indirect signals, such as photoperiodic cues, to anticipate changes in resource availability (Bronson 1989). With respect to seasonal reproduction in particular, photoperiodicity also determines biological processes even when animals are kept in human care

where typical seasonal fluctuations in resource availability are dampened or no longer exist (Swanson et al. 1996; Zerbe et al. 2012).

However, animals also respond to changing situations on an ad hoc basis that is independent of seasonal or photoperiodic cues. On a hot day, they may seek shade and reduce food intake; on a cold day, they may increase intake to meet higher thermoregulatory energy demands. A typical behavioural ad hoc mechanism in animals living in either unpredictable or highly seasonal environments that is not necessarily coupled to photoperiod triggers may be to ingest whatever food is available even beyond immediate satiety, in order to store energy as adipose tissue for leaner times (Bosch et al. 2015).

Bears are considered typical representatives of this latter mechanism. On the one hand, seasonal changes in food intake

and body mass can be observed in captive bears that correspond in their timing to those in the wild (Hilderbrand et al. 1999a; McCain et al. 2013). The capacity of bears for storing surplus energy as adipose tissue and, as a consequence, to become extremely obese, is well known (Nelson et al. 1973; Mustonen et al. 2009; Ely et al. 2013). In particular in bears from temperate habitats, enormous variation in adipose tissue mass has been reported in the wild linked to hibernation (Nelson et al. 2014), as well as a propensity for obesity in captivity (Frank et al. 2006). However, even bears from more tropical environments that do not hibernate have been reported to become obese in captivity, such as spectacled bears (also known as Andean bears, *Tremarctos ornatus*; Clauss et al. 2010b; Lisi et al. 2013).

The Andes provide a wide variety of habitats and altitudes including cloud forests, grasslands and dry forests, and the bears prefer the humid and evergreen cloud forests (Rios-Uzeda et al. 2006). The natural diet of the omnivorous spectacled bear contains more than 80 plant or prey species (staple foods include Bromeliaceae, fruits and berries; occasional foods include smaller mammals and livestock; Goldstein et al. 2006; Christiansen 2008; Van Horn et al. 2014). Spectacled bears are polyoestrous and facultative seasonal breeders (Garcia-Rangel 2012). Reproductive seasonality in spectacled bears is considered an adaptation to the temperate climate in which the species evolved, in contrast to its current tropical distribution (Spady et al. 2007). Because the natural habitat of spectacled bears spreads across both sides of the equator (Garcia-Rangel 2012), reports on potential seasonal behaviour must be interpreted with caution. For the wild in general, a mating season between March and October has been reported, though hemisphere and latitude were not specified, and a link with the fruiting season has been suggested (Garcia-Rangel 2012). In captivity the beginning of female oestrus for the northern hemisphere is reported to be in February/March, with a clustering of births in December–February (Spady et al. 2007). Even considering the high variability in gestation period length in the species, which includes a possible period of diapause (Garcia-Rangel 2012), such a birth cluster also suggests increased mating activity in the spring. Because the births cluster at a time when, in a temperate environment, conditions for raising young are not favourable, it appears plausible that spectacled bears have retained a reproductive seasonality from their natural habitat triggered by photoperiodic cues that is not modified by resource provision in captivity (Spady et al. 2007). For specimens kept in captivity in the southern hemisphere, a typical six-month shift in birthing pattern is apparent (Spady et al. 2007).

In an ongoing effort to provide enrichment for spectacled bears (Fischbacher and Schmid 1999), feeder boxes were installed, as repeatedly used for carnivores at Zurich Zoological Garden and other zoos (Carlstead et al. 1991; Jenny and Schmid 2002; Gilbert-Norton et al. 2009), with the aim of introducing a degree of unpredictability in the otherwise predictable food supply to the bears. The use of these feeders facilitated an estimation of seasonal changes in food intake from the feeders, and in the energy required to move between the feeders. Additionally, the bears were weighed regularly in an ongoing effort to control their body mass and prevent obesity (Clauss et al. 2010b). With these data, we tested the following hypotheses:

1. If spectacled bears, as a tropical bear species, do not show an environmentally-triggered seasonal pattern of metabolism, they either (a) show body mass variation related to changes in energetic costs of thermoregulation during winter, which they do not compensate for by increasing food intake at this time (body mass change but no intake change); or (b) maintain a constant body mass throughout the year by increasing food intake at times of increased costs of thermoregulation (no body mass change but intake change).

