Influence of Enclosure Conditions and Visitors on the Behavior of Captive Malayan Tapir (*Tapirus indicus*): Implications for Ex-Situ Management and Conservation

Kalai Arasi Arumugam*, Lim Qi Luan*, Wan Norhamidah Binti Wan Ibrahim*, Marina Binti Mohd. Toh @ Mohd. Tah*, Christina D. Buesching and Geetha Annavi***

* Biology Department, Faculty of Science, Universiti Putra Malaysia, 43400, Serdang, Selangor Darul Ehsan, Malaysia.
**Wildlife Conservation Research Unit, Department of Zoology, Recanati-Kaplan Centre, University of Oxford, Tubney House, Abingdon Road, Tubney, Abingdon, Oxfordshire OX13 5QL, UK.

DOI: 10.29322/IJSRP.8.7.2018.p7906
http://dx.doi.org/10.29322/IJSRP.8.7.2018.p7906

Abstract- The population of Malayan tapirs (*Tapirus indicus*) in the wild is experiencing a radical decline mainly due to habitat destruction throughout their regions. Therefore, as an initiative measure to sustain the population, ex-situ conservation was established. However, the ability of captive management to maintain and breed endangered species has been proved challenging. In this study, we investigated how the behavior of Malayan tapirs in captivity is affected by enclosure conditions; type (*semi-natural* versus zoo enclosures/*artificial*) and weather (temperature and humidity), and visitors. Behaviors (categorized as resting, locomotion, ingestion, swimming, investigative) were observed using instantaneous sampling over 20 minute periods with intervals of 30 seconds, and analyzed using generalized linear mixed-effects model, glmer. Enclosure type had a significant effect on feeding behavior where tapirs in *semi-natural* enclosures fed more frequently than tapirs in *artificial* environments, mirroring natural feeding activity. Significant adverse effects from background noises and visitors caused tapirs in *artificial* enclosure to be more alarmed and increased their investigative behaviors. High number of visitors overall lowered the activity of tapirs, while low humidity caused tapirs to suffer from dryness, and thus resulted in frequent ingestion (drinking) and locomotion behavior which indicative of thermal stress. Overall from this study, it is concluded that unsuitable enclosure conditions of extreme dryness and number of visitors are prone to be potential stressors that lower the activity pattern which possibly alter the natural behaviors of Malayan tapir in captivity. Therefore, further evaluation on exhibit design and management practices are encouraged to identify variables that could increase the well-being of captive Malayan tapirs.

Index Terms- Malayan tapir, behavior, visitors, humidity, enclosure condition

I. Introduction

Captivity often results in behavioral changes, abnormalities or stereotypic behaviors in wild animals [1,2]. This is particularly hazardous for endangered species, because it can affect their reproductive behaviors, hence their reproductive success, physiology and life expectancy due to social, and demographic changes [3-6]. For example, female Southern white rhinoceros (*Ceratotherium simum simum*) show an increase in their adrenal stress response in captivity that subsequently affects their reproductive physiology [7]. Therefore, zoos worldwide take measures to enhance animal husbandry primarily implementing environmental and behavioral enrichments [8]. To design appropriate species-friendly enclosures, we need to understand the focal species' specific needs that can be determined only through scientific research and behavioral observation.

In this study, we focus on the Malayan tapir (*Tapirus indicus*) which is currently listed as an endangered species by the International Union for Conservation of Nature (IUCN) Red List with an estimated population size of approximately 2,500 individuals in the wild [9]. Malayan tapir are susceptible to extinction due to increased hunting pressure, accidental trapping, and large scale deforestation resulting in habitat loss [9]. Because tapirs are strongly K-selected mammal [10], they have extremely low reproductive rates and produce one calf per parturition [9, 11, 12] after a gestation period of up to 399 ± 3 days [12, 13] with a calving interval of up to 14-18 months [12].

Malayan tapirs are important seed dispersers for a wide variety of plant species [14, 15] and are able to carry and excrete seeds across distances of up to 3.3 kilometers [14, 16]. Therefore, it is crucial to conserve this species at a sustainable population size to maintain the biodiversity of Malayan ecosystems. In recognition of these imperatives, Malayan tapirs are currently bred in government-organized ex-situ breeding programs in Malaysia, but studies that investigate potential stressors that could affect the conservation and welfare of captive individuals are still lacking.

