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Original Investigation

Foraging activity and food selection in Asiatic black bear orphaned cubs in absence of social learning from a mother

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ABSTRACT

In different groups of mammals the role of social learning in ontogeny of foraging behaviour is variable. Normally developed foraging skills are necessary for the survival of orphaned cubs, released into the wild after rehabilitation. The development of foraging behaviour in Asiatic black bears (*Ursus thibetanus*) has been poorly studied, and the role of learning from the mother remains undefined. Here we investigated the ontogeny of three aspects of foraging behaviour (foraging activity, diet composition and food selection) and compared our observations with literature data on wild adult bears. Two observers (including the author) reared three orphaned Asiatic black bear cubs from the age of three to 20 months in a natural environment in the Far East of Russia. We performed *ad libitum* observations of the cubs' foraging behaviour during daily excursions in the forest, totaling 2000 h of visual observations. The crop of trees and shrubs was estimated visually in grades (0–5) every 10 days. We found that the seasonal dynamics of the cubs' foraging activity correlated with food abundance and their nutritional requirements, allowing fattening for winter survival. The diet composition of the orphaned cubs was species-specific, close to that of wild conspecifics, although showing age-related and geographical specificity. The cubs assessed the edibility of foods via taste and olfaction analyzers, trying various food items and selecting those consumed by wild bears. We conclude that in the ontogeny of Asiatic black bear foraging behaviour, the seasonal dynamics of diet composition and foraging activity are based on inborn mechanisms, while food preferences develop through trial and error, i.e. individual learning. Therefore, we discovered that Asiatic black bear orphaned cubs, grown in a natural environment under the limited care of two observers and with supplemental feeding, are able to learn feeding on natural foods from the age of five months.

Introduction

Behaviour is a combination of innate, individually and socially learned components (Krushinskiy, 1960; Mazur and Seher, 2008; Zentall and Galef, 1988), but their contribution to the behavioural ontogeny remains a controversial issue in animal behavioural ecology. Inborn, or genetically determined, elements in foraging behaviour exist in most animals and represent inherited behavioural predispositions to forage in certain areas on certain foods (Boissy, 1995; Fragaszy and Visalberghi, 1996). Individual learning through trial and error is the primary mechanism of learning, documented for most vertebrate species (Fox, 1969; Thorpe, 1956; Van der Post and Hogeweg, 2006). Social learning from a mother and from unrelated conspecifics in the ontogeny of foraging behaviour is wide-spread in different orders of mammals, such as Chiroptera (Page and Ryan, 2006; Wright et al., 2011), Primates (Boinski and Fragaszy, 1989; Lefebvre, 1995; Luef and Pika, 2013; Voelkl et al., 2006), Rodentia (Aisner and Terkel, 1992; Galef and Clark, 1972), Cetacea (Sargeant and Mann, 2009), Carnivora (Mazur and Seher, 2008) and Artiodactyla (Hessle, 2009). Currently the rehabilitation of large mammalian carnivores is a rapidly developing method in wildlife conservation, especially concerning Ursidae species (Beecham, 2006; Rogers, 1985; Van Dijk, 2005). Orphaned animals grow in absence of a mother and other close adult relatives, thus having fewer opportunities for social learning than cubs reared in a family group. Understanding the mechanisms of foraging behaviour development and the role of social learning in it is a keystone in successful rehabilitation of animal orphans, because their survival depends on the adequacy of their foraging skills.

Most species of bears are omnivorous, opportunistic feeders, whose diets vary seasonally, yearly, geographically, and by habitat (Hwang et al., 2002). Contrary to other carnivores, bears need

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to consume large amounts of different plant foods and invertebrates, which forces them to move constantly in search of food sources and to develop various skills of food discovery and manipulation (Huber, 2010). Bears are characterized by large brain size, well-developed memory, behavioural plasticity and curiosity (Gilbert, 1999; Gittleman, 1986), and all these traits usually correlate with high learning ability (Fragaszy and Visalberghi, 1996; Lefebvre and Giraldeau, 1996; Reader, 2003). The share of learned skills compared to inherited ones in bears seems to be greater than in other carnivores (Huber, 2010). Annual foraging activity in adult brown bears (*Ursus arctos*) is graded into 4 periods: hibernation, walking hibernation, normal activity and hyperphagia (Nelson et al., 1983). No reliable data is available concerning the foraging activity of wild bear cubs living with a mother. It was suggested that food selection in wild brown bear cubs is based on the inborn knowledge about taste and smell of some components of the environment, but also developed with the help of trial and error, individual learning and imitation of their mother's behaviour (Pazhetnov, 1990). In American black bears (*Ursus americanus*), the hypothesis that food-conditioned foraging behaviour is transmitted vertically from sows to cubs was not proved. Food conditioning in young bears was strongly affected by their rearing conditions, but not by their mother's behaviour (Mazur and Seher, 2008). In any case, the process of decision making about edibility of food items has not yet been studied comprehensively in bears.

The Asiatic black bear (*Ursus thibetanus*) is listed as a vulnerable species on the IUCN Red List of Threatened Species; currently its population declines due to high rates of poaching and habitat degradation (Garshelis and Steinmetz, 2008). Foraging behaviour of wild Asiatic black bears has been intensively studied in Russia (Bromley, 1965, 1956; Khramtsov, 1997; Kolchin, 2011; Pizyuk and Seryodkin, 2008; Pizyuk, 2006; Seryodkin et al., 2003, 2002; Skripova, 2013, 2006; Tkachenko, 2002), Japan (Hashimoto et al., 2003; Huygens and Hayashi, 2001; Huygens et al., 2003; Mizukami et al., 2005), Taiwan (Hwang et al., 2002) and China (Malcolm et al., 2014). The full list of the food items, consumed by wild adult Asiatic black bears in the Russian Far East, was provided by G.F. Bromley (Bromley, 1965, 1956). Based on visual observations of rehabilitated orphaned Asiatic black bear cubs in the Ussurijskiy State Reserve (Primorskiy region, Russia), K.V. Skripova registered 50 plant species and presence of insects (unidentified ants and wasps) in their diet (Skripova, 2006). Only 13 plant species overlapped in these two lists of diet composition (Bromley, 1965; Skripova, 2006). Besides the studies in Ussurijskiy Reserve (Skripova, 2006) and our own research (Kolchin, 2011; Pokrovskaya, 2013), the ontogeny of Asiatic black bear foraging behaviour has unlikely been ever studied. The role of social learning from a mother or other conspecifics in development of food habits remains unstudied. In the Russian Far East, annually dozens of cubs become orphans after the winter den hunt and are fated to death or imprisonment (Kolchin, 2011). Orphaned bear cubs under rehabilitation represent a perfect model for investigating the development of foraging behaviour in absence of social learning through imitation of a mother's behaviour.

