

Developmental stability of foraging behavior: evaluating suitability of captive giant pandas for translocation

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Abstract

The behavioral competence of captive-bred individuals – an important source population for translocation programs – may differ from that of wild-born individuals and these differences may influence post-release survival. Some behaviors will be more robust, or developmentally stable, than others in the face of the environmental novelties of captivity. Here, we investigated developmental stability of foraging behavior by quantifying bamboo feeding behavior in captive-bred and wild-born giant pandas, *Ailuropoda melanleuca*. As an energy-limited species adapted to a low-nutrition diet, any reductions in feeding efficiency may compromise post-release survival. Using video of 22 captive pandas, we measured several components of the panda's elaborate bamboo feeding behavior repertoire. We found that captive-born and wild-born pandas displayed the same repertoire of feeding behaviors, suggesting developmental stability in these motor patterns, but that they employed them differently with different parts of the bamboo. Captive-born pandas devoted less time and effort to handling and chewing leaves while allocating more effort to the consumption of large culms than did wild-born pandas. Captive-born pandas also handled small culm and stripped small culms to prepare them for consumption less often than did wild-born pandas. All of these behavioral differences indicate that wild-born pandas in captivity behave in a manner more similar to wild pandas, and focus their behavioral effort on more nutritious bamboo. Thus, these aspects of captive-born panda feeding behavior may be compromised, and were not developmentally stable in the captive environment. These behavioral differences are cause for concern and should be the subject of future study to determine whether they forecast compromised fitness in translocations. Evaluating developmental stability and behavioral competence should be a key component of captive-release translocation programs, serving to guide pre-release training and selection of individuals to be released.

Introduction

Conservation breeding as a tool for species recovery has assumed an increasingly prominent role in recent years (Conde *et al.*, 2011), largely a result of the increasing use of captive-bred animals as a source for translocation programs (Seddon, Armstrong & Maloney, 2007). For example, 94% of species recovery plans in the US include a recommendation for *ex situ* conservation breeding (Tear *et al.*, 1993). However, despite increasing success rates for translocation programs (Seddon & Armstrong, 2016), the success rate for translocations using captive-bred animals remains substantially lower than those using animals of wild origin. Behavioral deficiencies arising from effects of the captive environment on development are thought to be a primary

factor limiting the success of captive-release programs (Fischer & Lindenmayer, 2000; Mathews *et al.*, 2005; Jule, Leaver & Lea, 2008). The captive environment often fails to provide appropriate learning opportunities for skills important for post-release survival. Among these skills necessary for survival are antipredator behavior, navigational abilities, social competence, and foraging skills.

With the exception of antipredator behavior (Griffin, Blumstein & Evans, 2000; Shier, 2016), developmental effects of captivity on behaviors important to improve post-release success have not been well studied (Mathews *et al.*, 2005). While the negative consequences of inadequate antipredator behavior are readily evident, compromised foraging behavior can lead to similarly poor outcomes if animals cannot find, recognize, handle, process and consume

sufficient amounts of food. Indeed, starvation is a major cause of mortality in reintroduced captive carnivores (Jule *et al.*, 2008). Compromised foraging behavior has long been known to negatively influence post-release survival (Kleiman, 1989) and some studies have shown that provision of natural food items and other forms of foraging enrichment in captivity can enhance foraging skills and post-release survival (Reading, Miller & Shepherdson, 2013; Shier, 2016). Experience with natural food items can enhance foraging abilities through a variety of mechanisms including recognizing, locating, capturing and handling food items. Pheasants *Phasianus colchicus* reared with more natural diets were quicker at handling food items, spent less time foraging and had higher survival rates post-release than those reared with more artificial diets, indicating that the rearing environment influenced learning and development of these foraging skills (Whiteside, Sage & Madden, 2015). Similarly, captive-released golden lion tamarins with more efficient foraging techniques experienced higher survival (Stoinski & Beck, 2004).

An important consideration in designing captive-release programs is the extent to which behaviors important for survival are developmentally stable. Developmental stability can be defined as the set of mechanisms selected to maintain relatively constant phenotypic expression in the face of environmental irregularities (Debat & David, 2001). Some behaviors will have greater developmental stability and thus be more resistant to alteration by captive environments. The behaviors most vulnerable to perturbation, then, are those that require conditions and experience available in nature but not in captive environments. An important research goal in captive-release programs is thus to evaluate the developmental stability of behaviors important for survival post-release. Few studies of foraging behavior have addressed this issue directly (but see Mathews *et al.*, 2005), although as noted above providing experience with natural diets can lead to enhanced foraging success. In some cases, some aspects of foraging behavior may be more developmentally stable than others. For example, recognition of prey is developmentally stable in captive environments in jade perch *Scortum barcoo*, but efficiency of prey capture increased with pre-release experience hunting and consuming live prey (Reid, Seebacher & Ward, 2010).

