Naturalising diet to reduce stereotypic behaviours in slow lorises rescued from wildlife trade

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Abstract Providing a natural diet is a key component to improving animal welfare and can potentially reducing stereotypic behaviours in captivity. Wild slow lorises (*Nycticebus* spp.) are threatened by illegal wildlife trade, and in Thailand, confiscations from illegal wildlife trade has led to a large number of Bengal (*Nycticebus bengalensis*) and greater slow lorises (*N. coucang*) in rescue centers such as Bang Phra Wildlife Domestic Research Station (Bang Phra). Due to limited enclosure space and availability of natural food items, welfare may be compromised for these confiscated animals. Slow lorises in most rescue centres including Bang Phra are mainly fed with fruit and vegetables rather than their natural diet of exudates, nectar and insects. Our project aimed to increase wild-type activities and reduce stereotypic behaviours in captive slow lorises at Bang Phra by modifying the diet (especially adding exudates of gum *Arabic*) using environmental enrichment devices. From May to August 2019, we implemented four diet conditions on 30 individuals: baseline, gum presented in two feeding devices and insects presented in a box. Diet conditions changed individual behaviours, with more time spent feeding and foraging, less time spent resting, and less stereotypic behaviours. Fixed gum was the most successful device to encourage increased feeding (40.4 % vs ~ 3.5 % during baseline conditions) and foraging (16.3 % vs ~2.5% during baseline conditions), whilst significantly decreasing stereotypic behaviours (3.2 % vs ~16.5 % during baseline conditions). Animals with small body sizes are often placed in small cages in rescue centres despite their needs in the wild. At the same time, species with specialist diets may not thrive in rescue centres that lack the funds or infrastructure to procure food items perceived to be specialised. With wild numbers declining rapidly, rescue centres must provide adequate space and wild type diets to ensure the health and well-being of these globally threatened primates.

1. Introduction

A major threat to many animal species is the illegal wildlife trade (Challender et al., 2015; Roe, 2015). Rescue centres play a role in the mitigation of this trade, holding confiscated animals as evidence for trials or preparing them for return to the wild (Gupta and Chakraborty, 2005). Lack of funds, knowledge of specialised species, and prioritised care of charismatic taxa often means that animals are kept in inappropriate conditions that violate the five freedoms of animal welfare (Bergin and Nijman, 2018). Furthermore, limited space means that rescue centres fill up quickly, resulting in smaller spaces and compromised welfare for confiscated animals. If rescue centres are to fulfil their role in the wildlife trade cycle, these aspects need to be improved (Nijman, 2010).

Slow lorises (*Nycticebus* spp.) are nocturnal primates native to South-East Asia. They are listed on Appendix I of the Convention on International trade in Endangered Species of Wild Fauna and Flora (CITES), and all species are protected by governments in every country to which they are endemic (Nekaris and Nijman, 2007). In Thailand, the two endemic species *Nycticebus bengalensis* and *N. coucang*, and the non-native *N. pygmaeus* are traded as pets. They also feature as tourist attractions in the form of "photo props" whereby tourists at beaches and bars such as Phuket pay to get their photograph taken with a wild-caught animal (Osterberg and Nekaris, 2015). Improved confiscation of these animals has meant an inundation of animals in rescue centres, but lack of prosecution means that after confiscation, street vendors quickly acquire new animals, meaning the problem persists (Osterber and Nekaris, 2015).

A major factor affecting care of slow lorises in rescue centres is providing them with an appropriate diet. Captive *Nycticebus* spp. are typically fed a diet mainly of fruits, which results in many health problems including dental disease, obesity, wasting and kidney failure (Cabana and Nekaris, 2015). Unusually, slow lorises are exudativorous, meaning that they are

anatomically and physiologically adapted to eat mainly tree gums and saps (Swapna et al., 2010; Starr and Nekaris, 2013; Cabana et al., 2019). For gouging exudates, slow lorises have a specialised tooth comb, and can make 100s of holes in trees per night (Starr and Nekaris, 2013). Campera et al. (2020) demonstrated that a good dentition and the ability to gouge for gum was a vital characteristic of successful slow loris releases to the wild. Being the only venomous primates, the toothcomb is also the venom injection mechanism. Confiscated slow lorises often have their front teeth removed to avoid their injecting venom (Plesker and Schulze, 2013; Nekaris and Starr, 2015), meaning feeding them with gum requires alternative techniques. For example, Gray et al. (2015) provided gum to slow lorises without teeth in three ways including spreading it on a pinecone, enclosing it in a banana leaf, and or freezing it in grass bundle. Many rescue centres simply do not have access to gum, resulting in the death or declining health of animals (Nekaris and Gibson, pers. obs.).