2. If spectacled bears have an environmentally triggered seasonal metabolism, changes in body mass and food intake occur in the same direction at the same time that either (a) corresponds to the photoperiodicity of their natural habitat, or (b) has adapted to their captive habitat in the northern hemisphere.

Methods

Subjects
Data from four bears between June 2012 and October 2013 were evaluated: three females, "Sisa" (mean body mass ± SD: 80.0 ± 3.3 kg, born in 1992), "Cashu" (64.3 ± 2.0 kg, born 2002) and "Cocha" (61.0 ± 2.6 kg, born 2002), and one male, "Apu" (136.4 ± 6.2 kg, born 1997, moved to Zurich in June 2010). The female "Cashu" left Zurich in June 2013.

Housing
The bears were housed in the Zurich Zoological Garden, sharing their area with six ring-tailed coatis (*Nasua nasua*). The female bears were group housed. The exhibit has been described in detail by Fischbacher and Schmid (1999) and consists of indoor dens and a large outdoor exhibit, which can be separated into three compartments using swing bridges over trenches into units of 1210, 630 and 700 m². Bears were released into the outdoor exhibit from approximately 0945 to 1600 in winter, and had permanent access to the outdoor enclosures during the summer. The outdoor enclosure was cleaned stepwise with the bears still having access to the two other compartments. Except when the indoor dens were being cleaned, bears had access to them. Additionally, the outdoor exhibits offered various den-like resting opportunities filled with straw as insulation material. Daily temperatures were not recorded, but the average temperature was available from the Federal Office of Meteorology and Climatology "MeteoSwiss" (Fig. 1), and showed the typical seasonal fluctuation of a temperate climate in the northern hemisphere.

Diet and feeding
The daily diet consisted of fruit, vegetables and a pelleted feed designed for bears ("Bärenwürfel" 3350, Kliba Nafag, Kaiseraugst, Switzerland) (Fischbacher and Schmid 1999; Clauss et al. 2010b).
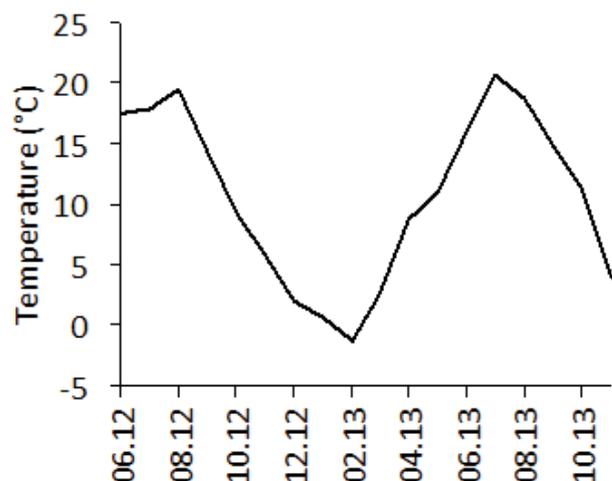

Figure 1. Temperature in Zurich within the time of data collection (Federal Office of Meteorology and Climatology MeteoSwiss; Station Zurich/Fluntern, 47° 22.7' N / 8° 33.9' E).

According to the supplier, the latter contained, on an as fed-basis, 22.5% crude protein, 14% neutral detergent fibre, 3.5% crude fibre, 6% crude fat and 6.3% crude ash, and was composed of grain and soy products as well as poultry meal. The diet fed besides the pellets varied seasonally due to the availability of different vegetables (e.g. lettuce, chicory, cooked potatoes, carrots) and fruits (e.g. apples, oranges, pears, melons), and due to daily adjustments in the amounts fed depending on the previous day's food consumption by the bears. As a rough estimate derived from sporadic weighing of the food items offered, the total daily diet provided approximately 0.8 kg dry matter (or 12.9 MJ ME) per female and 1.4 kg dry matter (or 21.3 MJ ME) per male bear. The feeding instructions allowed only minor deviations from these amounts. In particular, keepers were allowed to reduce these amounts when many leftovers occurred, but were restricted to adding only a few fruits or a handful of pellets per day when they had the impression that the bears consumed all diet items offered. Diet items were scattered all over the bear area twice daily, with the group of females and the male having alternating access to all compartments during the day, and pellets were placed into various objects for enrichment (Fischbacher and Schmid 1999). Therefore, individual intake was unknown. The diet also contained trout (once a week), and honey and nuts approximately once every other month. The fish were offered live in a small pond in the bear area. According to the animal caretakers, the bears caught the fish only occasionally.