Therefore, we undertook this study to identify potential stressors (quantified through behavioral observations) for both male and female Malayan tapirs in captivity by evaluating 1) the effects of enclosure type (*semi-natural* and *artificial* enclosures), and 2) the presence and number of human visitors (which has been shown to increase the faecal cortico-stress hormone levels in related species such as black and white rhinoceros (*Diceros bicornis* and *Ceratotherium simum*): [17]) and to have substantial effects on the behavioral repertoire of others [5, 18]. In addition, we assessed 3) the relationship between tapir behaviors and weather variables (i.e., temperature and humidity), as wild animals kept under environmental conditions that differ from their natural habitat are prone to exhibit stereotypical behaviors [19].

II. MATERIALS AND METHODS

A. Study Sites and Subjects

This study was conducted in Peninsular Malaysia in three enclosures (Sungai Dusun Padlock A (SDA), Padlock B (SDB) and Padlock C (SDC)) at the Sungai Dusun Wildlife Reserve Centre: 3.4075° N, 101.2382° E (henceforth termed '*semi-natural'*) and in two zoo enclosures (Zoo Negara (ZN): 3.2091° N, 101.7582° E, and Zoo Melaka (ZM): 2.2765° N, 102.2989° E; henceforth termed '*artificial'*). *Semi-natural* enclosures in this study are surrounded by forest and no visitors permitted therefore the amount of background noise are minimal compared to *artificial* enclosures that are surrounded by buildings, traffics and open to visitors, whereas, the other captive facilities are akin between *semi-natural* and *artificial* enclosures (Table 1). We observed a total of 7 adults, three in the *semi-natural* (male = 2, female = 1) and four in *artificial* (male = 2, female =2).

Table 1: Description of study sites

Place	**Enclosure type**	**Surrounding**	**Visitors Permitted (yes/no)**	**Fence height (high/low)**
Zoo Negara (ZN)	artificial	buildings	yes	high
Zoo Melaka (ZM)	artificial	traffic	yes	low
Sungai Dusun Wildlife Reserve Centre Padlock A (SDA)	semi-natural	forest	no	high
Sungai Dusun Wildlife Reserve Centre Padlock B* (SDB)	semi-natural	forest	no	high
Sungai Dusun Wildlife Reserve Centre Padlock C* (SDC)	semi-natural	forest	no	high