The captive environment can cause an increase in stereotypic or other abnormal behaviours of slow lorises (Novak et al., 2006; Moore et al., 2015; Khudamrongsawat et al., 2018). Over one out of three Bengal slow lorises in Bang Phra Wildlife Domestic Research Station, Thailand, showed abnormal behaviour divided into six types: rocking, pacing, circling, up down moving, disc spinning, and reaching above the head (Khudamrongsawat et al., 2018). Meanwhile, Moore et al. (2015) found that 33% of Indonesian slow lorises (*N. coucang, N. hilleri, N. javanicus*) in a rescue centre displayed abnormal behaviours including pacing, rocking and circling, which was related with sex composition and number of conspecifics in the same cage. Tarou et al. (2005) suggested that environmental enrichment and training can decrease the occurrence of such abnormal behaviours.

Environmental enrichment (e.g., food, enclosure, and social modifications) can promote natural behaviours in animals in captivity, and improve their welfare (Tarou and Bashaw, 2007).

Enrichment can also increase active behaviours, especially social behaviours (Putri et al., 2014; Gray et al., 2015). Gray et al. (2015) suggested that environmental enrichment may increase the rate of reintroduction success for captive slow lorises by helping them to regain health and physical strength lost in captivity. Thus, to improve slow loris welfare, and increase their chance to be released to the wild, we investigated the effect of enrichment on slow loris behaviours at Bang Phra Wildlife Domestic Research Station.

The aim of our study was to examine the behavioural impact of increasing natural dietary items in the diet of confiscated slow lorises using enrichment devices. We examined if slow lorises in Bang Phra Wildlife Domestic Research Station presented stereotypic behaviour in the baseline condition. We then presented gum in three environmental enrichment procedures in an attempt to decrease stereotypies and increase wild-type behaviours. We discuss our results in the light of the management of neglected species such as slow lorises in rescue centres, and give suggestions for improving diet and its presentation, especially in rescue centres that host a large number of slow lorises.

2. Methods

2.1 Study site

Bang Phra Wildlife Domestic Research Station (Bang Phra) is located in Chonburi province, eastern Thailand (13°13'19.6"N 100°59'59.3"E). Around 1,500 animals are under the care of the rescue centre. 68 percent of animals in Bang Phra were confiscated animals from illegal wildlife trade and the majority of them are non-native species, while 32 percent are donated from people. In recent years, Bang Phra has experienced an inundation of some native species including *Aonyx* spp. and *Nycticebus* spp. that were confiscated from illegal wildlife trade. In May 2019, 99 slow lorises were housed at Bang Phra; 77 slow lorises were donated from people, who presumedly kept them as pets, and 22 were confiscated from illegal wildlife trade. Bengal

slow lorises (*N. bengalensis*) are larger than other slow lorises species, weighing up to 2100 g. Compared to other lorises, this species has shorter ears and a light-coloured head. The greater slow lorises (*N. coucang*) weight about 800 g and are richly coloured with crimson red on their flanks and head, which is characterised by a darker and more pronounced forking pattern (Mittermeier et al., 2013). All keepers at Bang Phra work during the daytime between 8:00 to 17:00. For slow lorises, the standard diet was fruits, vegetables, crickets, eggs and vitamin water once a day at 15:00 when slow lorises were still asleep.

Slow lorises were all housed outdoors and kept on a natural light cycle and housed alone or in groups. 18 were kept in semi-natural "large" cages (a minimum of 4.0 x 3.5 x 4 m; iron mesh; adjoining others large cages) and 14 in "medium" cages (a minimum of 1.5 x 3.0 x 1.5 m; iron mesh; adjoining others medium cages) purpose built for slow lorises. Due to the large number of confiscations, 67 animals were kept in "small" bird cages (a minimum of 0.4 x 0.6 x 0.4 m; wire mesh covered with plastic; a minimum distance from other small cages was 0.1 m). Slow lorises were housed in 5 different zones including zone 1 (solitary semi-natural large cages zone), zone 2 (solitary medium cages zone), zone 3 (small building where many small cages were placed), zone 4 (hospital building where animals were kept in small cages) and zone 5 (solitary storage building where many slow lorises were housed in small cages; other species were kept in this zone as well) (Fig. 1). Slow lorises in large and medium cages were housed nearby conspecifics within 50 m radius (i.e., the distance between zone 1 and 2 is around 50 m - the largest possible distance between cages), whereas the 37 slow lorises in small cages were kept in 2 m radius of each other and nearby other species such as *Python bivittatus*, *Athene brama* and *Atelerix albiventris* (zone 4 and 5). From the subsample of slow lorises of this study, there are only five housed in small cages that were kept nearby other species.