Here, we examine developmental influences of captivity on the feeding behavior of giant pandas *Ailuropoda melanoleuca*, a dietary specialist almost exclusively reliant on bamboo as a food source. Although recently down listed from Endangered to Vulnerable on the International Union for the Conservation of Nature's Red List of Threatened Species (Swaisgood, Wang & Wei, 2016), pandas have just started on the path to recovery, and conservation breeding and translocation will remain an important component of the conservation strategy for the future (Swaisgood, Wang & Wei, 2017). The highly fragmented nature of panda habitat requires a dual strategy of increased landscape connectivity and release of captive-bred individuals into small, isolated populations as a form of genetic rescue. To date, release of captive pandas has met with mixed success and

some individuals have been known to lose body condition after release, indicating possible deficiencies in foraging behavior.

Although the giant panda is a member of the order Carnivora, it has a number of unusual characteristics that set it apart from other large mammals in this order, all of them related to pandas' specialized bamboo diet (Schaller *et al.*, 1985). While some have argued that the panda's specialized diet has contributed to its decline and even that it is an evolutionary "dead-end," all evidence points to the contrary, and the panda is exquisitely adapted to its lifestyle and its decline can be solely attributed to anthropogenic change to its habitat (Wei *et al.*, 2015). Pandas retain the standard digestive anatomy of a carnivore, requiring other compensatory adaptations to enable this foraging strategy. While giant pandas have a number of anatomical adaptations to their bamboo diet, such as modified dentition, a well-developed sagittal crest and zygomatic arches supporting powerful jaw muscles (Endo *et al.*, 2003) and an extended radial sesamoid which facilitates the handling of bamboo for consumption (Salesa *et al.*, 2006), pandas compensate by spending a large portion (55%) of their daily activity foraging. To meet its energetic needs, the panda must be selective in its choice of bamboo, making foraging decisions based on bamboo age, species, part of the plant as well as tracking seasonal changes in nutritional value of these characteristics (Nie *et al.*, 2015b; Li *et al.*, 2017b). Processing bamboo for consumption by pandas requires an elaborate behavioral repertoire that, presumably, improves the digestibility and nutritional value of bamboo. As further testament to the panda's long history of adaptation to a diet of bamboo, they also have specialized symbiotic gut microbes that facilitate digestion of bamboo (Zhu *et al.*, 2011). Although much is known about pandas' foraging strategies in the wild, there have been no developmental studies and no determination of how pandas learn to forage on bamboo. However, there is a period of extended maternal care from 1.5 to 2.5 years and, as pandas begin to eat bamboo at about 1 year of age, plenty of opportunities for socially facilitated learning to take place.

Even with these strategies designed to optimize intake and digestion of nutritional food, pandas are considered an energy-limited species. Pandas appear to minimize energy expenditure (Nie, Swaisgood, Zhang *et al.*, 2012a; Nie, Zhang, Swaisgood *et al.*, 2012b) and have one of the lowest metabolic rates in mammals to compensate for low energy intake rates (Nie *et al.*, 2015a). Due to the panda's reliance on behavioral strategies to increase intake and processing rates, any deficits in behaviors functioning to increase feeding efficiency are expected to have significant negative consequences. It is unlikely the panda could simply spend more time foraging, as it already allocates more than half its time to foraging, and digestive tract capacity and gut transit time preclude the consumption of greater bulk (Schaller *et al.*, 1985; Nie *et al.*, 2015b). Thus, if captive rearing even marginally compromises foraging efficiency, released pandas are predicted to rapidly lose body condition as their energetic requirements exceed energy intake.

Our study was designed to evaluate whether captive rearing alters bamboo feeding behavior to inform strategies for the emerging giant panda translocation program. A test of the effects of captivity can be found in differences in behavior between animals captured in the wild and brought into captivity versus those born and raised in captivity (Mathews *et al.*, 2005). As both categories of panda currently experience the same conditions and feeding opportunities, this design controls for other confounding factors that may influence feeding behavior, isolating the effects of provenance (captive born vs. wild born). Our research question was centered on the developmental stability of bamboo feeding behavior in pandas. Specifically, we hypothesized that rearing conditions may influence the development of bamboo feeding style and efficiency and predicted that captive rearing might compromise feeding efficiency.