A part of the pelleted food was offered by computer-controlled feeder boxes (two feeder boxes in each compartment), installed in November 2011 (six months prior to the beginning of data collection) as enrichment devices to induce searching and locomotion in the bears. The amount of pellets claimed by each bear from these devices was continuously recorded. Several individually randomised time slots (15–60 min each) per day when the boxes would dispend food were provided to each bear. Bears were recognised by the feeder boxes via microchip transponders. If the bear visited the feeder box within one of these time slots, it received pelleted feed in a known amount (between 10 g and 30 g DM) and the computer recorded a successful visit. Amounts offered during one feeder visit were changed irregularly by changing the time setting for the screw conveyor to deliver food from the feeder's storage supply to its outlet. Feeders were refilled regularly. Unsuccessful visits (when the bear approached a box outside its allocated time slot) were also recorded. Because the shortest distance between feeding boxes (along the path used by the bears) was known, this facilitated the estimation of the minimum distance each bear moved on each single day.

Body mass recording
Body mass was measured at least monthly for each bear using a mobile scale (Clauss et al. 2010b). The body mass on individual days was extrapolated by assuming a linear change between two measurements. For further energetic calculations, we assumed that differences in body mass between days represented adipose tissue depletion or accretion.

Calculations
Maintenance energy requirements (MER, in metabolisable energy ME) were estimated as 0.6 MJ ME/kg$^{0.75}$ (Bermingham et al. 2014), for each day. This corresponds to an estimate of 2.3 times the basal metabolic rate using the equation for species in the order Carnivora from McNab (2008). The ME content of body fat was assumed to be 0.04 MJ per gram, with an efficiency of ME utilisation of 0.76 for body fat accretion as described for fattening pigs (Alexander et al. 2011; NRC 2012). Energy utilisation of depleted body fat was considered to be very efficient with 15% heat loss (NRC 2006). The minimum energy requirement for

Table 1. Average composition of the scattered feed component of the total diet that was not offered via feeder boxes to spectacled bears (*Tremarctos ornatus*) at the Zurich Zoological Garden.

Category	Items	Average percentage of the diet (% dry matter)
Fresh	Vegetables (lettuce, carrot, chicory, leaves); fruits (apple, pear, orange, melon)	72
High calories	Nut, raisin, honey, raspberry syrup	5
Proteins	Egg, trout	3
Basis and enrichment	Pellets	20

walking the distances between the feeder boxes was calculated with an equation depending on distance travelled, body mass and speed, assuming an average walking speed of 5 km/h (Best et al. 1981; Taylor et al. 1982). Following the recommendation of Clauss et al. (2010a), the ME content of the pelleted diet was estimated using its crude nutrient composition and the equation for dogs of the NRC (2006); the ME content of the scattered diet (Table 1) was estimated in the same way, using previously published data for nutrient composition from a standard textbook (Souci et al. 1989). The ME content of the pellets was 14 MJ/kg, and the scattered feed part of the diet provided a total of 3.6 MJ/kg. Calculations were performed with Microsoft Excel for Mac 2011 version 14.5.5 (Microsoft Corporation, Redmont, Washington, USA). For a detailed evaluation the period of 2012–2013 was selected, as feeder boxes worked without interruption during this time.

Results

There was a marked seasonal variation in the food intake and hence ME obtained from the feeder boxes (Fig. 2A) and in the additional ME required for movement between feeders (Fig. 2B). Both measures increased, in all bears, in September 2012 (and, to a lesser extent, in September 2013). Both measures dropped again in December 2012.