153 ***2.2 Data collection***

154 2.2.1 Study subjects

155 The first author collected data between the 11 May 2019 and the 11 August 2019 on the
156 behaviour of 30 slow lorises that she observed between 18:00 to 06:00 from Monday to Friday
157 (Table 1) by using continuous sampling on each individual (Martin and Bateson, 2007). Using red
158 light to detect the slow lorises during their active period, they were always visible to the
159 observer. The slow loris ethogram consisted of ten behaviours and four postures (Rode-
160 Margono et al., 2014) (Table 2). We studied two species, Bengal slow loris (*N. bengalensis*) and
161 greater slow loris (*N. coucang*), which are native to the northern and southern parts of Thailand
162 respectively. We observed and collected data from the studied individuals (25 of *N. bengalensis*
163 and 5 of *N. coucang*) that were chosen randomly among the captive slow lorises living in Bang
164 Phra for at least one year, to decrease the effect of stress related to human presence.

165

166 2.2.2 Enrichment conditions

167 The observation period was divided into six conditions for three months: 1) baseline condition
168 for two weeks; 2) insect enrichment condition for two weeks; 3) baseline condition for two
169 weeks; 4) hanging gum enrichment condition for two weeks; 5) baseline condition for two
170 weeks; 6) fixed gum enrichment condition for two weeks. We collected baseline data to
171 investigate the behaviours of slow lorises before providing the enrichment. During baseline
172 condition, the routine diet was provided, consisting of fruits and vegetables including corn,
173 pumpkin, cucumber, lentils, banana, papaya, apple and guava. For insect enrichment, we placed
174 live crickets into plastic boxes with a minimum size of 20 x 25 x 18 cm for small cages and 25 x
175 25 x 18 cm for large cages. We placed the boxes in the cages of slow lorises. For the gum
176 enrichments, we chose branches with an approximate length of 15-20 cm and drilled 3-4 holes
177 in each branch, which were then filled with gum *arabic*. Gum *arabic* was bought from a local
178 market without a label specifying nutritional information. We installed the gum enrichments in

two ways, hanging or fixing them inside the cages. In enrichment conditions, slow lorises obtained both routine food at 15.00 during their inactive period and natural food from enrichments during observations. Slow lorises obtained the diet enrichment when the individual observation started during the diet enrichment condition. The first time we provided enrichment, we took notes on exploring behaviour that we defined as watching and sniffing while resting or touching the enrichment (foraging). Since this behaviour was noted only for the first time and for the diet enrichments, for the analysis, we coded this behaviour as either resting or foraging according to the definitions (Table 2).

2.3 Data analysis

We analysed differences in behaviours between the enrichment conditions and baseline condition by using the Generalized Linear Mixed Model (GLMM). The total number of observation minutes in each stage was the same; we thus did not include any weight (i.e., known values that varies from observation to observation and are used to control for different observation efforts) in the analysis. We set diet condition, cage size (small, medium, large), animal alone or in group, dental problem, species and sex as predictors. We checked for multicollinearity of the predictors via the "vif" function in the package "car" (all predictors having a score lower than 2.6). We included individuals and zone where the cages were housed as random effects. We used the "glmmTMB" function in the "glmmTMB" package as this function is used to take into account zero-inflated data and is particularly used to deal with zero-inflated count data. We tested different fit functions for count data (poisson, genpois, compois) and included or excluded a zero-inflation term based on the lowest AICc score. We ran pairwise contrasts using a Bonferroni-Holm post hoc correction via the function "emmeans" in the package "emmeans". We ran the analysis via R software v 4.0.4 and considered $p = 0.05$ as level of significance.

205 ***2.4 Ethical note***

206 The experiment was carried out according to the Oxford Brookes University Research Ethics
207 Committee and guidelines and the Association for the Study of Animal Behaviour (ASAB) on the
208 observation, handing and care of animals in field research under study.

209

210 **3. Results**

211 **3.1 General pattern of activity budget**

212 We collected 32,400 minutes of behavioural data from 30 slow lorises (1,080 minutes per
213 individual – 180 minutes in each diet condition). We provided three types of environmental
214 enrichment including insect enrichment, hanging gum enrichment and fixed gum enrichment to
215 large (Fig.2) and small cages (Fig.3).