Materials and methods

Subjects and study site

We conducted bamboo feeding trials with 15 adult female and 7 adult male giant pandas (9 captive born, 13 wild born) 5–9 years of age at the China Conservation and Research Center for the Giant Panda in the Wolong Nature Reserve Sichuan China. Of the 13 wild-born pandas, five entered captivity before they reached 2 years old while the remaining eight entered captivity between 3 and 16 years of age. Giant pandas were housed individually in concrete walled, open-air enclosures measuring 72 m² with an adjoining 18 m² indoor den. Subjects were fed bamboo *ad libitum* and their diet was supplemented with bread, milk, carrots and apples. Details of housing and husbandry can be found in Swaisgood *et al.* (2000).

Data collection

We conducted feeding trials during the breeding season (March–May) between 09:00 and 16:00 h, and videotaped 10-min trials for future decoding, completing a total of 1–16 trials per individual that met our criteria of uninterrupted feeding bouts. Including only uninterrupted (for <1 min) 10-min feeding bouts ensured that our observations only included pandas that were motivated to eat bamboo, thus mitigating against variation in motivation that may influence results. We provided 5–10 bamboo culms ~ 3 meters in length, with a diameter of 2–10 cm, including a range of sizes and leaf/culm combinations. To begin a trial, caretakers placed bamboo in enclosures 2–3 times daily, and observers visited enclosures within 30 min. Once a panda was observed beginning to feed, we began to videotape feeding behavior. We did not commence behavioral observations while pandas had access to bread or other supplemental food.

Feeding and processing behaviors (Table 1) were categorized by leaf/culm and by culm size: large (>greater than 2 cm in diameter) and small (<2 cm in diameter). We reviewed videotape recordings using frame-by-frame playback to capture details impossible to detect and record in

real time. For behaviors that lasted more than a few seconds (behavioral states) we recorded the duration of each behavioral bout. Bouts were separated by >5 s interruption in behavioral states. For short-duration behaviors (events) we recorded the frequency of the behavior. Inter-observer reliability was calculated using kappa statistic which corrects for agreement due to chance, and a criterion of 90% agreement was set.

Data analysis

Because our data were zero inflated, we followed Welsh *et al.* (1996) recommendations. To construct the first dataset, we reduced data to a binary format indicating the behavior was/was not observed. The second dataset included all the non-zero values, allowing us to model these two aspects of the data separately and to estimate model parameters independently (Welsh *et al.*, 1996). Histograms, normal probability plots of residuals and quantile–quantile plots were used to check goodness of fit.

We modeled binary and presence data using generalized linear mixed effects models (*glmer* function of the *lme4* package in R (Bates *et al.*, 2013)). For response variables (Table 2) we examined provenance and sex as explanatory variables. We used individual identity as a random variable to account for variation between individuals and uneven sample sizes for each individual (Pinheiro *et al.*, 2007). We analyzed binary data using logistic regression. For the presence data, we fit generalized linear mixed models (GLMM) with a negative binomial distribution and we included both the frequency and duration of behaviors. We used a negative binomial distribution as opposed to Poisson because negative binomial distributions are a natural and flexible extension of the Poisson distribution but allow for over-dispersion relative to the Poisson (Hoffman, 2003). We considered models containing the main effects and all possible interactions. For both types of model, we used the *glmulti* package that compares all candidate models and ranks them based on their Bayesian information criterion (BIC) values (*glmulti* package (Calcagno & de Mazancourt, 2010)).

Because both animal's age and the length of time in captivity may influence behavior, we further investigated behavioral differences in our presence dataset using GLMMs with age and years in captivity as explanatory variables and identity as a random variable. We used R Studio (Version 0.98.981; R Studio Inc. 2009–2013; R Version 3.0.2) for Mac OS X for all analyses and the R package *ggplot2* (Wickham, 2009) for creating graphics.

Results

Binary data

Our models demonstrated that captive-born pandas were more likely to strip large culm ($n = 133$, $r = -0.21$, $P < 0.05$, BIC = 214.08; Fig. 1a) and bite large culm ($n = 133$, $r = -0.21$, $P < 0.05$; BIC = 214.50; Fig. 1b) than were wild-born pandas.

Table 1 Giant panda bamboo sampling and feeding ethogram.