Prior to the present study attempts to reduce body mass levels of the bears at this facility to normal levels – 100–175 kg for males and 60–82 kg for females (Stirling and Derocher 1990; Nowak 1991; Macdonald 2007) – led to a reduction in body mass in two overweight animals while not compromising growth in several adolescent animals. After this period, a seasonal fluctuation in body mass was evident, whereby body mass peaked in the three females more or less simultaneously in January 2013, although the pattern of increase from September 2012 onwards differed between individuals (Fig. 2C). In the male, the body mass increase started later than in the females and did not coincide with the period of increased food intake from feeders, and also peaked later, in April 2013 (Fig. 2C).

The average ±SD and maximum (the latter given in parentheses) additional ME required for movement was calculated as 0.25±0.15 (1.08) MJ ME/d and 0.19±0.15 (1.17) MJ ME/d, for the male and the females, respectively, which is equivalent to 0.57±0.35 (2.47)% and 0.75±0.57 (4.39)% of the daily ME requirements. The average ±SD (maximum) additional ME gained from adipose tissue stores during times of body mass loss was calculated as 0.005±0.004 (0.03) MJ ME/d and 0.002±0.003 (0.04) for the male and the females, representing 0.04±0.03 (0.2)% and 0.023 ± 0.045 (0.60)% of the
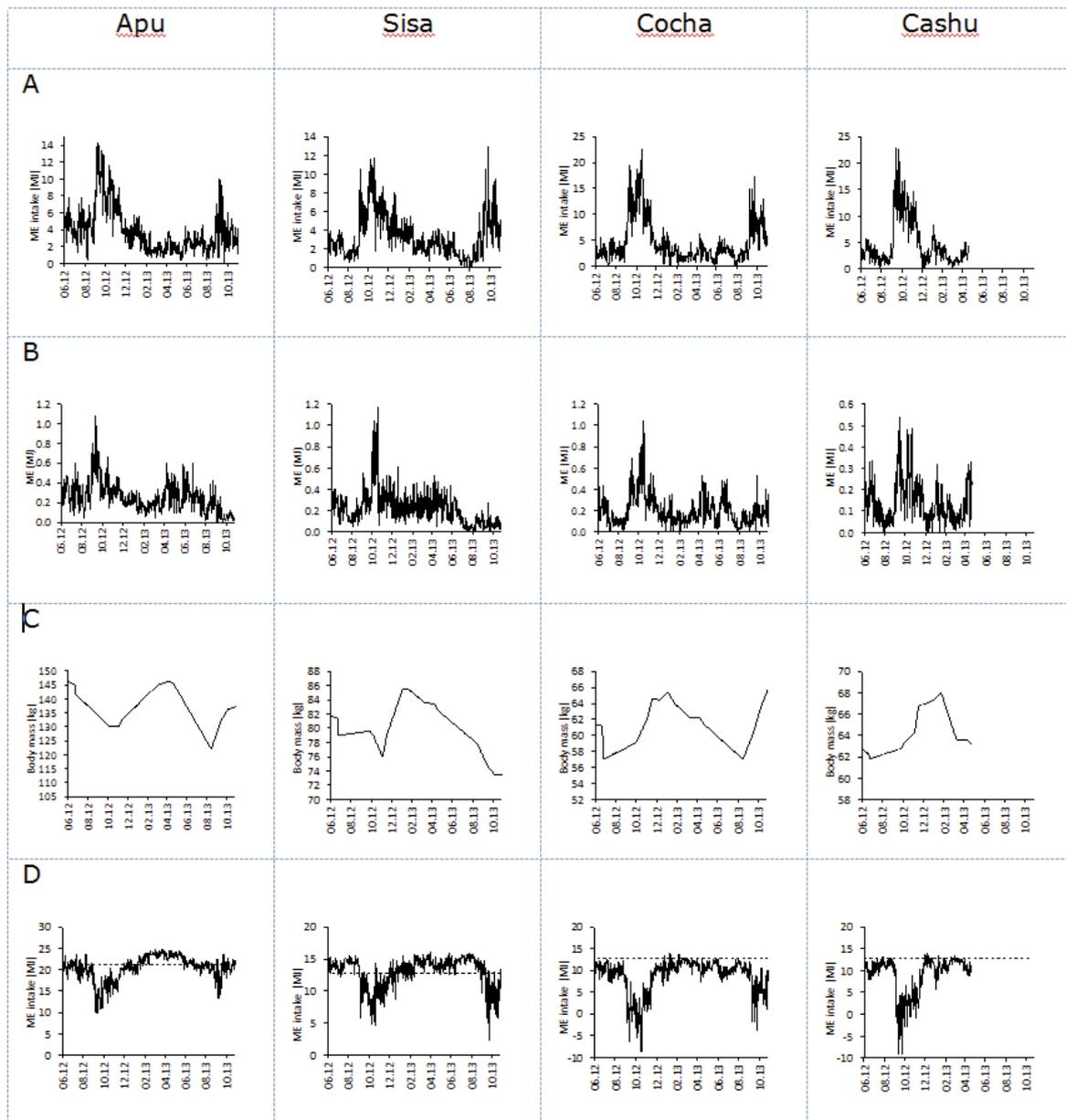
Figure 2. Seasonal patterns in a male (Apu) and three female spectacled bears (*Tremactos ornatus*) of A) metabolisable energy (ME) intake via feeder boxes, B) ME requirement for minimum movement estimates, C) body mass, D) calculated additional ME intake from the scattered feed part of the total diet. The horizontal line in D indicates the total amount of ME offered, on average, to the animal.