216

217 50% of studied slow lorises (15 out of 30 individuals) present stereotypic behaviour. 27% of slow
218 lorises (3 from 11 individuals) that were housed with conspecific species in large or medium
219 cages presented stereotypic behaviours. 63% of solitary slow lorises in small cages (12 from 19
220 individuals) presented stereotypic behaviours. The most common stereotypic behaviour across
221 the six stages was rocking at 48.6% , followed by up-down movement, pacing, circling and
222 reaching above the head at 19.5%. 15.6%, 9.2% and 7.1% respectively.

223

224 Slow lorises were less inactive, had less stereotypic behaviours, and travelled less during the
225 fixed gum and hanging gum diet conditions than during baseline conditions (Table 3). The insect
226 diet condition determined a decrease of stereotypic behaviours, but not in inactivity and
227 travelling behaviours, compared to baseline conditions (Fig.4). Feeding and foraging time was
228 higher during all the natural diet conditions than during baseline conditions (Fig.5), and feeding
229 time during gum enrichments was higher than during insect enrichment. The time spent in other
230 behaviours did not change between diet conditions. Additional factors influenced the

231 behaviours: animals housed socially had higher feeding and foraging time than solitary animals;
232 animals in small cages spent more time foraging and less time showing social behaviours than
233 animals in large cages; males spent more time foraging and less time inactive, and had more
234 stereotypic behaviours than females. *Nycticebus coucang* spent less time engaging in social
235 behaviours than *N. bengalensis*.
236
237 The first time the natural diet was provided, individuals took time to explore it. For hanging gum
238 enrichments they explored for 229.1 (SE 37.8) seconds; for fixed gum enrichment they explored
239 59.6 (SE 11.4) seconds before feeding. For insect enrichment, they explored on average 139.6
240 (SE 22.8) seconds after live crickets were put into the plastic boxes.
241
242 **4. Discussion**
243 Here, we found that improved diet using environmental enrichment devices influenced slow
244 loris activity, especially feeding, foraging and stereotypic behaviour. Studied slow lorises
245 engaged in foraging and feeding behaviours in natural diet conditions more than the baseline
246 conditions. Insect enrichment produced behaviour similar to slow lorises in their natural
247 habitats, where feeding and foraging behaviours comprise more than 20-30% of activity (Rode-
248 Margono et al., 2014; Reinhardt et al., 2016; Al-Razi et al., 2020; Das and Nekaris, 2020). The
249 amount of feeding and foraging was even higher in the gum enrichment conditions (40-55%)
250 than in the natural habitats, suggesting that gum consumption is particularly needed in captive
251 animals. Travelling time is also similar between individuals in natural diet conditions and
252 individuals in natural habitat (25-35% of activity; Al-Razi et al., 2020; Das and Nekaris, 2020),
253 while animals in baseline conditions spent much more time travelling (~50%). Having similar
254 activity patterns as a consequence of environmental enrichment including improved substrates
255 and diet might bring benefits on the psychology and welfare of captive animals as showed by
256 previous work (Mellen and MacPhee, 2001).

Low welfare in captivity may create atypical behaviours such as aggression, over-grooming, repetitive behaviour, inappropriate social behaviour, and stereotypies, defined here as repetitive behaviour with no known function (Tarou and Bashaw, 2007). Slow lorises exhibited high levels of stereotypic behaviours in the baseline condition. Khudamrongsawat et al. (2018) also found that 73% of studied slow lorises in Bang Phra displayed at least one of three types of stereotypic behaviours. Abnormal behaviours such as stereotypies and abnormal aggression can be influenced by unsuitable living conditions, poor diet and human handling in captivity (Novak et al., 2006). In this study, the number of stereotypic behaviours significantly decreased with environmental enrichment as found in other mammals (e.g., *Mus musculus*, Jones et al., 2011; *Phoca vitulina richardii*, Chudeau et al., 2019). As one would expect, supplying a natural diet produced a positive welfare outcome (Hosey, 2013). We thus recommend that the relatively simple measure of providing more substrates and a gum diet not be considered enrichment but instead be implemented wherever slow lorises are in captivity.

Despite their small body size, wild slow lorises have home ranges of up to 30 ha (Campera et al., 2020). Thus, we expected cage size to be related to the frequency of stereotypic behaviours but that was not the case as also found out by numerous studies (Herron et al., 2001; Shyne, 2006; Moore et al., 2015; Poindexter and Nekaris, 2017). Indeed, lorises in both small and large cages still showed stereotypic behaviours. This may be because even the largest cages are only a fraction of lorises' wild home ranges.