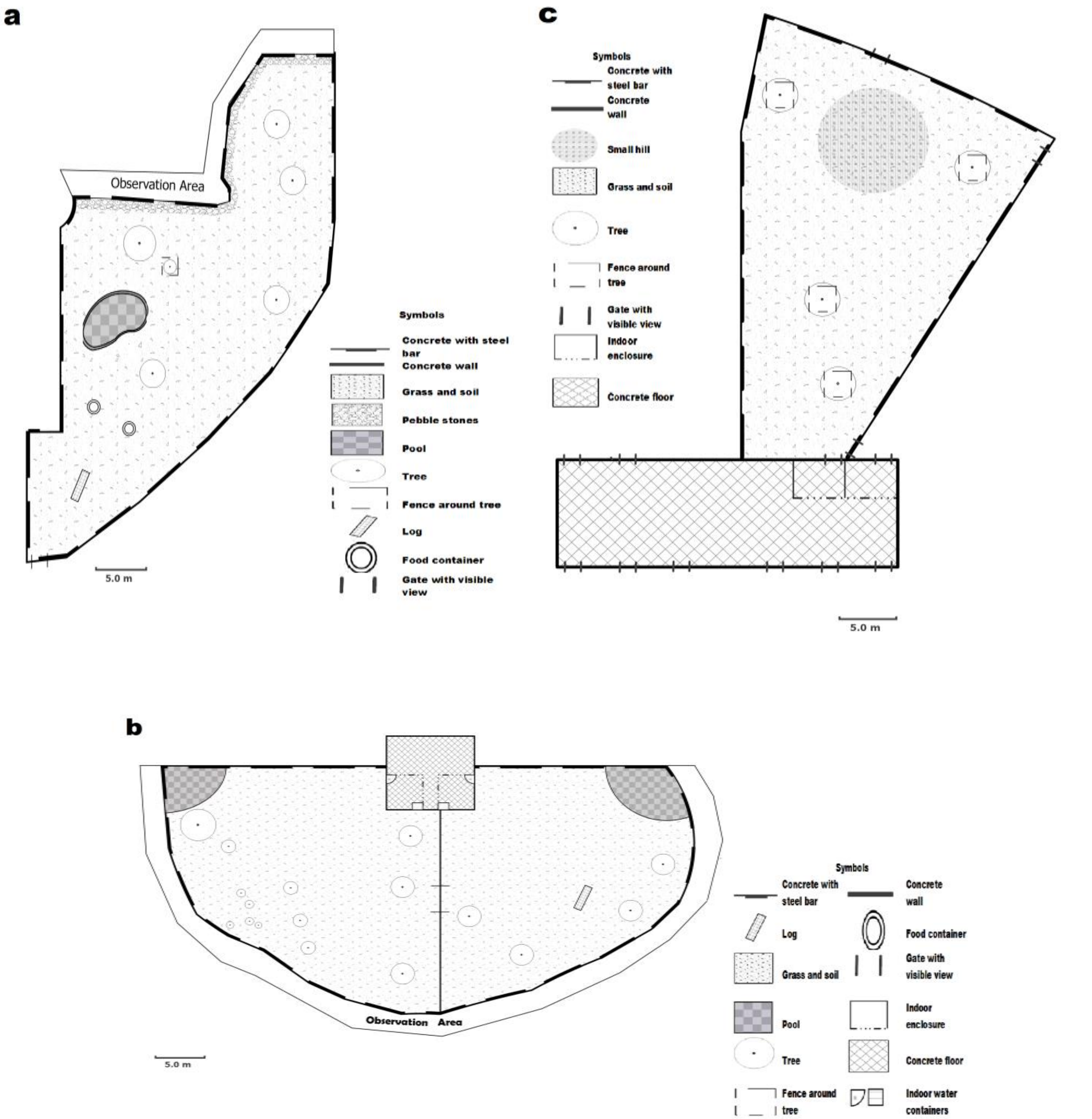
*The same male individual was placed in different enclosures at different times: SDB (March-July), SDC (August onwards).

B. Behavioral Observation

The behavioral observations were conducted over a period of 24 weeks (6 months) between March and August 2016, divided into two week periods and alternating between *semi-natural* and *artificial* enclosures to control for any variation due to month and weather. Tapir behaviors were recorded by instantaneous sampling method using a digital video camera (Brand: Sony, Modal: FDR-AXP35) and camera traps (Brand: Scout Camera, Modal: DTC-560K) with video mode wherever direct observations were not possible. Behaviors were recorded during a continuous 20-minute sampling period at an interval of 30 seconds with a 15 minute break in between different sampling periods [20, 21] for 8 consecutive hours from 0900 to 1700. Number of visitors that visited tapirs' enclosure during each sampling period were counted manually at *artificial* enclosures, and the outdoor temperature and humidity were recorded using Hygro-Thermometer Clock (Extech Instruments, Model: 445702) during each sampling period at all enclosures and averaged per week for each individual. The layout of each enclosure were drawn and measured using SketchUp Pro 2016 Software Version 16.1.1449 (Fig. 1).

C. Ethogram

An ethogram compiled from literature reviews of *Tapirus* sp. and other mammals belonging to the order Perissodactyla was used in this study [7, 21-24; Table 2].


a
Observation Area
5.0 m
Symbols
Concrete with steel bar
Concrete wall
Grass and soil
Pebble stones
Pool
Tree
Fence around tree
Log
Food container
Gate with visible view
c
Symbols
Concrete with steel bar
Concrete wall
Small hill
Grass and soil
Tree
Fence around tree
Gate with visible view
Indoor enclosure
Concrete floor
5.0 m
b
Observation Area
5.0 m
Symbols
Concrete with steel bar
Concrete wall
Log
Food container
Grass and soil
Gate with visible view
Pool
Indoor enclosure
Tree
Concrete floor
Fence around tree
Indoor water containers