daily requirement in these periods. When calculating the amount of ME theoretically necessary to meet calculated requirements of maintenance, movement and potential fat accretion, after subtracting the ME intake from feeder boxes and from potential fat mobilisation, it was evident that this amount was always within the range of the estimate for the amount of scattered food offered (Fig. 2D). In the case of the two younger females, however, the intake of the pellets from feeder boxes exceeded the estimated requirements for maintenance and fat accretion for a certain time period (September/October), leading to a calculated negative ME intake from the scattered diet (Fig. 2D). No noticeable

corresponding decrease in scattered food intake was reported by the animal keepers.

Discussion

Our study reveals seasonal changes in body mass and food intake in spectacled bears at the Zurich Zoological Garden between June 2012 and October 2013. In contrast to the typical timing of herbivores in the temperate zone, an increase in body mass (and hence food intake) was not evident over summer and autumn with a subsequent decrease over the winter period. Rather, a decline

over summer and autumn was evident, with an increase in food intake from feeder boxes in early winter, followed by a general increase in body mass in late winter. In particular, the increased activity and intake at the feeder boxes did not occur at the time of body mass increase, but markedly preceded it, with differences between the peaks in feeder box use and body mass of 70–130 days in the females and approximately 200 days in the male. The resulting impression is that of generally increased activity, as evidenced by feeder box usage, at the onset of increased food intake and body mass accretion. Subsequently, bears relied on their usual diet that was scattered across their enclosures to accrue body mass. These findings do not support hypothesis 1 (no seasonal metabolism); bears did not adjust food intake simply to keep body mass constant, nor did body mass fluctuate simply according to thermoregulatory energy requirements. In contrast, body mass reached a peak in females at the time of the lowest ambient temperatures towards the end of January. Therefore, the findings support hypothesis 2, of seasonal metabolism and behaviour.

The timing of the increase in food intake and body mass coincides with the beginning of oestrus in females, as reported by Spady et al. (2007) for spectacled bears in the northern hemisphere in February/March. Therefore, our findings support the interpretation of Spady et al. (2007) that spectacled bears do not adapt to (seasonal) climatic conditions of their respective zoological institution but retain their natural seasonality. Such behaviour is highly suggestive of a seasonal physiology linked to photoperiodic cues (Zerbe et al. 2012).

The difference between the male and the female bears in the present study also supports the interpretation that it is not a reaction to a seasonal shift in ambient temperature and hence energy requirements for thermoregulation that explains the observed pattern, but a mechanism related to reproduction. For females, increased activity related to the onset of oestrus should be coupled with an accretion of body reserves that will serve a potential conceptus. In brown bears (*Ursus arctos*) and black bears (*Ursus americanus*), differences in reproductive success between populations have been linked to differences in female body mass (Stringham 1990; Hilderbrand et al. 1999b). For males, however, an accretion of body reserves during the time of female oestrus is not a priority compared to finding female partners for reproduction. In many mammals, a loss of male body condition is a typical side-effect of a breeding or rutting period (Miquelle 1990). Thus, a body mass decrease in mature males but an increase in mature, non-lactating females was reported during the breeding periods of black bears (Noyce and Garshelis 1998). Similarly, body mass increased in the male spectacled bear noticeably later in the year than in the three females in the present study.