Wild slow lorises feed mainly on plant exudates all year round, but even more so in the cooler or drier seasons (Swapna et al., 2010; Das et al., 2014). For example, Bengal slow lorises (*N. bengalensis*) spent 80.9% of their feeding time consuming gum, while nectar and insects comprised the remaining 3.2% and 2.3% of the diet respectively (Das et al., 2014). After

283 providing the animals in this study with gum, slow lorises readily exhibited gouging behaviour,
284 which has also been linked to a decrease in dental problems (Cabana and Nekaris, 2015).
285 Moreover, slow lorises presented more rubbing behaviour when exudates were provided for
286 the first time resulting in gums sticking to their mouths and faces. They learned quickly and did
287 not present rubbing behaviour the second time exudates were offered. Cabana and Plowman
288 (2014) showed that adding exudates and insects and removing fruit from their captive diet
289 improved the activity budget of pygmy slow lorises, while abnormal behaviours reduced.
290 Moreover, slow lorises consumed a more energetically appropriate diet when natural gum-
291 based diets were provided to them (Cabana and Plowman, 2014). Indeed, the benefits of feeding
292 this main natural food item to slow lorises are numerous, and feeding it in an enriching way,
293 encouraging exploration and gouging increase its benefit.
294
295 **5. Conclusion**
296 Slow lorises are still heavily threatened due to habitat loss and illegal wildlife trade for food, pets
297 and medicines (Shepherd et al., 2005; Nekaris and Starr, 2015; Miard et al., 2017), including in
298 Laos, Cambodia and Thailand (Nekaris et al., 2010). Wildlife trade is the main factor determining
299 the decline in slow loris population (Nekaris and Streicher, 2008). This widespread trade in these
300 species results in their frequent appearance in the countries' rescue centres. Moreover, many
301 slow lorises faced negative experiences during transport in trade that can impact their
302 rehabilitation, so the rescue centres should adjust to these problems and provide suitable
303 conditions to promote animal welfare (Fuller et al., 2017).
304
305 Providing slow lorises with environmental enrichment, especially gum enrichments, encouraged
306 active and natural behaviours (Shyne, 2006), including feeding and foraging (c.f. Gray et al.,
307 2015). Increasing substrates and providing permanent gum and insect feeding opportunities
308 should be considered as essential aspects of husbandry for captive slow lorises, providing them

with opportunities to consume exudates and catching their prey. In rescue centres, moving the slow lorises to semi-natural enclosures where they have enough space could also lead to increased social interactions between conspecifics and allow an increased range of natural behaviours. The success of reintroduction programmes may ultimately be linked with environmental enrichment, social interaction with conspecifics, and appropriate enclosures for captive slow lorises. More and more animals with dietary, social and behavioural specialisations are being rescued from illegal wildlife trade and entering rescue centres. Indeed, many rescue centres are the only captive holders of some of the world's most threatened species (Trayford and Farmer, 2013). Despite the challenges that such species bring to caretakers, we highly encourage these caretakers to strive to find as natural solutions as possible.

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464 **Table captions**

465

466 **Table 1.** Study subjects at the Bang Phra Wildlife Domestic Research Station, including
467 information about species (B: *Nycticebus bengalensis*; C: *N. coucang*), sex, cage sixe, social
468 housing, zone where the case was housed, dental problem, and observation time. The
469 observation time was the same each week, two observations in each of the six dietary conditions
470 object of this experimental study.