The goal of our study was to investigate whether social learning is obligate for normal development of species-specific food habits (foraging activity, food choice and food selection) of orphaned Asiatic black bear cubs. To this aim, we compared food habits of orphaned cubs from our experiment and that of wild adult conspecifics in other areas of Russian Far East (Bromley, 1965, 1956; Kolchin, 2011; Seryodkin et al., 2003; Tkachenko, 2002). In particular, we explored the following questions: (1) do orphaned cubs feed on the same foods as wild adult conspecifics in that region, (2) do they show similar seasonal trends in diet composition and foraging activity as wild bears do and (3) how do they estimate the edibility of food items in absence of a mother. Because of the rehabilitation goals of the entire project, we had to follow certain procedures and precautions, not necessary in our study design, such as the permanent presence of observers to provide the cubs with protection from predators, accompanying the cubs in the most productive feeding patches according to seasonal phenology of plant foods, supplemental feeding, making tree sap available to them to drink and using an outdoor enclosure. This approach forced us to deviate somehow from an ideal study design aimed to assess if the foraging behaviour of orphaned cubs would develop normally in the absence of their mother, and we considered this issue in the discussion section.

Material and methods

Study area

The study was conducted on the western slopes of Central Sikhote-Alin Mountains in the watershed of the river Durmin (48°04′ N, 135°50′ E), on the territory of the game preserve «Durminskoe». The study area represents the typical habitat of Asiatic black bears in the southern part of the Russian Far East. Highland relief, drained by the Durmin river and its tributaries, characterizes it. Prevailing altitudes are 400–500 m a.s.l. Climate is ultra-continental with prolonged cold winters and rainy summers (Petrov et al., 2000). The study area was situated in the northern subzone of coniferous-broadleaf forests of the Russian Far East (Kolesnikov, 1969). The main assemblage is formed by broadleaf cedar forests, modified by anthropogenic activity. The most typical tree species on the mountain slopes are Mongolian oak (*Quercus mongolica*) and Korean pine (*Pinus koraiensis*), accompanied by elm (*Ulmus japonica*), birches (*Betula alba*, *B. costata*), asp (*Populus tremula*), Mandshurian walnut (*Juglans mandshurica*), ash (*Fraxinus mandshurica*), maples (*Acer mono*, *A. tegmentosum*) and Amur linden (*Tilia amurensis*) (Kolesnikov, 1969) in the river bottomland.

Ethics statement

This study was carried out in accordance with the recommendations of the Civil Code of the Russian Federation, Article 26 «Keeping and breeding of wildlife in semi-free conditions and artificially created habitat». In March 2009 we obtained an approval for transportation and rearing Asiatic black bear cubs from the Federal Service for Veterinary and Phytosanitary Surveillance in Primorsky Krai and Sakhalin Oblast.

Subjects and rearing conditions

Our study was conducted within the orphaned Asiatic black bear cubs rehabilitation pilot project (Pizyuk and Sagatelova, 2009). The conditions of our experiment differed from ideal ones, because the safety and fitness of the cubs were the first priorities in the rehabilitation process. In March 2009 three Asiatic black bear cubs (two males and one female) aged 2.5–3 months were taken for rehabilitation after their mothers were killed during the winter den hunt. One male cub (Yasha) came from Primorskiy region, and twins (male Shum and female Shiksha) came from Khabarovskiy region. The cubs were reared using the original methods of Dr V.S. Pazhetnov (Pajetnov and Pajetnov, 1998), who has conducted the rehabilitation of brown bear cubs in European Russia for over 30 years. According to these methods, the cubs were raised until weaning age (20 months) under the limited care of two observers (including the author), being constantly exposed to natural surroundings. To prevent human habituation, we minimized tactile and vocal communication between the cubs and observers during all experimental work (except for necessary procedures); the cubs never met any other humans. During the active season (from spring to fall), cubs spent nights in an outdoor enclosure in a remote forest area (1 km away from the game preserve). The enclosure was a spacious (3.1 m × 1.5 m × 1 m) metal cage with a wooden box (0.95 m × 0.78 m × 0.6 m) inside, which the cubs used as a sleeping den. The enclosure remained locked during the night, and they were unable to leave it until we opened it in the morning before taking the cubs on their daily excursion. The main purpose of the enclosure was to protect them from predators (e.g. the Amur tiger *Panthera tigris*, and the brown bear) when the cubs were left in the forest alone, without observers.

Every day (except for days with extremely inclement weather) in April–October 2009 and in April–August 2010, the surrogate family (three bear cubs and one or two observers) conducted excursions into the forest, lasting 6–8 h. Contrary to the Pazhetnov's method, observers accompanied the cubs during their excursions into the forest to provide them with protection from predators. We did not specifically control or affect their behaviour, except for the indirect influence of our presence. In April 2009, during the first forest excursions, the cubs imprinted on the both observers as surrogate parents and started demonstrating pronounced following reaction towards both of them (Lorenz, 1937; Pazhetnov, 1990; Slonim, 1976). Observers selected the routes of the excursions according to seasonal dispersal of main feeding objects, including those places that showed the highest abundance of feeding objects in certain season. Wild female bears usually behave in that way while raising cubs (Pazhetnov, 1990). The forest enclosure was also moved three times from one biotope to another (river valley, dividing ridge and hillside) to get closer to rich feeding spots. During excursions cubs foraged on natural foods and investigated the territory. We never interfered with the feeding behaviour of the cubs during excursions, except for the case of tree sap. In April–May 2009 and 2010, we regularly damaged with an axe the base of tree trunks (birches (mostly *B. costata*), maples and Manchurian walnut) to let the cubs drink the sap of these trees. We performed this procedure because in the spring wild female bears damage tree trunks with their teeth to facilitate cubs' sap drinking, and continue to do so until cubs are able to damage trees themselves (Kolchin, 2011).