Several limitations of the present research must be mentioned that are linked to necessary assumptions and constraints on data collection. Assuming body mass changes to represent only changes in adipose tissue, for example as found during weight reduction in domestic cats (Butterwick and Markwell 1996) and dogs (Larsson et al. 2014), is a simplification. For bears, seasonal changes in body mass might affect adipose tissue as well as muscle. However, given the comparatively small calculated contribution of ME from adipose tissue, which is also in contrast with hibernating bear species where adipose stores have to cover the total requirements, the related calculation error can be considered minor.

The most obvious weakness in our calculations is that they led to an assumed negative intake of the scattered food items. This is most probably not due to a miscalculation of the ME content of the offered diet (Clauss et al. 2010a), but to an underestimation of the energy requirements of these animals. Factors not taken into account in our calculations, due to a paucity of data, were the actual daily movement of the animals beyond the minimum that

could be estimated from the distance between the feeder boxes and the number and order of visits, as well as additional costs of thermoregulation. In particular, it could be expected that changes in activity, measured here only as visits to the feeder boxes, led to more distinct changes in the overall locomotion-derived requirements. Deriving ME requirements from an equation established for domestic dogs might have introduced another source of error, and individual energy requirements are subjected to relevant variation due to, for example, breed, coat length, age, temperament and activity in dogs (Kienzle and Rainbird 1991; Harper 1998).

The reported observations demonstrate typical conditions in a zoo setting. Rather than feeding a definitively fixed amount, animal keepers adjusted the diet fed to their impression of the previous day's consumption, within the limits allowed by the defined feeding instructions. This was not done excessively (e.g. a few fruits more or less per day) and in fact facilitated a reduction in body mass in an obese animal before the present study (Clauss et al. 2010b). Hence, small discrepancies between the estimated amount of scattered food required by the bears and the typical "average" daily offer were in reality met by such daily adjustments. Additionally, in the case of the females, one animal might sometimes have compensated for such differences by consuming food intended for, but not required by, another animal (Fig. 2D).

Maintenance of appropriate body mass whilst providing seasonal variation in food quantities offered is challenging in bears, given their typically voracious appetites. The successful manipulation of the amount of scattered feed offered by keepers in the present study, whilst avoiding undesirable consequences such as obesity, reflects a high degree of animal husbandry skill within the keeping team. One important aspect is the palatability of the diet items used. In the management system described in the present study, a pelleted diet item with a comparatively low fibre content (3.5 % crude fibre as fed) was used that nevertheless has, to our experience, a lower palatability, and energy density, than preferred items such as nuts, honey, or meat. Accommodating fluctuating intake behaviours in zoo animals with non-preferred diet items may help reduce the risk of obesity.

Body mass of spectacled bears varies considerably within a range of 100–175 kg for males and 60–82 kg for females (Stirling and Derocher 1990; Nowak 1991; Macdonald 2007). Measured average body mass of the bears at Zurich Zoological Garden was within these limits. Prior to the present study, reducing the amount of food offered led to a distinct body mass decrease in one of the female bears (Sisa) at Zurich Zoological Garden (Clauss et al. 2010b). A seasonal body mass pattern became obvious in this bear after the weight loss. Although long-term data on the period when this animal was obese is lacking, it could be suggested that seasonal body mass shifts may be a sign of an ideal or adequate body condition, as opposed to obesity. Monitoring body condition, and managing animals so as to permit the expression of their typical seasonality, are important goals in captive bear husbandry.

In conclusion, the feed boxes offered to the bears in the present study not only facilitated a change in seasonal intake patterns, but in particular offered an apparent outlet for seasonally changing feeding behaviour patterns putatively related to the onset of a breeding season. Their inclusion in overall dietary management helps achieve the aim that bears should be exposed to a mix of predictable and unpredictable foraging opportunities (Gilbert-Norton et al. 2009). Seasonal changes in body mass did not follow the typical cycle expected in the temperate zone (Fig. 1), but followed the pattern observed in free-ranging animals, which suggests that genetically fixed photoperiodic cues are involved. Managing the seasonal metabolism of bears, even the non-hibernating species, is an important challenge in zoo animal husbandry.