Behavior	F, D ^a	Definition	L, C ^b
Bamboo sampling			
Sniff accept	F	When selecting a culm, panda places nose to within less than 5 cm of bamboo and inhales deeply, then eats selected culm or leaf.	L, C
Sniff reject	F	As above, but panda casts aside without eating	L, C
Make wad	F, D	Panda strips leaves from several branches by grasping culm in the forepaws and pulling clumps of leaves off of branches with the teeth. Several such clumps are gathered together in the forepaw, their mass compacted and inserted into the side of mouth to be bitten and chewed.	L
Handle	F, D	Manual manipulation of bamboo prior to consumption; includes picking up and handling the bamboo culm to move them into position for consumption.	L, C
Strip culm	F, D	Panda grasps culm in forepaws and peels off outer later using incisors and premolars; head and paws are moved in opposite directions to facilitate action.	C
Bamboo feeding			
Chew	F, D	Panda opens and closes its mouth during mastication of leaf or culm.	L, C
Bite	F, D	Use of teeth to break off part of leaf or culm for consumption.	L, C
Chews per bite		Chew Frequency/Bite Frequency	L, C

^aF, frequency; D, Duration of behavior.

^bL, bamboo leaf; C, bamboo culm; culms were also analyzed based on size of greater than or less than 2 cm.

Presence data

Means and standard deviations of all response variables are reported in Table 2. Best models from GLMMs showed that captive-born giant pandas handled bamboo leaves for shorter durations ($n_{obs} = 18$, $n_{pandas} = 12$, $r = 0.65$, $P = 0.091$, BIC = 125.02; Fig. 2a), handled small culm less frequently ($n_{obs} = 65$, $n_{pandas} = 18$, $r = 0.30$, $P = 0.135$, BIC = 239.46; Fig. 2b) and stripped small culm less frequently ($n_{obs} = 96$, $n_{pandas} = 15$, $r = 0.46$, $P < 0.01$, BIC = 816.45; Fig. 2c) and for shorter durations ($n_{obs} = 93$, $n_{pandas} = 15$, $r = 0.39$, $P < 0.01$, BIC = 894.58; Fig. 2d) than wild-born pandas.

Captive-born and wild-born giant pandas differed with regard to the use of several behaviors used during feeding (Table 2). Captive-born giant pandas chewed bamboo leaves less frequently ($n_{obs} = 60$, $n_{pandas} = 14$, $r = 0.50$, $P = 0.086$, BIC = 654.90; Fig. 3a), bit leaves for shorter durations ($n_{obs} = 59$, $n_{pandas} = 14$, $r = 0.56$, $P = 0.05$, BIC = 630.38; Fig. 3b) and had more chews per bite ($n_{obs} = 60$, $n_{pandas} = 14$, $r = -0.43$, $P < 0.05$, BIC = 280.98; Fig. 3c) than wild-born pandas. When extrapolated to the number of hours per day giant pandas eat (14 h/day; Schaller *et al.*, 1985), these differences can result in substantial disparities between bamboo feeding by captive-born versus wild-born individuals (Table 3).

Changes in feeding behavior as a function of age at capture and time spent in captivity

Pandas that were captured from the wild at an older age showed higher frequency of handling ($r = 0.378$, t -value = 2.200, $P = 0.027$) and longer durations of stripping bamboo culm less than 2 cm in diameter ($r = 3.96$, t -value = 1.97, $P = 0.0481$). As wild-born pandas lived in

captivity for longer periods, time spent biting bamboo leaves decreased ($r = -10.22$, t -value = 5.46, $P = 0.061$); however, this relationships was only marginally significant.

Discussion

Captive-reared animals designated for release to the wild in translocation programs should undergo behavioral evaluation to determine whether their behavior is compromised by the developmental effects of captivity (Kleiman, 1989; Mathews *et al.*, 2005; McPhee & Carlstead, 2010). We evaluated the degree to which feeding behavior is developmentally stable in giant pandas born and reared in captivity, reasoning that any deviation in foraging behavior from that observed in wild-born counterparts living under the same circumstance is potential cause for concern. Presumably, wild-born pandas gained adequate foraging experience – direct or socially mediated during the period of dependency on the mother – to meet energetic demands and survive. A first step toward understanding whether captive-born pandas' foraging behavior will compromise post-release survival is a detailed analysis of their feeding behavior, as we have provided here. A strength of this study is that our comparison holds other variables constant with regard to current environmental conditions and thus isolates the effects of the rearing environment as causal for behavioral differences (Mathews *et al.*, 2005). By contrast, comparisons of captive-born with wild-living animals would be less informative because observed behavioral differences may be the outcome of different circumstances between the two study groups. Although we do not yet know how these behaviors map on to foraging efficiency and survival if these pandas are released to the wild, we did find a number of differences in the way captive-born and wild-born pandas process bamboo and the parts of the plant they focus on when feeding. These differences are cause for concern and should be the subject of future study

Table 2 Means \pm SD (obtained from the presence only dataset) of bamboo feeding and sampling behaviors. Frequencies and durations are reported for a 10-min sampling period.