After each day's excursion, the cubs received supplementary feeding: infant milk formula "Malyutka"® (at the age 2.5–3 months), later replaced by a cereal made of oats, buckwheat, millet and wheat with minerals and vitamins. The milk formula was a Russian product, composed of demineralized whey powder, a mixture of vegetable oils, maltodextrin, skim milk, probiotics, whey protein concentrate, lactose, minerals, omega-3 and omega-6, complex vitamins choline, soy lecithin, taurine, nucleotides, inositol and L-tryptophan. We regulated the amount of supplementary feeding according to cubs' body size and energy demands in various seasons (Pazhetnov et al., 1999): it varied from 200 ml of milk formula per cub in March 2009 to 2 l of porridge in September–October 2009. We provided supplementary feeding to the cubs because their daily foraging activity was limited by the duration of our excursions (6–8 hours per day). We gave them artificial food after the excursions to compensate for the absence of access to natural foods in the rest part of the day.

From early November 2009 until April 2010, cubs (fitted with plastic yellow ear-tags) hibernated in the forest in the artificial den – a wooden box inside their enclosure, winterized with fir twigs. After their emergence from the den, excursions into the forest were continued. In late August 2010, the cubs (aged 20 months) were released into the wild in the surroundings of the study area. We choose that time for release because the heavy crop of Mongolian oak should have assisted them in transitioning to an independent life on natural foods.

Data collection

To quantify social learning, it is necessary to investigate (a) the presence or absence of a learning experience for each individual, and (b) whether the behavioural outcome was different for those animals that did versus those that did not have a learning experience (Heyes, 1994). Here we compared our data with those concerning wild adult conspecifics to assess possibility of normal development of foraging behaviour in Asiatic black bear in absence of a mother. We observed 2884 bouts of foraging behaviour of orphaned cubs during 1200 hours of observation, in 2009, and 3004 bouts during 800 hours, in 2010. The term «foraging bout» here is defined as a continuous uninterrupted act of foraging behaviour towards the same food items (i.e. foods of the same species and with the same part consumed). Foraging bouts of the three cubs were recorded *ad libitum* (Altmann, 1974), i.e. permanently during all excursions into the forest. For each foraging bout we established the following parameters: (a) date and time, (b) identity of the cub, (c) taxonomic status of the food item (plant or animal species), (d) consumed part of the food item (leaves, leafstalks, flowers, fruits or eggs, larvae, offspring, etc.), (e) was the food item consumed or chewed and spit out and (f) duration of a foraging bout (sec).

Body mass measurements

We weighed the cubs before an excursion in the morning prior to any food consumption. Between the ages of 3–7 months, the cubs were weighed in a canvas bag via using a hanging mechanical beam scale (maximum weight 20 kg, scale interval 0.1 kg); cubs aged 8–20 months – in the iron cage (1 m × 0.5 m × 0.5 m) via hanging spring balance (maximum weight 100 kg, scale interval 1 kg). In 2009, we weighed the cubs every two days between March and April, in May – every five days, in June – every ten days, in July – every 15 days, in August – at the beginning and at the end of the month, in September–October – every five days. In 2010, we weighed the cubs 1–2 times a month. In total, we made 38 mass measurements per each cub in 2009 and 6 measurements per cub in 2010.

Foraging activity

The daily foraging activity (in %), or the role of foraging in daily time budget, was counted as the time spent daily on foraging behaviour, divided by the total time of the excursion. It was assessed separately for each cub in 2009 (N = 135 days) and in 2010 (N = 98 days). We chose six feeding plants, which are the most important in the diet of this species during the fattening period: Amur cherry *Padus Maackii*, Korean pine *Pinus koraiensis*, Mongolian oak *Quercus mongolica*, Manchurian walnut *Juglans mandshurica*, Manchurian filbert *Corylus mandshurica* and hardy kiwi *Actinidia kolomikta* (Bromley, 1965; Khramtsov, 1997; Kolchin, 2011; Seryodkin et al., 2003). Throughout the study we determined the onset and the end of vegetation and fructification periods for these trees, shrubs and lianas in the study area. We estimated their relative crop abundance every 10 days according to Kapper-Formozov scale of visual evaluation of crops of berries, fruits, acorns and seeds of trees and shrubs in grades from 0 to 5 (0 – total crop failure, 1 – bad crop, 2 – low crop, 3 – medium crop, 4 – good crop, 5 – rich crop) (Cherkasov et al., 1981).

Diet composition

To determine the cubs' diet composition we classified all food items into 7 categories according to taxonomic status and eaten part: (1) herbs (leaves, leafstalks, flowers, inflorescence, onions and roots of herbaceous plants); (2) vegetative parts of trees and shrubs (leaves, buds and bark); (3) soft mast (fleshy fruits and berries); (4) hard mast (dry fruits: seeds, acorns, nuts); (5) insects (imago, nymphs and eggs of ants, wasps, bumblebees and hornets);

(6) vertebrates (small live animals, eggs or spawn, offspring and carrion of mammals, birds, reptiles, amphibians and fish); (7) sap of trees (birch and maple syrup). The role of wood mushrooms in the bear diet is negligible, so we did not include it in our analysis. Different parts of the same plant (e.g. leaves, flowers and fruits) were considered different food items. All food items were ranked according to frequency of their occurrence in the diet of the cubs: (a) staple (consumed frequently, >80 times totally for each cub or during very long foraging bouts, >30 min), (b) alternative (consumed occasionally, 20–80 times totally) and (c) marginal (rarely consumed, <20 times totally) foods (as done by Koike, 2010).

To evaluate the seasonal dynamics of diet composition we calculated the role of each food category in the diet of cubs according to their share in foraging activity. It was calculated as the time each cub spent daily on foraging on food items within seven categories (see above) divided by the total time of daily foraging. For the most frequently eaten food items, we showed their share among the other objects within a food category (see Fig. 1). We divided each study period into four seasons (spring (1st April–31st May), early summer (1st June–15th July), late summer (16th July–31st August) and fall (1st September–31st October)) and calculated the mean role of each food category in each season. We compared the mean role of each food category between two consecutive seasons (e.g. spring 2009 and early summer 2009, etc.) and that for the same seasons of two years (e.g. spring 2009 and spring 2010). The daily and seasonal roles of food categories were calculated separately for each cub and then averaged for three of them.

Food preferences

To study food preference development we estimated the number of edible food items (tasted firstly and tasted before) and the number of inedible food items (tasted firstly and tasted before) separately for each month. If a cub tried a new food item and fully consumed several of them (e.g. several leaves, fruits, eggs, etc.), we considered it edible, and if a cub chewed the new food item for a few seconds and then spit out, we considered it inedible. For each inedible item we counted the number of times the cubs tasted the item before rejecting it completely, separately for 2009 and 2010. We also recorded all instances where the cubs experienced alimentary toxicosis symptoms (Gossel, 1994) after feeding on natural foods and analyzed the literature on the possible reasons for it.