Studied individual	Sex	Cage size	Social	Zone	Dental problem	Observation time (twice for each diet condition)
No.1 (C)	Female	Large	Social	1	No	Mon 18.00-19.30
No.2 (C)	Female	Large	Social	1	No	Mon 19.30-21.00
No.3 (C)	Female	Large	Social	1	No	Mon 21.00-22.30
No.4 (B)	Female	Large	Social	1	No	Mon 22.30-00.00
No.5 (B)	Female	Large	Social	1	No	Tue 00.00-01.30
No.6 (B)	Female	Large	Social	1	Yes	Tue 01.30-03.00
No.7 (B)	Female	Large	Social	1	No	Tue 18.00-19.30
No.8 (B)	Female	Large	Social	1	Yes	Tue 19.30-21.00
No.9 (B)	Female	Large	Social	1	Yes	Tue 21.00-22.30
No.10 (B)	Male	Medium	Alone	2	No	Wed 00.00-01.30
No.11 (B)	Female	Medium	Social	2	No	Wed 03.00-04.30
No.12 (B)	Female	Medium	Alone	2	No	Wed 18.00-19.30
No.13 (B)	Female	Medium	Social	2	No	Wed 19.30-21.00
No.14 (B)	Male	Small	Alone	3	No	Wed 22.30-00.00
No.15 (B)	Male	Small	Alone	3	Yes	Thu 00.00-01.30
No.16 (B)	Male	Small	Alone	3	Yes	Thu 01.30-03.00
No.17 (B)	Male	Small	Alone	3	No	Thu 03.00-04.30
No.18 (B)	Male	Small	Alone	3	No	Thu 04.30-06.00
No.19 (B)	Male	Small	Alone	3	Yes	Thu 18.00-19.30
No.20 (B)	Male	Small	Alone	3	No	Thu 21.00-22.30
No.21 (B)	Male	Small	Alone	3	No	Thu 22.30-00.00
No.22 (B)	Male	Small	Alone	3	No	Fri 00.00-01.30
No.23 (C)	Male	Small	Alone	3	No	Fri 01.30-03.00
No.24 (B)	Male	Small	Alone	3	Yes	Fri 04.30-06.00
No.25 (B)	Male	Small	Alone	5	Yes	Fri 19.30-21.00
No.26 (C)	Male	Small	Alone	5	Yes	Fri 21.00-22.30
No.27 (B)	Male	Small	Alone	5	Yes	Fri 22.30-00.00
No.28 (B)	Male	Small	Alone	5	Yes	Sat 01.30-03.00
No.29 (B)	Female	Small	Alone	4	No	Sat 03.00-04.30
No.30 (B)	Female	Small	Alone	4	No	Sat 04.30-06.00

Table 2. Ethogram used in behavioural observations of captive slow lorises (adapted from Rode-Margono et al., 2014).

Behavior	**Definition**
Feeding	Actual consumption of a food item
Foraging	Movement associated with looking for food
Grooming	Allogroom, lick or use tooth comb on own fur
Other	Other behaviours
Resting	Remain stationary, eyes open
Sleeping	Remain stationary, eyes close and head between the knees
Social	All interaction with conspecifics
Stress	Non-repetitive behaviours associated with extreme levels of stress
Stereotypic	Abnormal repetitive behaviours
Travelling	Continuous, directed movement from one location to another
Posture	**Definition**
Clinging	Clinging to mesh horizontally/vertically with four limbs
Horizontal suspension	Hanging from two feet
Sitting	Remain stationary with placing on the ground or branches
Standing	Remain stationary in upright position using two or four limbs

Table 3. Activity budget as percentage of time (mean and SE) spent by 30 slow lorises considering baseline and enrichment conditions during June to August 2019. (BC=baseline condition, IN=insect enrichment condition, HG=hanging gum enrichment condition, FG=fixing gum enrichment condition).

	BC 1	IN	BC 2	HG	BC 3	FG
Feeding	2.9 (0.8)	7.6 (1.0)	4.9 (1.1)	30.7 (3.0)	4.1 (1.0)	40.4 (1.0)
Foraging	4.5 (1.0)	15.9 (1.3)	1.3 (0.3)	10.5 (1.3)	1.4 (0.4)	16.3 (1.6)
Grooming	7.8 (1.2)	9.9 (1.8)	8.5 (1.3)	6.6 (0.9)	6.7 (1.2)	6.4 (1.2)
Resting	13.1 (1.4)	9.9 (1.0)	9.4 (1.3)	6.7 (1.1)	10.9 (1.5)	6.2 (1.3)
Sleeping	2.7 (1.5)	0.7 (0.5)	1.5 (0.7)	1.2 (0.5)	1.2 (0.8)	1.8 (0.9)
Social	1.5 (1.1)	0.4 (0.3)	1.8 (0.9)	0.1 (0.1)	1.1 (0.9)	0.1 (0.1)
Stereotypic	14.7 (3.9)	7.6 (2.0)	16.8 (4.1)	7.2 (2.4)	18.4 (4.3)	3.2 (1.2)
Stress	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.2 (0.2)	0.1 (0.1)	0.0 (0.0)
Travelling	51.0 (3.9)	46.9 (3.3)	53.3 (3.9)	35.8 (4.1)	54.3 (4.1)	25.2 (2.3)
Other	1.8 (0.7)	1.0 (0.5)	2.5 (1.1)	1.0 (0.5)	1.8 (0.7)	0.4 (0.2)

Table 4. Significant results from the Generalised Linear Mixed Models in addition to the significant differences in dietary conditions (included in the same models) that are summarise in Fig.4 and Fig.5.