Behavior	Provenance	
	Captive	Wild
Bamboo sampling		
Sniff accept leaves frequency	1.00 \pm 0.01	1.50 \pm 0.76
Sniff accept culm <2 cm frequency	1.33 \pm 0.59	1.52 \pm 0.67
Sniff accept culm >2 cm frequency	1.29 \pm 0.56	1.38 \pm 0.74
Sniff reject leaves frequency	0.08 \pm 0.41	0.05 \pm 0.26
Sniff reject culm <2 cm frequency	3.00 \pm 2.97	3.00 \pm 2.39
Sniff reject culm >2 cm frequency	3.00 \pm 2.65	1.50 \pm 1.22
Make leaf wads frequency	16.88 \pm 19.58	22.61 \pm 18.27
Make leaf wads duration (sec)	37.69 \pm 38.47	53.39 \pm 50.52
Handling leaves frequency	2.33 \pm 3.27	2.20 \pm 0.84
Handling leaves duration (sec)	6.62 \pm 2.50^a	9.90 \pm 9.27^a
Handling culm <2 cm frequency	1.68 \pm 1.07	2.29 \pm 2.70
Handling culm <2 cm duration (sec)	19.31 \pm 27.14	20.21 \pm 21.80
Handling culm >2 cm frequency	1.48 \pm 0.87	1.06 \pm 0.25
Handling culm >2 cm duration (sec)	13.36 \pm 17.66	9.11 \pm 7.03
Stripping culm <2 cm frequency	19.82 \pm 14.92^b	31.38 \pm 19.62^b
Stripping culm <2 cm duration (sec)	32.36 \pm 22.55^b	41.61 \pm 33.60^b
Stripping culm >2 cm frequency	22.87 \pm 21.05	22.88 \pm 19.09
Stripping culm >2 cm duration (sec)	34.82 \pm 32.02	36.04 \pm 32.82
Bamboo feeding		
Chewing leaves frequency	60.24 \pm 58.94^a	80.89 \pm 79.40^a
Chewing leaves duration (sec)	0.92 \pm 5.39	0.37 \pm 1.82
Chewing culms <2 cm frequency	99.48 \pm 88.64	150.12 \pm 93.91
Chewing culms <2 cm duration (sec)	11.93 \pm 22.18	14.49 \pm 24.99
Chewing culms >2 cm frequency	104.62 \pm 90.11	100.78 \pm 91.52
Chewing culms >2 cm duration (sec)	9.03 \pm 16.94	6.23 \pm 14.19
Biting leaves frequency	15.53 \pm 20.39	14.39 \pm 20.32
Biting leaves duration (sec)	37.61 \pm 36.29^b	93.65 \pm 70.98^b
Biting culms <2 cm frequency	35.83 \pm 23.80	41.00 \pm 22.49
Biting culms <2 cm duration (sec)	53.97 \pm 74.18	83.70 \pm 88.36
Biting culms >2 cm frequency	24.85 \pm 16.22	20.77 \pm 19.38

Table 2 Continued.

Behavior	Provenance	
	Captive	Wild
Biting culms >2 cm duration (sec)	36.29 \pm 60.95	31.92 \pm 70.92
Chews per bite on leaves frequency	4.97 \pm 3.71^b	3.59 \pm 1.41^b
Chews per bite on <2 cm culms frequency	3.92 \pm 1.49	3.95 \pm 1.09
Chews per bite on >2 cm culms frequency	5.30 \pm 1.54	4.87 \pm 1.06

Bold indicates variables where provenance (captive vs. wild) was included in the best generalized linear mixed models with subject ID as a random variable.

^aIndicates trends at $P < 0.08$ for the explanatory factor of provenance (captive vs. wild).

^bIndicates significant differences at $P < 0.05$ for the explanatory factor of provenance (captive vs. wild).

to determine whether they forecast compromised fitness post-release. More optimistically, the basic motor components employed during feeding, which are both nuanced and somewhat complex, appear to be developmentally stable, occurring routinely in both captive-born and wild-born pandas.