Data analysis

We performed statistical analysis in STATISTICA 8.0. We considered the outcomes of the tests statistically significant when the *P*-value was lower than 0.05. Mean values are given in a form of mean ± standard deviation (sd). We compared the role of different food categories in the cubs' foraging activity between four seasons using one-way ANOVA with post hoc Tukey HSD. We used the Spearman Rank test to describe the correlation between the relative crop of main fattening plant foods and the foraging activity of the cubs during periods of fructification of these plants.

Results

Foraging activity

The daily foraging activity of three orphaned cubs fluctuated between 0 to 92.8% of their daily time budget (Fig. 1). In the spring and early summer 2009 the orphaned cubs showed low foraging activity (<20%). In spring 2010, the small peaks of foraging activity (up to 50%) referred to extended bouts of drinking tree sap (birch and maple syrup). In late summer and fall, the foraging activity of the cubs correlated positively with the seasonal dynamics of the crops of six trees and shrubs during the periods of their fructification (Fig. 1). During periods when only plant foods with low or medium crop were available, cubs spent 15–45% of their daily time budget on foraging. In the fall in both years, during the periods of abundant fructification of staple fattening foods, the cubs' foraging activity strongly increased and arrived at the mean value of 45–50% (with maximum values of 90% in August 2009 and 75% in August 2010). In 2009, we recorded two definite peaks of foraging activity, which coincided with rich crop of *Padus maackii* in August ($rs = 0.76$, $N = 40$, $P < 0.001$) and with good crop of *Pinus koraiensis* in late September ($rs = 0.53$, $N = 42$, $P < 0.001$). In 2010 we observed one peak of foraging activity, which coincided with a good crop of *Quercus mongolica* in August ($rs = 0.75$, $N = 37$, $P < 0.001$) (Fig. 1). Since the middle of October 2009, the cubs' foraging activity gradually decreased, and on 7th November 2009, the cubs stopped foraging and began hibernating. The cubs fed almost exclusively on *Padus maackii* (95.5 ± 14.1% of time spent daily on foraging during the period of its fructification, $N = 75$) in August 2009, on *Pinus koraiensis* (90.3 ± 20.4%, $N = 66$) in September and early October 2009, on *Juglans mandshurica* (68.7 ± 35.4%, $N = 17$) in late October 2009 and on *Quercus mongolica* (92.1 ± 17.6%, $N = 26$) in August 2010 (Fig. 1). By October 2009, prior to denning, the body mass of the bear cubs increased six fold compared to their initial mass in March 2009 (Fig. 2). During the 5.5 months of hibernation, the cubs lost 36.6 ± 2.6% of their body mass. In spring 2010, the cubs continued to put on mass again, and by August 2010 they gained nearly all of their maximum body mass, which was registered in October 2009.

Diet composition

The diet of the orphaned cubs consisted of plants (at least 57 food items within 42 species of mostly angiosperm plants), insects (imago, eggs and nymphs of insects, including at least six species of ants and two species of wasps) and vertebrates (live birds, their eggs and chicks of at least four species within the orders Passeriformes, Cuculiformes, and Galliformes, amphibian spawns, and carrion of vertebrate animals (except for fish)) (see appendix 1). Of all plant food items, 13 played a staple role in the diet of the cubs, 10 had an alternative role and 33 were the marginal foods. The diet of the orphaned cubs varied seasonally (Fig. 3, Table 1, appendix 1). From spring until mid-summer of both years, the staple foods were green vegetation (leaves and leafstalks, rarely flowers, of herbs, trees and shrubs). Herbs comprised the greatest share of their diet in spring and early summer. In spring 2010, the cubs spent much time drinking the sap of birches and maples. Insects were the staple foods in both years since May until mid-summer: in May and June cubs ate mostly ants and their brood, and in July wasps as well. During the late summer 2009, cubs consumed almost exclusively soft mast – fleshy fruits of *Padus maackii*. During the fall of 2009 and late summer 2010, hard mast (seeds of *Pinus koraiensis*, nuts of *Juglans mandshurica* and acorns of *Quercus mongolica*) represented the staple foods. Alternative foods were fruits of *Actinidia kolomikta*, *Lonicera edulis*, *Rubus idaeus* during the late summer, and some hard mast (*Corylus mandshurica*, *Tilia amurensis*) in fall. Vertebrate animals (their offspring, eggs and carrion) played an insignificant role in the diet of the orphaned cubs (≤4% of their foraging activity in all seasons). The role of herbs in spring 2009 was smaller than in spring 2010, while the role of tree leaves was vice versa ($P < 0.001$ for both). The role of soft mast was higher in late summer 2009 than in late summer 2010, and vice versa for hard mast ($P < 0.001$ for both). No significant individual differences between cubs have been found.