Response	Predictor	Estimate	Std. Error	Z	P
Feeding	Group[a]	2.05	0.73	2.81	0.005
Foraging	Cage size[c]	1.07	0.43	1.43	0.014
	Group[a]	1.84	0.38	4.81	<0.001
	Sex[b]	0.89	0.33	2.68	0.007
Inactive	Sex[b]	-0.91	0.30	-3.04	0.002
Social	Cage size[c]	-8.32	1.50	-5.55	<0.001
	Cage size[d]	-4.11	1.22	-3.37	<0.001
	Species[e]	-2.99	0.98	-3.04	0.002
Stereotypic	Sex[b]	8.67	3.34	2.60	0.009

Reference values: [a] social; [b] male; [c] small; [d] medium; [e] *Nycticebus coucang*

Figure captions

Fig. 1. Map of the Bang Phra Wildlife Domestic Research Station that housed rescued slow lorises. Only slow lorises were housed in areas 1-3 while areas 4-5 housed other species as well.

Fig. 2. Three different environmental enrichments including insect enrichment, hanging gum enrichment and fixed gum enrichment in the large cages, where many furniture were available including plants, branches and nest boxes, using red light to detect the slow lorises.

Fig. 3. Three different environmental enrichments including insect enrichment, hanging gum enrichment and fixing gum enrichment in the small cages, where some furniture was available including small branches and nest boxes, using red light to detect the slow lorises.