Acknowledgements

References

Alexander L., Salt C., Thomas G., Kienzle E., Butterwick R. (2011) Factorial analysis of energy requirements in entire and neutered growing female colony cats. *Congress of the European Society of Veterinary and Comparative Nutrition* 15:41.

Bermingham E.N., Thomas D.G., Cave N.J., Morris P.J., Butterwick R.F., German A.J. (2014) Energy requirements of adult dogs: A meta-analysis. *Plos One* 9:e109681.

Best R.C., Ronald K., Oritsland N.A. (1981) Physiological indexes of activity and metabolism in the polar bear. *Comparative Biochemistry and Physiology a–Physiology* 69:177–185.

Bosch G., Hagen-Plantinga E.A., Hendriks W.H. (2015) Dietary nutrient profiles of wild wolves: insights for optimal dog nutrition? *British Journal of Nutrition* 113:S40–S54.

Bronson F.H. (1989) *Mammalian Reproductive Biology*. Chicago: University of Chicago Press.

Butterwick R.F., Markwell P.J. (1996) Changes in the body composition of cats during weight reduction by controlled dietary energy restriction. *Veterinary Record* 138:354–357.

Carlstead K., Seidensticker J., Baldwin R. (1991) Environmental enrichment for zoo bears. *Zoo Biology* 10:3–16.

Christiansen P. (2008) Feeding ecology and morphology of the upper canines in bears (Carnivora: Ursidae). *Journal of Morphology* 269:896–908.

Clauss M., Kleffner H., Kienzle E. (2010a) Carnivorous mammals: nutrient digestibility and energy evaluation. *Zoo Biology* 29:687–704.

Clauss M., Zingg R., Ruckstuhl N., Jutz S., Hatt J.-M. (2010b) Weight reduction in spectacled bears (*Tremarctos ornatus*). *Abstract Book of the 6th European Zoo Nutrition Conference*, 6.

Ely J.J., Zavaskis T., Lammey M.L. (2013) Hypertension increases with aging and obesity in chimpanzees (*Pan troglodytes*). *Zoo Biology* 32:79–87.

Fischbacher M., Schmid H. (1999) Feeding enrichment and stereotypic behavior in spectacled bears. *Zoo Biology* 18:363–371.

Frank N., Elliott S.B., Allin S.B., Ramsay E.C. (2006) Blood lipid concentrations and lipoprotein patterns in captive and wild American black bears (*Ursus americanus*). *American Journal of Veterinary Research* 67:335–341.

Garcia-Rangel S. (2012) Andean bear *Tremarctos ornatus* natural history and conservation. *Mammal Review* 42:85–119.

Gilbert-Norton L.B., Leaver L.A., Shivik J.A. (2009) The effect of randomly altering the time and location of feeding on the behaviour of captive coyotes (*Canis latrans*). *Applied Animal Behaviour Science* 120:179–185.

Goldstein I., Paisley S., Wallace R., Jorgenson J.P., Cuesta F., Castellanos A. (2006) Andean bear–livestock conflicts: a review. *Ursus* 17:8–15.

Harper E.J. (1998) Changing perspectives on aging and energy requirements: Aging and digestive function in humans, dogs and cats. Journal of Nutrition 128:2632S–2635S.

Hilderbrand G.V., Jenkins S.G., Schwartz C.C., Hanley T.A., Robbins C.T. (1999a) Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology* 77:1623–1630.

Hilderbrand G.V., Schwartz C.C., Robbins C.T., Jacoby M.E., Hanley T.A., Arthur S.M., Servheen C. (1999b) Importance of dietary meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77:132–138.

Jenny S., Schmid H. (2002) Effect of feeding boxes on the behavior of stereotyping Amur tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich, Switzerland. *Zoo Biology* 21:573–584.

Kienzle E., Rainbird A. (1991) Maintenance energy requirement of dogs – what is the correct value for the calculation of metabolic body-weight in dogs. *Journal of Nutrition* 121:S39–S40.

Larsson C., Vitger A., Jensen R.B., Junghans P., Tauson A.H. (2014) Evaluation of the oral ^{13}C-bicarbonate technique for measurements of energy expenditure in dogs before and after body weight reduction. *Acta Veterinaria Scandinavica* 56:87.