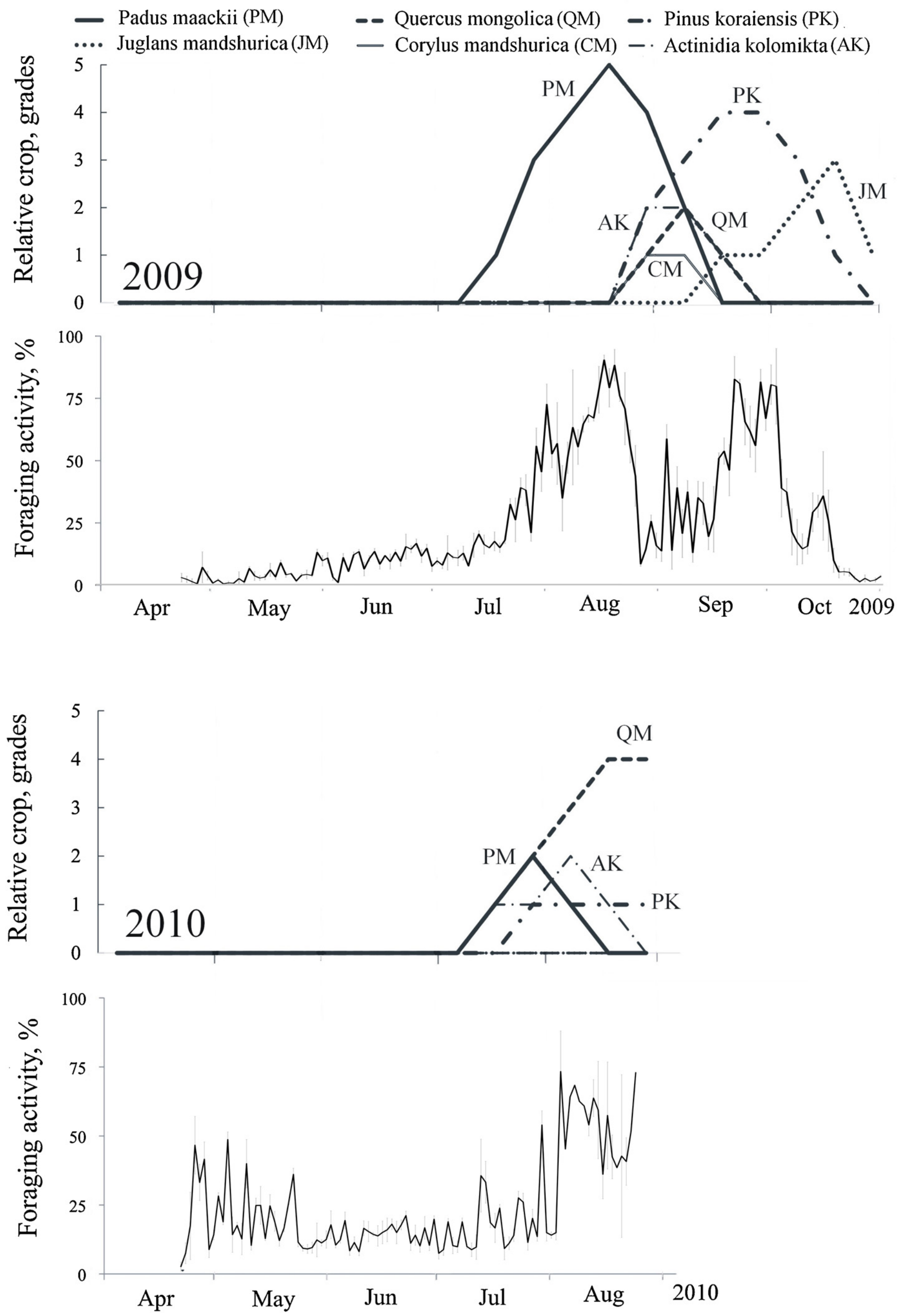

Fig. 1. Relative crop of six staple and alternative plant foods (PM – *Padus maackii*, QM – *Quercus mongolica*, PK – *Pinus koraiensis*, JM – *Juglans mandshurica*, CM – *Corylus mandshurica*, AK – *Actinidia kolomikta*) and daily foraging activity (black line – mean; grey error lines – sd) of three orphaned Asiatic black bear cubs in 2009 and 2010.

Table 1
Role of different food categories in the diet of Asiatic black bear orphan cubs in four seasons of the year. Post hoc Tukey HSD (difference from the previous season): *** $P<0.001$, ** $P<0.01$, * $P<0.05$, ns – not significant.

Year	2009				2010		
Season	Spring	Early summer	Late summer	Fall	Spring	Early summer	Late summer
Herbs	12.4 ± 6.5%	40.6 ± 12.0% (***)	1.2 ± 0.4% (***)	1.5 ± 0.3%	38.2 ± 1.6% (***)	38.7 ± 2.8% (ns)	4.7 ± 3.0% (***)
Trees, shrubs	42.5 ± 1.7%	11.7 ± 5.2% (***)	0.2 ± 0.1% (**)	0.1 ± 0.1%	17.7 ± 4.7% (***)	1.6 ± 0.7% (***)	0.4 ± 0.2%
Soft mast	0.0%	4.3 ± 1.0% (ns)	89.2 + 1.8% (***)	5.0 ± 1.0% (***)	0.0% (ns)	2.5 ± 0.8% (ns)	19.0 ± 10.9% (**)
Hard mast	0.0%	0.7 ± 0.1% (ns)	3.9 + 0.9% (ns)	90.2 ± 1.9% (***)	9.7 ± 0.6% (***)	0.7 ± 0.1% (ns)	54.7 ± 27.3% (***)
Invertebrates	30.8 ± 6.4%	27.5 ± 7.7% (ns)	2.0 ± 1.5% (**)	0.7 ± 0.1% (ns)	10.2 ± 2.9% (ns)	55.2 ± 3.8% (***)	18.8 ± 13.4% (***)
Vertebrates	3.4 ± 0.1%	1.3 ± 0.3% (**)	0.2 ± 0.2% (ns)	0.0% (ns)	0.7 ± 0.2% (ns)	1.5 ± 0.2% (ns)	2.1 ± 1.3% (ns)
Tree juice	1.9 ± 0.3%	0.0% (ns)	0.0% (ns)	0.0% (ns)	20.2 ± 4.5% (***)	0.0% (***)	0.0% (ns)

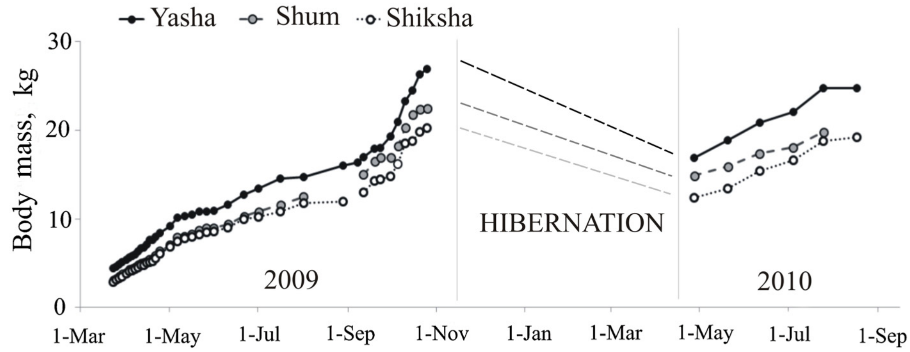

Fig. 2. Body mass dynamics of three Asiatic black bear orphaned bear cubs in the study period.