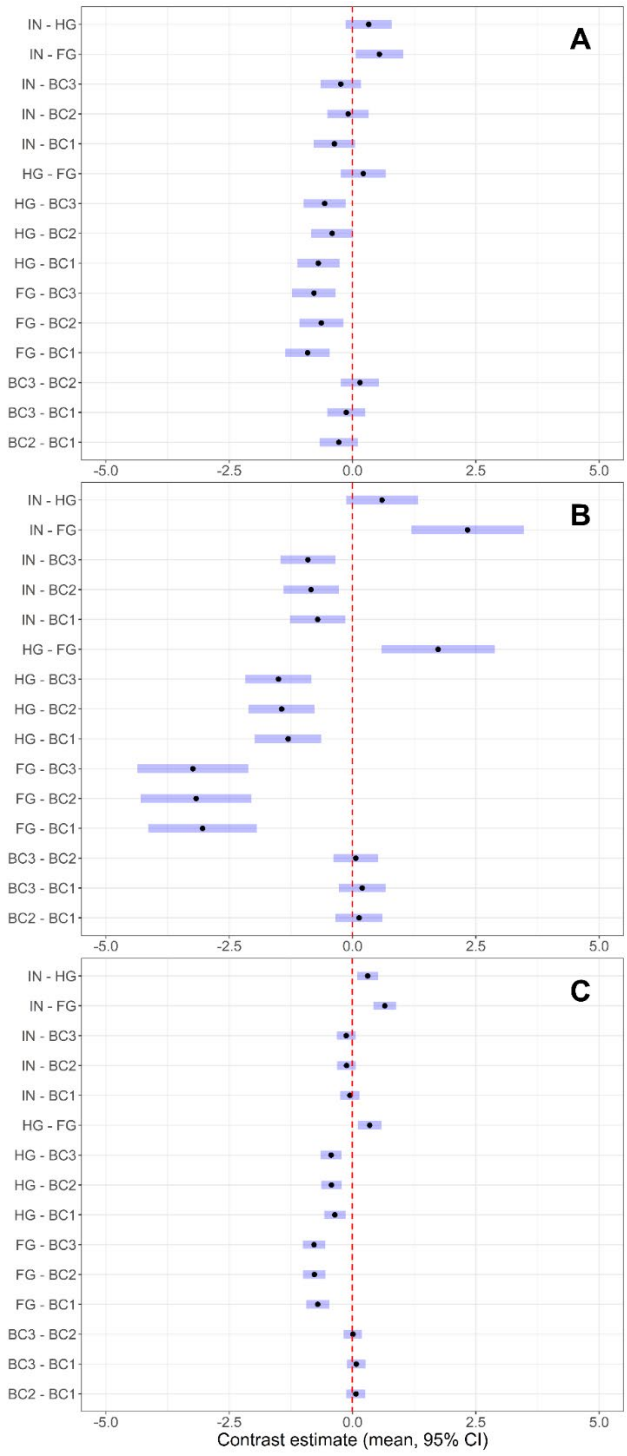
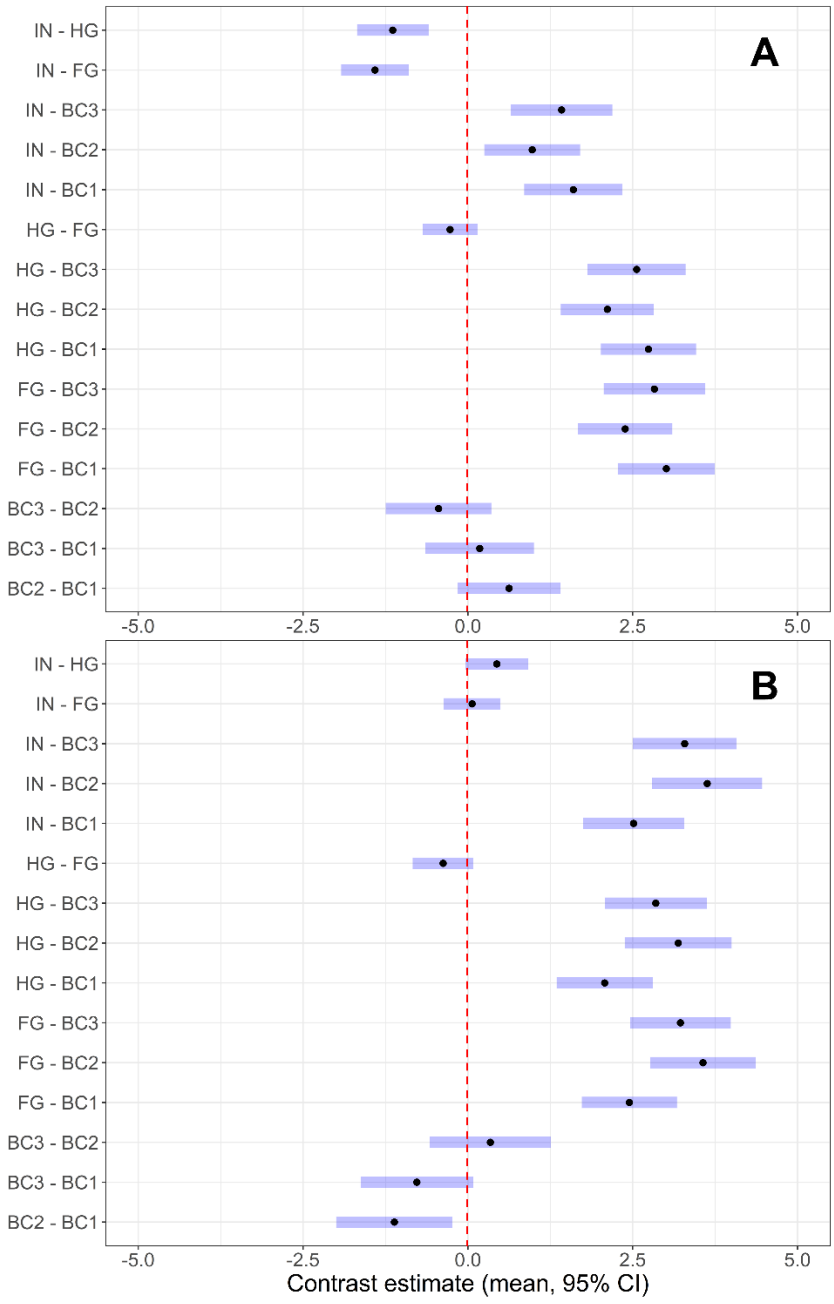


Fig. 4. Behaviours that were reduced when the natural diet conditions were provided to 30 slow lorises in captivity at Bang Phra Wildlife Domestic Research Station, Chonburi province, Thailand from June to August 2019. **A:** Inactive (resting or sleeping); **B:** Stereotypic; **C:** Travelling. Values are contrast estimated means and 95% confidence intervals for pairwise comparisons (after Bonferroni-Holm correction) between the six diet conditions (BC1-3=baseline diet conditions, IN=insect enrichment condition, HG=hanging gum enrichment condition, FG=fixing gum enrichment condition).



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554 **Fig. 5.** Behaviours that were increased when the natural diet conditions were provided to 30
555 slow lorises in captivity at Bang Phra Wildlife Domestic Research Station, Chonburi province,
556 Thailand from June to August 2019. **A:** Feeding; **B:** Foraging. Values are contrast estimated
557 means and 95% confidence intervals for pairwise comparisons (after Bonferroni-Holm
558 correction) between the six diet conditions (BC1-3=baseline diet conditions, IN=insect
559 enrichment condition, HG=hanging gum enrichment condition, FG=fixing gum enrichment
560 condition).