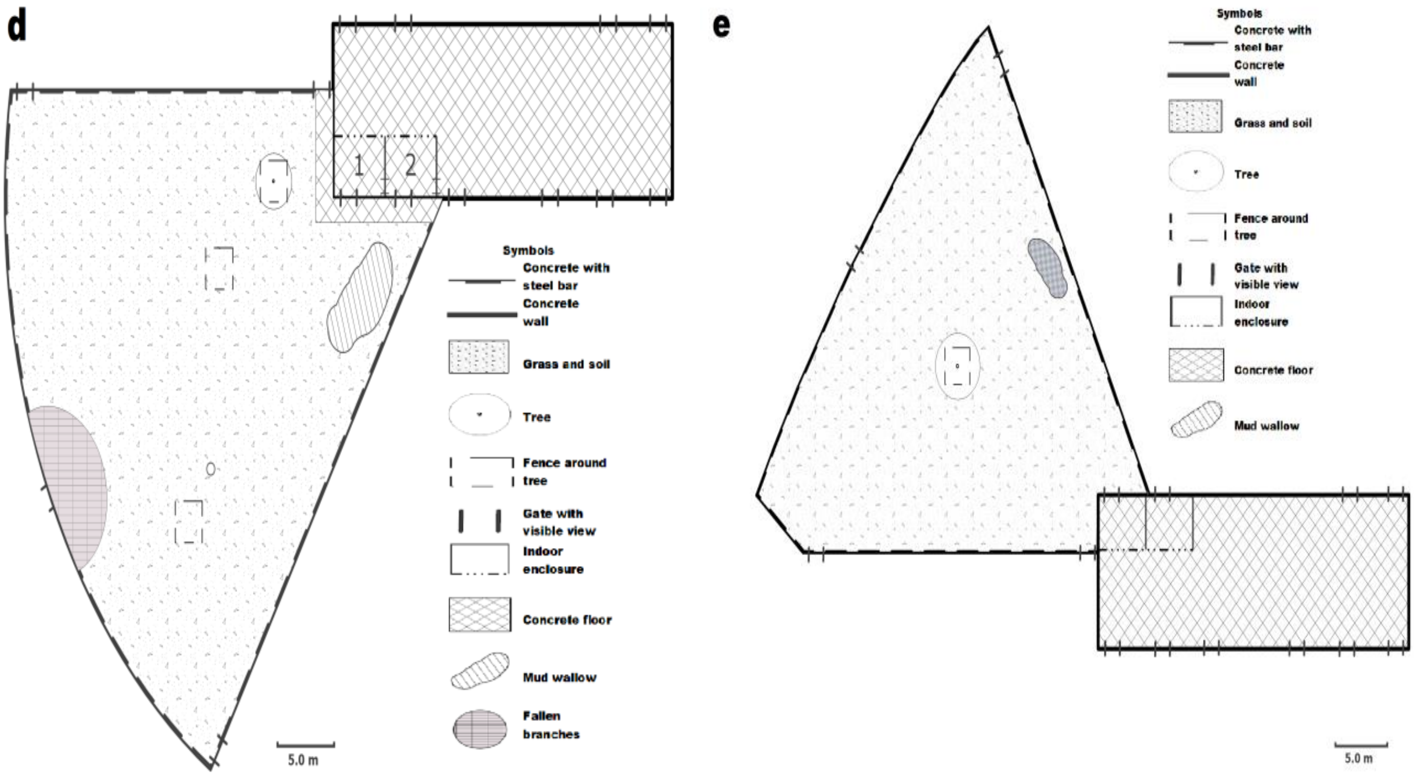


Figure 1: (a) Layout of Zoo Negara, ZN, (b) Layout of Zoo Melaka, ZM, (c) Layout of Sungai Dusun Wildlife Reserve Centre Padlock A, SDA, (d) Layout of Sungai Dusun Wildlife Reserve Centre Padlock B, SDB, (e) Layout of Sungai Dusun Wildlife Reserve Centre Padlock C, SDC