Food preferences

During forest excursions, the cubs checked the edibility of almost every encountered novel food item (plant, insect, small vertebrate or its remains). The orphaned cubs usually made a correct decision about the inedibility of a food item from the first or second trial (Yasha – 1.6 ± 1.0 trials (N = 29), Shum – 1.1 ± 0.3 trials (N = 15), Shiksha – 1.3 ± 0.9 trials (N = 13)). The number of food objects tasted (both tasted firstly and eaten before), which cubs considered edible, in both years was greatest in May and then gradually decreased from spring to fall (Fig. 4). During the spring and summer (April–August) of the first year of their life, the cubs tasted a greater variety of inedible objects (N = 40), than during the same period in the second year (N = 14).

In May 2010, the cubs experienced toxicosis after regular consumption of purple poisonous spathes (modified leaf around the spadix) of the perennial plant *Symplocarpus renifolius* (family Araceae). All three cubs fed heavily on spathes of this plant during four days in early May, then stopped and ate only edible leaves and leafstalks. Five days after they stopped eating the poisonous spathes, the cubs began to demonstrate symptoms of illness; they repeatedly emitted distress calls (whine and chuffing, see Pokrovskaya, 2013), fed much less than usual, did not play at all, moved very slowly, sometimes with muscle convulsions, or lay

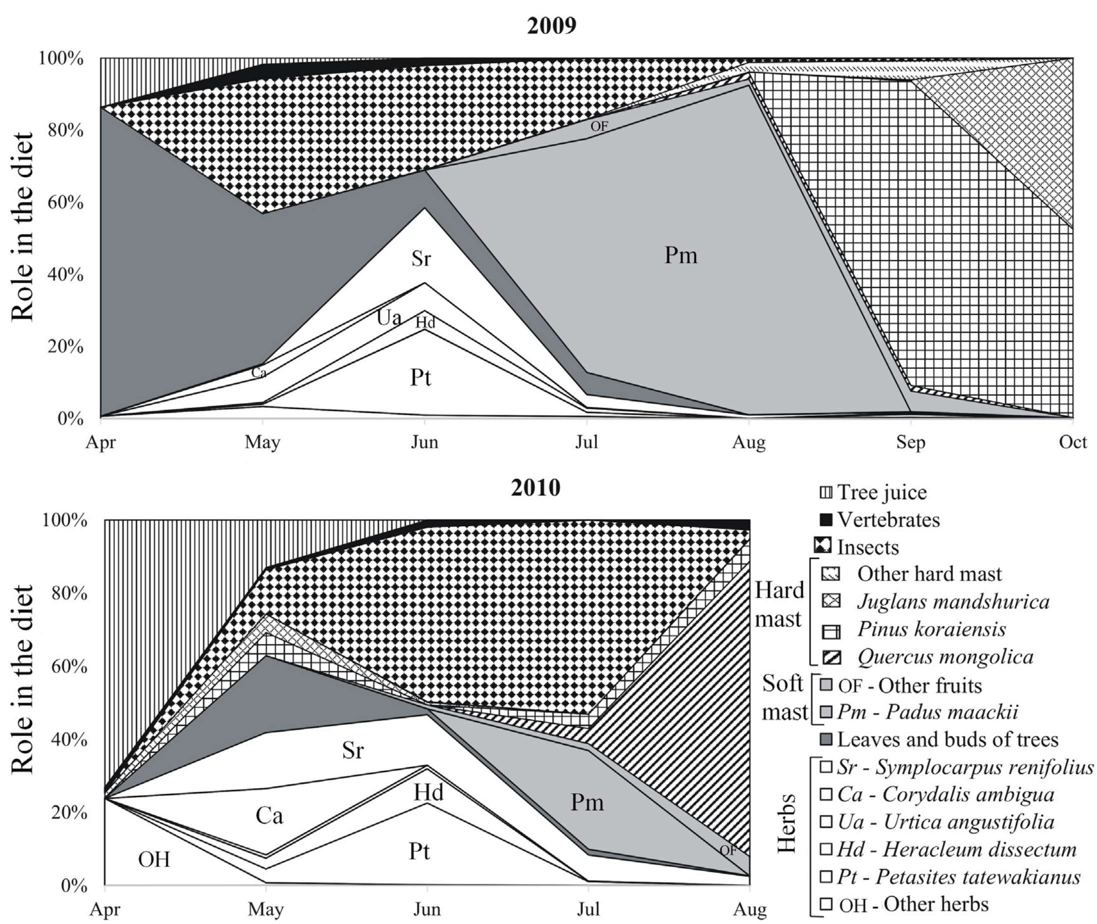

Fig. 3. Seasonal dynamics of the role of different food categories in the diet of Asiatic black bear orphaned cubs.

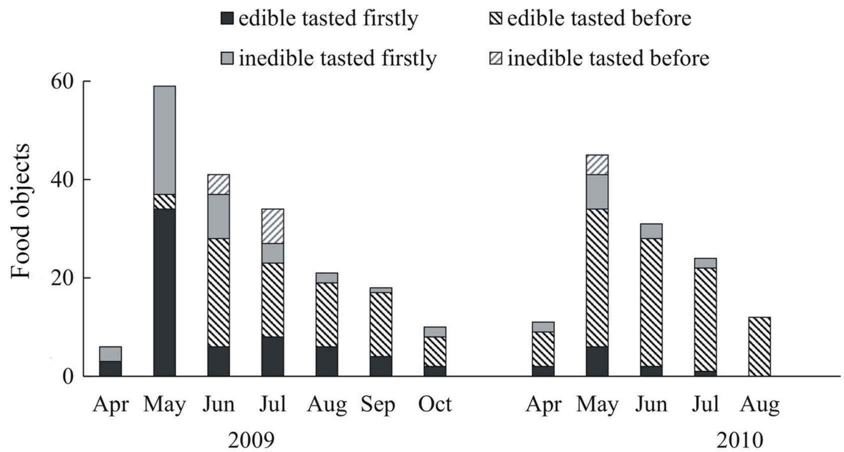

Fig. 4. Number of edible and inedible food objects, accepted and rejected by Asiatic black bear orphaned cubs in each month of years 2009 and 2010.

in a prone position and refused to follow observers, all while vocalizing. The cubs were fully recovered two weeks later the first signs of illness appeared.