Our results provide several lines of evidence indicating that captive-born pandas might have compromised feeding abilities. We consider any behavioral differences to be potentially maladaptive for life in the wild because of *a priori* assumptions that animals that have lived and foraged in the wild are more likely to demonstrate optimal feeding strategies (Mathews *et al.*, 2005). Captive-born pandas devoted less time and effort to handling and chewing leaves while allocating more effort to the consumption of large culms than did wild-born pandas. Pandas in nature typically show a preference for leaves over culms and smaller, younger culms over older, larger culms because leaves are typically more nutritious than culms and smaller culms are more nutritious than larger culms (Schaller *et al.*, 1985; Pan *et al.*, 2001; Nie *et al.*, 2015b; Li *et al.*, 2017b). Thus, by devoting more effort to handling, chewing and biting leaves, wild-born pandas living in captivity appear to behave more like their wild counterparts, and may have higher nutritional intake than captive-born pandas during a feeding session. Similarly, wild-born pandas more frequently handled small culm and stripped small culms to prepare them for consumption. This finding suggests that learning is involved in choosing to focus on smaller culms, as seen in both wild-born pandas in captivity and wild pandas. Selecting a larger food item may be an inherited ancestral trait common to most animal life, whereas recognizing the higher nutritional value of small culms in this case may require experience more readily available to wild pandas. These results suggest that captive-born pandas waste more time and effort on less nutritious bamboo than their wild-born counterparts.

Further evidence for the possible negative effects of captivity on feeding behavior can be found in our analyses incorporating age at time of capture and time spent in

captivity for wild-born pandas. With shorter developmental periods in the wild, wild-born panda feeding behavior was more likely to resemble the behavior of captive-born pandas in that they spent less time handling and stripping small bamboo culm. Furthermore, we found evidence that panda feeding behavior became more like captive-born pandas as they spent more time in captivity, as suggested by the decrease in time spent processing leaves.

The giant panda has a number of morphological, physiological and behavioral adaptations for its obligate bamboo

foraging strategy (Schaller *et al.*, 1985; Pan *et al.*, 2001; Zhu *et al.*, 2011; Nie *et al.*, 2015b; Li *et al.*, 2017b), all requirements to meet its energetic needs on a low-nutrition diet for this energetically on-the-edge species (Nie *et al.*, 2015a). Wild pandas spend approximately 14 h each day foraging, and most of the remaining time resting (Schaller *et al.*, 1985). Thus, we might predict there is little room for behavioral deficiencies that compromise the rate of intake, effective processing of bamboo for consumption or nutritional value of bamboo selected for consumption. Our results indicating that captive-born pandas' feeding behavior diverges from their wild-born counterparts are worrisome. Even small deficits in the ability to process bamboo or in decisions

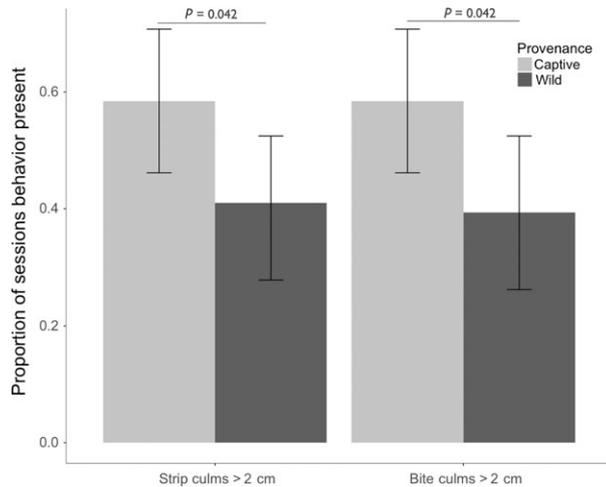


Figure 1 Differences in bamboo feeding and processing in captive-born versus wild-born giant pandas (binary data reduction such that each behavior is present or absent in an observation session). *P* values are obtained from the explanatory factor of provenance (captive vs. wild) in the best generalized linear mixed model. Error bars \pm SE.

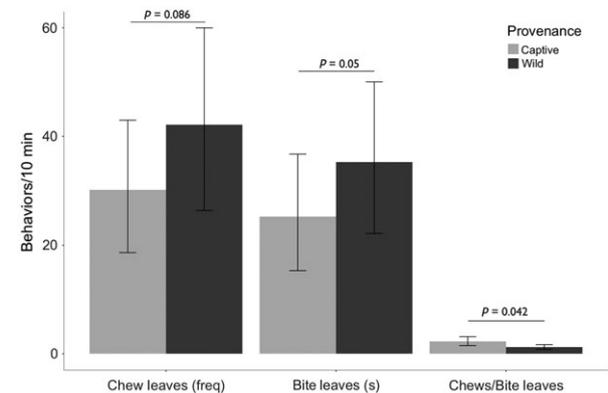


Figure 3 Differences in bamboo processing in captive-born versus wild-born giant pandas (presence data only such that only behaviors occurring at least once in an observation session are included in the analysis). *P* values are obtained from the explanatory factor of provenance (captive vs. wild) in the best generalized linear mixed model. Error bars \pm SE.