Lisi K.J., Barnes T.L., Edwards M.S. (2013) Bear weight management: a diet reduction plan for an obese spectacled bear (*Tremarctos ornatus*). *Journal of Zoo and Aquarium Research* 1:81–84.

Macdonald D.W. (2007) *The Encyclopedia of Mammals*. Oxford: Oxford University Press.

McCain S., Ramsay E., Kirk C. (2013) The effect of hibernation and captivity on glucose metabolism and thyroid hormones in American black bear (*Ursus americanus*). *Journal of Zoo and Wildlife Medicine* 44:324–332.

McNab B.K. (2008) An analysis of the factors that influence the level and scaling of mammalian BMR. *Comparative Biochemistry and Physiology A* 151:5–28.

Miquelle D.G. (1990) Why don't bull moose eat during the rut? *Behavioral Ecology and Sociobiology* 27:145–151.

Mustonen A.-M., Puukka M., Rouvinen-Watt K., Aho J., Asikainen J., Nieminen P. (2009) Response to fasting in an unnaturally obese carnivore, the captive European polecat *Mustela putorius*. *Experimental Biology and Medicine* 234:1287–1295.

Nelson O.L., Jansen H.T., Galbreath E., Morgenstern K., Gehring J.L., Rigano K.S., Lee J., Gong J., Shaywitz A.J., Vella C.A., Robbins C.T., Corbit K.C. (2014) Grizzly bears exhibit augmented insulin sensitivity while obese prior to a reversible insulin resistance during hibernation. *Cell Metabolism* 20:376–382.

Nelson R.A., Wahner H.W., Jones J.D., Ellefson R.D., Zollman P.E. (1973) Metabolism of bears before, during, and after winter sleep. *American Journal of Physiology* 224:491–496.

Nowak R.M. (1991) *Walker's Mammals of the World, Fifth Edition*. Baltimore: Johns Hopkins University Press.

Noyce K.V., Garshelis D.L. (1998) Spring weight changes in black bears in northcentral Minnesota: the negative foraging period revisited. *Ursus* 10:521–531.

NRC (2006) National Research Council: Nutrient requirements of dogs and cats. National Academy Press, Washington DC.

NRC (2012) *National Research Council: Nutrient Requirements of Swine.* Washington DC: National Academy Press.

Rios-Uzeda B., Gomez H., Wallace R.B. (2006) Habitat preferences of the Andean bear (*Tremarctos ornatus*) in the Bolivian Andes. *Journal of Zoology* 268:271–278.

Sadleir R.M.F.S. (1969) *The Ecology of Reproduction in Wild and Domestic Mammals*. London: Methuen.

Souci S.W., Fachmann W., Kraut H. (1989) *Food Composition and Nutrition Tables*, 4th edn. Stuttgart: Wissenschaftliche Verlagsgesellschaft.

Spady T.J., Lindburg D.G., Durrant B.S. (2007) Evolution of reproductive seasonality in bears. *Mammal Review* 37:21–53.

Stirling I., Derocher A.E. (1990) Factors affecting the evolution and behavioral ecology of the modern bears. *Proceedings of the International Conference of Bear Research and Management* 8:189–204.

Stringham S.F. (1990) Grizzly bear reproductive rate relative to body size. *Proceedings of the International Conference of Bear Research and Management* 8:433–443.

Swanson W.F., Brown J.L., Wildt D.E. (1996) Influence of seasonality on reproductive traits of the male Pallas› cat (*Felis manul*) and implications for captive management. *Journal of Zoo and Wildlife Medicine* 27:234–240.

Taylor C.R., Heglund N.C., Maloiy G.M.O. (1982) Energetics and mechanics of terrestrial locomotion. 1. Metabolic energy-consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology* 97:1–21.

Van Horn R., Appleton R., Amanzo J. (2014) Andean bears in two Peruvian forests are rarely photographed with meat. *International Bear News* 23:20–22.

Zerbe P., Clauss M., Codron D., Bingaman Lackey L., Rensch E., Streich W.J., Hatt J.-M., Müller D.W.H. (2012) Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history. *Biological Reviews* 87:965–990.