Discussion

Initially we will discuss the role of several methodological assumptions (see Methods), aiming to increase success of the rehabilitation, on the results of our study. Both the presence of observers during excursions and the use of the forest enclosure, in which the cubs were locked during all resting times, provided them with protection from predators. Had the cubs been left alone in the forest, most likely they could have been predated upon by the Amur tiger, as this species is the main predator for bear cubs in the Russian Far East (Bromley, 1965; Kolchin, 2011; Skripova, 2013; Yudin and Yudina, 2009). Our presence had minimally affected the food selection and food choice of cubs, although we never taught them to eat anything (except for facilitation of drinking tree sap). However, the routes were not chosen by the cubs, but were planned by the observers according to the seasonal distribution of rich feeding patches. This fact was likely to impact both the selection of foods by the cubs and their foraging activity. In this case their behaviour was much closer to the wild type when the cubs follow the mother bear during foraging trips, but not to the behaviour of the orphans living and foraging independently in the forest. The forest enclosure affected neither their foraging activity, nor the food choice, because we measured foraging activity and food choice only during forest excursions when cubs moved and acted naturally. We provided the cubs with supplementary feeding to model the natural situation when bears are able to forage throughout the day. This factor did not strongly influence the food selection and food choice of cubs, but probably affected their daily foraging activity and body mass growth. We suggest that in absence of supplementary feeding the cubs would have spent their whole daily time budget on foraging, and that they would have gained less fat during the fattening period. On the other hand, the amount of daily supplemental feeding was negligible compared to the cubs' daily intake of natural foods, so we believe that the role of food supplementation was less important for fattening than the natural foods. Therefore, our presence, supplementary feeding and the forest enclosure altogether enhanced the cubs' survival by reducing their vulnerability and increasing their fitness, which are the main goals of rehabilitation. All of these conditions were critical to the cubs' survival in the wild and would have been provided naturally by their mothers. Although these methodological implications just minimally biased our results, we are unable to apply our conclusions to the wild orphaned or mother-reared cubs.

Fattening, monophagia and hyperphagia

The fattening period of bear foraging behaviour is characterized by monophagia, i.e. switching the foraging activity to a single food item which is the most abundant and available at that moment (Gilbert, 1999). Hyperphagia is characterized by an increase of foraging in order to maximize energy accumulation (Nelson et al., 1983). Moderate monophagia of bears under abundant crop conditions of one food species reduces the energy cost of movement and searching for other foods. Increased foraging time, decreased activity, selection and availability of higher quality food items, changes in assimilation efficiency, or reduced levels of baseline or maintenance energy expenditure are possible mechanisms that facilitate the increase of mass involved in preparing for hibernation (Sheriff et al., 2013). We found that the number and amplitude of the peaks of foraging activity of the orphaned Asiatic black bear cubs correlated with the number of staple fattening plant foods (*Padus Maackii*, *Quercus mongolica* and *Pinus koraiensis*). The rapid increase of cubs foraging activity and selection of calorific and abundant foods was caused by the need to reduce their expenditures on locomotion in search of foods and to accumulate fat for a successful hibernation. Similar dynamics of foraging activity have been recorded for orphaned brown bear cubs (Gordienko, 2010; Palomero et al., 1997; Pazhetnov, 1990) and for wild adult Asiatic black bears inhabiting broadleaf forests with cyclical productivity of trees (Huygens et al., 2003; Koike, 2010; Kolchin, 2011).

As cubs grew, the distance between them during forest excursions increased. Although the cubs could separate from each other and feed independently on different food objects on a distance up to 100 m and more. Nevertheless, no significant individual differences have been found in the daily foraging activity of cubs. Our data confirms that the high level of foraging activity during the fall, yearly variations in food habits and a tendency to monophagia and hyperphagia are inborn traits in the Asiatic black bear, occurring in the behaviour of all three orphaned cubs much in the similar way as it occurs in wild Asiatic black bears and other species of Ursidae.

Seasonal dynamics of the diet

Diet composition of the orphaned Asiatic black bear cubs varied in different months according to the seasonal phenology of plants, cycles of productivity of trees and shrubs and life cycles of insects. Similar patterns of seasonal dynamics of diet composition have been shown for wild Asiatic black bears in Russia (Bromley, 1965; Seryodkin et al., 2003; Tkachenko, 2002) and other subspecies of Asiatic black bear inhabiting Japan (Hashimoto et al., 2003; Huygens et al., 2003; Koike, 2010) and Taiwan (Hwang et al., 2002). Staple and alternative foods are green vegetation in spring, soft mast and insects in summer and hard mast in fall. The marginal foods in spring are hard mast from the previous fall crop and other fruits in fall. Seasonal food habits of orphaned cubs showed inter-annual variations: cubs used alternative and marginal foods in response to the yearly variation in staple food amounts, with high variability of food habits during late summer and fall and low variability in spring and early summer, presumably due to the fall fluctuation in fruit production between years. The same pattern was previously shown for adult wild Japanese black bears (*U. t. japonicus*) (Koike, 2010). This suggests that the effect of the inter-annual crop abundance variability is more significant than the effect of cubs' age, but this assumption should be statistically verified on the bigger sample size.

Of all the plant food items that we recorded in the diet of orphaned cubs ($N = 57$), only 26% overlapped with the list of food items consumed by the wild Asiatic black bears in Russia (Bromley, 1965). Of the 13 staple plant food items, eaten by cubs, 54% were previously found in the diet of wild adult conspecifics (Bromley, 1965). G.F. Bromley collected the data on the feeding habits of bears from various geographical locations, and averaged it for bears of different ages and between years with different crops of plant foods. This, together with our special experimental conditions, may be the reason for the difference in diet composition between wild adult bears and the orphaned cubs. We were the first to discover that the Asiatic black bear on the Russian Far East feeds on corydalis (*Corydalis ambigua*), nettle (*Urtica angustifolia*), Fisher's ligularia (*Ligularia fischeri*), equisetum (*Equisetum hiemale*), Korean elder (*Sambucus coreana*), and Siberian ginseng (*Eleutherococcus senticosus*). These plants comprised an important part of the cubs' diet (Kolchin, 2011; our data), although we cannot conclude, based solely on our data, that these plants would be present in the diet of wild adult conspecifics. Our data also differs from those collected via visual observation of the orphaned Asiatic black bear cubs' foraging behaviour in the Ussurijskiy Reserve (Skripova, 2013, 2006). Only 42% of all plant food items from the diet of the cubs in our experiment and 62% of the staple plant foods were found by K.V. Skripova (Skripova, 2006). At least two food items, listed by Skripova, were rejected (considered inedible) by the cubs in our experiment (e.g. leaves of *Juglans mandshurica* and flowers of *Caltha sylvestris*). Probably, these differences are due to regional variability in floristic composition in the Primorskiy (Skripova, 2006) and Khabarovskiy (our data) regions of the Russian Far East.