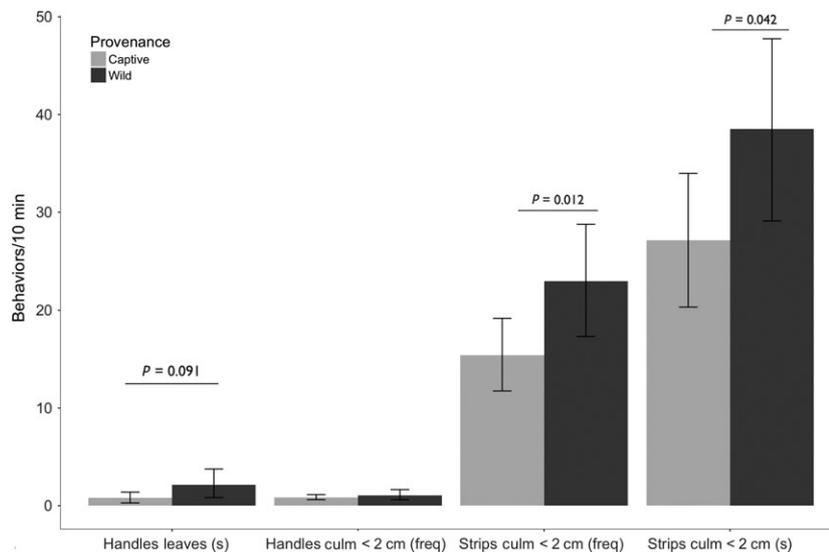


Figure 2 Differences in bamboo processing in captive-born versus wild-born giant pandas (presence data only such that only behaviors occurring at least once in an observation session are included in the analysis). *P* values are obtained from the explanatory factor of provenance (captive vs. wild) in the best generalized linear mixed model. Error bars \pm SE.

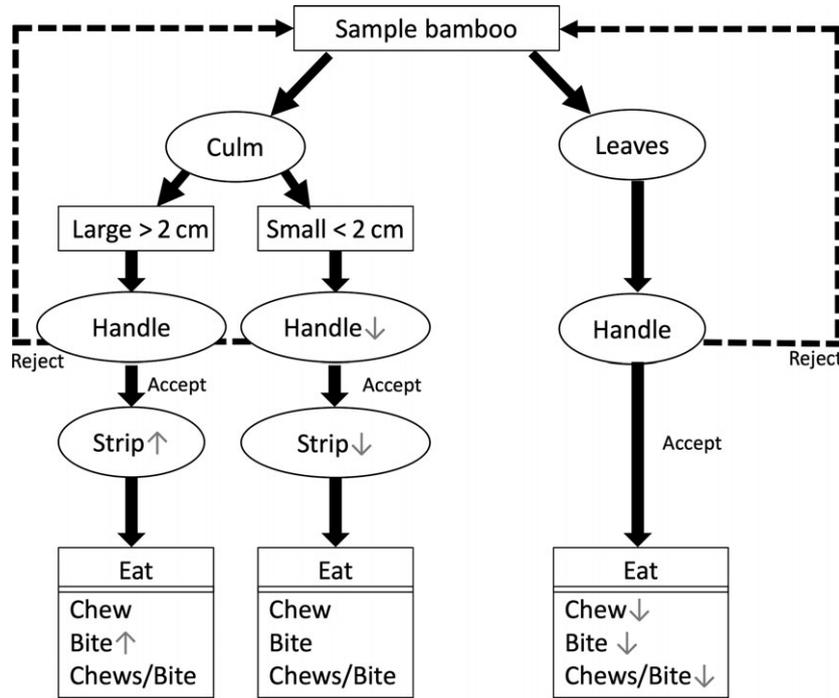


Figure 4 Flow diagram showing bamboo processing and feeding behaviors performed by giant pandas. Plain arrows link two successive behaviors indicating the progression of the main feeding procedure with dotted arrows representing rejection of bamboo. Light gray arrows next to behaviors signify whether captive-born giant pandas displayed significantly higher (up arrow) or lower (down arrow) levels of behavior than wild-born giant pandas.

Table 3 Differences between captive-born and wild-born giant pandas in bamboo feeding and sampling behaviors per day based on 14 h of feeding. Only behaviors that had provenance (captive vs. wild) as an explanatory variable in the best generalized linear mixed model are presented.