Studies of the brown bear nutritional physiology showed that bears during the fattening period tend to consume a mixed diet, consisting both of protein (salmon) and carbohydrates (fruits) if both of these food items are abundant (Robbins et al., 2007; Rode and Robbins, 2000). We did not notice a considerable protein intake by the orphaned cubs during the fall. In the diet of the Asiatic black bear insects, but not fish, represents the main source of protein, and their abundance is the greatest during mid-summer and decreases with the beginning of the fattening period. The exploitation of different food resources by sympatric bear species reduces the diet overlap between these species (Fortin et al., 2007). Our data contradict the observations of the wild Formosan black bears (*U. t. formosanus*), which showed a very large proportion of ungulates (both killed and scavenged) and a very small proportion of insects in their diet (Hwang et al., 2002). This difference could be caused by the low age of cubs in our experiment, which were unable to catch and kill large ungulate prey and only consumed the remains of dead animals, while the data on Formosan bears was collected mostly from adult bears. Contrary to the more carnivorous brown bear, the Asiatic black bear, as well as the American black bear, is largely herbivorous and frugivorous (Koike, 2010; Kolchin, 2011). However, in Taiwan, Bhutan, Iran, India and Japan, where livestock depredation by adult Asiatic black bears is often registered (Chauhan, 2005; Gutleb et al., 2005; Hwang et al., 2002; Sakamoto and Aoi, 2005; Sangay and Vernes, 2008).

Therefore, in absence of social learning from a mother, the orphaned bear cubs demonstrated species-specific seasonal dynamics in the diet composition, although the exact composition of food species varied according to the age of the cubs and inter-annual differences in crop abundance of staple plant foods. However, while still having milk teeth, the orphaned cubs were unable to damage tree bark to extract tree and required our assistance. In several cases they used the trees damaged by other bears as an example of social learning via facilitation (Reznikova, 2004). We suspect that as growth and physical development progresses, the cubs will learn by trial and error to gnaw tree bark for sap extraction.

Food selection

During normal uterine development exposes a human or animal infant is exposed to certain gustatory sensations that are more pleasurable than others (Galef, 1981). Responses to novelty can be classified as neophilia or neophobia (Voelkl et al., 2006). While tasting various food items, the orphaned bear cubs in the first year of life made mistakes (tried inedible foods) more often than in the second year of life. Yearlings had already formed their positive or negative preferences towards the majority of food items and did not waste time on analyzing their edibility, even during the first encounter with the item after hibernation. Cubs assessed the edibility of food items not only by the visual appearance of the food item, but also with help of taste and olfactory receptors. The same patterns in food selection process, i.e. tasting everything and spitting out the inedible objects, were shown for orphaned brown bear cubs (Pazhetnov, 1990). Therefore, orphaned bear cubs learn to choose edible food items by individual learning, i.e. by trial and error method (Pazhetnov, 1990; Gordienko, 2010; our data). However, we found no individual differences in food preference between cubs; all three cubs considered the same foods edible and refused to eat the others. That suggests that some information about preferable tastes and smells is an inborn knowledge. We suppose that wild bear cubs growing with a mother would spend less time on tasting inedible food items compared to orphaned cubs, although the data on development of food preferences in wild bear cubs is lacking.

Multiple incidents of the consumption of poisonous purple spathes of *Symplocarpus renifolius* by the orphaned cubs denote that they do not have a strictly fixed inborn knowledge of food preferences, but they learn to choose food items by individual learning, more or less effectively. *Symplocarpus* is known to have curative features and is used in medicine, but may be toxic when consumed in large amounts (Saadi and Modal, 2013). Plants of Araceae contain crystals of calcium oxalate, which causes intense irritation when handling or consuming the raw plant tissue (Mayo et al., 1997). It has been suggested that the oxalate crystals could function as deterrents to herbivores (Franceschi and Horner, 1980), which may cause intense sensations of burning in the mouth and throat, swelling and choking, in larger doses – severe dyspepsia, and breathing difficulties, up to convulsions, coma, and death (Gossel, 1994). Other studies found that not calcium oxalate, but a proteolytic enzyme is responsible for the severe irritation caused by this plant (Arditti and Rodriguez, 1982). Therefore, literature data supports our prediction that cubs experienced severe toxicosis after consuming spathes of *Symplocarpus*. In both years, the green leaves and leafstalks of *Symplocarpus* were the most preferable vegetation in the cubs' diet throughout the whole active season. Both leaves, leafstalks and spathes of *Symplocarpus* are regularly consumed by adult wild bears (Bromley, 1965; Kolchin, 2011), but they do not suffer much from toxins, probably because their body mass is much greater than the cubs', and therefore the relative concentration of poison in an adult is lower. During the 30 years of the orphaned brown bear rehabilitation project only a single case has been recorded of an orphaned cub dying after consuming a poisonous bogbean (*Menyanthes trifoliate*) (Pajetnov and Pajetnov, 1998). This may be regarded as a mistake in the individual's learning program.

Conclusion

To summarize, the food habits (foraging activity, food choice and food selection) of the orphaned Asiatic black bear cubs reared in the wild in the Russian Far East generally correspond with those of other wild Asiatic black bears throughout the species' area. Without direct social learning the orphaned cubs showed hyperphagia and monophagia during the fall and accumulated enough fat for hibernation, feeding almost exclusively on natural foods. Most likely, differences in diet composition with that of wild bears depend on the geographical variety of floristic composition, inter-annual variety in crop abundance, age-related features in the feeding habits, as well as on the research methods. We assumed that the cubs assessed the edibility of food items via trials and errors, and the positive or negative reaction to each food item was inborn, inherited from their parents. We conclude that vertical transmission of food habits is likely facultative in bears, because the orphans developed normal species-specific food habits at the proper age without social learning from a mother, rather from inborn knowledge, individual learning and indirect social learning from unrelated conspecifics (our unpublished data). Our results suggest that orphaned bear cubs are able to learn foraging independently from the age of 5 months, if they are permanently exposed to natural foods in a natural environment, but that they should still be protected from predators by a surrogate mother and/or a secure enclosure. Our findings suggest that permanent access to the natural environment of orphaned bears cubs should be recommended for rehabilitation facilities. To investigate the share of inborn, individual and social learning in ontogeny of bear foraging behaviour, special research is required, comparing orphaned and wild bear cubs.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2015.02.007

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