Behavior	Provenance	
	Captive	Wild
Bamboo sampling		
Duration of handling bamboo leaves (min)	9.27	13.86
Frequency of handling culm < 2 cm	141.12	192.36
Frequency of stripping culm < 2 cm	1664.88	2635.92
Duration of stripping culm < 2 cm (min)	45.30	58.25
Bamboo feeding		
Frequency of chewing leaves	5060.16	6794.76
Duration of biting leaves (min)	52.65	131.11
Number of chews per bite on leaves	4.97	3.59

regarding which bamboo parts to selectively consume may alter the energy balance toward a net negative, potentially increasing morbidity and mortality.

Our results provide no direct evidence regarding the causal mechanisms explaining these developmental effects of captivity on feeding behavior. Plausible explanations include observational learning from the mother, the availability of variable bamboo that affords learning and more rapid learning due to the severity of consequences from foraging inefficiencies for wild pandas unsupplemented with more

nutritious non-bamboo food items (i.e. motivational effects on learning). Of note for this study is that captive-born cubs were reared by mothers for only ~6 months, whereas wild-born pandas were reared by the mother for ~18 months, and panda cubs do not begin to eat bamboo until 10–12 months of age. The duration of maternal rearing in captivity can influence behavioral expression in pandas, and cubs reared with mothers for longer periods are known to spend more time manipulating bamboo, suggesting social facilitation and learning opportunities (Snyder *et al.*, 2003). It is thus possible that maintaining captive-born pandas with mothers for 18 months will address these potential deficiencies in bamboo feeding behavior, especially if the mother is also wild born.

Conservation implications

While it is promising that giant pandas are beginning to recover in their native habitat, much work still needs to be done to keep the panda on the path to recovery (Swaisgood *et al.*, 2017). Although some wild populations have stabilized, there are many small and isolated populations that require genetic rescue through supplementation from captive breeding programs. This is why the Chinese government has invested so heavily in conservation breeding for pandas, and has begun to release captive-reared pandas back to the wild (SFA, 2015). However, three of the first eight captive-released pandas have perished within a year of release

(unpublished data), indicating that the release program should be improved. Cause of death is not known with certainty, but poor body condition and limited energy reserves from deficient foraging could contribute to mortality from disease, social aggression or other immediate causes.

The current pre-release training program addresses some of the concerns raised by our research. For example, release candidates are reared in large, naturalistic outdoor enclosures and have access to native, live bamboo, as well as supplemental bamboo provided by caretakers. These features of the pre-release training program may provide improved direct experience and learning opportunities. Release candidates are reared in these enclosures with their mothers to at least 2 years of age, so they also have greater opportunities for social learning, albeit typically from mothers reared in captivity that may not be able to model the best bamboo foraging behavior. These improvements will no doubt enhance post-release success, but empirical demonstration is required to determine whether this environment encourages the development of more wild-typical feeding behavior. To develop an optimal training program we need to understand the degree of developmental stability associated with bamboo foraging behavior across varying possible pre-release training environments. The application of behavioral knowledge has done much to enhance the success rate for breeding pandas (Swaisgood *et al.*, 2006; Martin-Wintle *et al.*, 2015, 2017; Li *et al.*, 2017a) and a similar approach promises likewise to increase post-release success. Targeted research addressing training for bamboo feeding in pre-release enclosures, coupled with behavioral observations of released pandas compared to wild pandas, should be conducted and evaluated with regard to post-release outcomes such as body condition and survival.

The panda translocation program is under intense scrutiny (Guo, 2007) and the value of each individual panda is high, thus all best practices stemming from the growing field of translocation biology (Seddon *et al.*, 2007) should be implemented. In addition, our study has possible ramifications for the number of animals required for release. To the extent that captive-reared pandas are behaviorally compromised and thus have lower survival probabilities post-release, the number of animals required for release must be adjusted upward to account for any negative impact of behavioral incompetence on fitness (McPhee & Silverman, 2004).

Our study is the first to systematically evaluate the effects of captivity on giant panda suitability for release to the wild. While at present we do not know whether these differences will relate directly to post-release survival, it is reasonable to assume that deviations from the wild behavioral phenotype may place captive-reared individuals at a disadvantage (Mathews *et al.*, 2005). Furthermore, documentation of wild-born panda behavior in captivity will be important for setting behavioral targets for release candidates, providing guidance for the types of behavioral profiles managers should promote or consider when selecting suitable release candidates. Evaluation of behavioral competence should be more broadly considered in conservation breeding and translocation programs, and behavioral data such as these comparing

captive-born and wild-born animal behavior can be useful in developing behavioral criteria to determine individual release suitability.

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