Table 2: Ethogram used for this study

Behavioral Grouping	**Behavior Subgrouping**	**Description**
Ingestion	Eating	The animal in upright position ingesting edible material using the tongue, teeth and mouth, with movement of upper and lower jaw to crush, chew and swallow.
	Drinking	Intake of liquid by using snout to suck water.
Locomotion	Walking	The movement of feet (forefeet and hind feet) by alternately setting each pair of feet forward, with at least one pair of feet on the ground.
	Running	The quick forward movement using two feet by alternatingly making a short jump off either pair.
Stationary	Standing	The animal remains stationary in an upright position either in a bipedal or quadrupedal manner.
Swimming	Swimming	Sitting, standing, lying or swimming in the water with their head out of the water, leading with their snout or fully submerged in the water.
Aggression	Bite	Opening and closing of the jaws with the teeth grasping a conspecific or an object.
	Kick	Movement of one leg lifting off the ground and rapidly extending forward toward conspecific or object.
	Push	The animal uses force by pressing the head, neck, shoulder, chest, body or rump against conspecific or an object in an attempt to move it violently.
Resting	Lying Down	The animal rests on the ground in a horizontal or prostrate position while fully or partially conscious.
	Sitting	The animal in a position where its forelimb extended straight and rump on the ground.
	Sleeping	The animal is in a complete state of unconsciousness; in a dormant state, with eyes closed, resting on the ground.
Investigating	Alert/ Observing	The body is in sitting or standing position, raising its head and staring at another species or objects with eyes wide open and alert to surroundings.
	Smelling	The inhalation of air by touching or extending the snout towards an object, sites or in the air.

D. Data Analysis

All statistical analyses were run in the R Statistical Package Version 3.3.2. We fitted generalized linear mixed-effects models using the glmer function in lme4 package [25] and model averaging based on information criteria, AICc (Akaike's Information Criterion; [26] in MuMIn package [27]. The Y-axis represents the frequency of behaviors (number of times a behavior occurred at each sampling point, see Table 2) averaged per week for each individual. The fixed effects included enclosure type, sex, weather, and number of visitors. We standardized the visitor, temperature and humidity variables to a mean of zero and a standard deviation (SD) of two [28]. The weather variables were inter-correlated (i.e. if temperature (^{o}C) increased, humidity (%) decreased; $r = -0.80$, $p<0.05$), thus we included only humidity in the models. Individual identity and month were included as random effects in all models to control individual-specific and weather-dependent variation. We used an information-theoretic (IT) approach to select sets of plausible models and to estimate the overall importance of each fixed effect [29, 30]. Models were ranked by their AICc value, such that the top model had the lowest AICc value [29] and we considered the top model to be the only plausible model if model rank (ΔAICc) was ≤ 7. A model's relative Akaike weight (ω) was calculated as the model's relative likelihood (exp [−0.5 * ΔAICc]), divided by the sum of the likelihoods for all models considered (whether plausible or not). We used the 'average method' (averaged over all plausible models in which the given parameter was included, weighted by the summed weights (ω) of these models to estimate model-averaged parameters [26, 30]. The 95% confident interval for model-averaged parameter estimates were calculated using the model.avg function in R. The relative importance of each fixed effect was calculated as the total ω of all plausible models that included the fixed effect of interest.

III. RESULTS

A. Enclosure Type

Enclosure type had a significant effect on the feeding behavior of tapirs with individuals kept in *semi-natural* enclosures (SDA, SDB and SDC) fed more frequently than those kept in *artificial* enclosures (ZN and ZM) (Table 3A; Fig. 2a). Tapirs in *artificial* enclosures performed more investigative behaviors than tapirs in *semi-natural* enclosures (Table 3E; Fig. 2b). There were no pools in the *semi-natural* enclosures, thus swimming behavior was investigated in *artificial* only where we observed that tapirs swam more frequently in ZM enclosure compared to ZN (Table 3D; Fig. 2c).

B. Humidity

Humidity had a significant effect on most of the recorded behaviors. Tapirs were found ingesting, moving and resting more frequently during low humidity (55-69%) and warmer temperatures (31-33^{o}C) (Table 3A, 3B and 3F; Fig. 3a, 3b and 3c). In addition, we observed swimming behavior was continuously increasing with increase in humidity (Table 3D; Fig. 3d).

C. Number of Visitors

The higher the number of visitors, the less locomotion was observed (Table 3B; Fig. 4a). Tapirs also swam (Table 3D; Fig 4b) and investigate (Table 3E; Fig 4c) less frequently when the visitor numbers were high. In contrast, tapir resting behavior increased with higher visitor numbers (Table 3F: Fig 4d).

Table 3: Model-averaged parameter estimates over all submodels with Delta Akaike's Information Criterion (ΔAICc) < 7; see Table S1-S7) testing the relationship between variables and groups of behaviors in both, *artificial* and in *semi-natural* enclosures. All continuous data were standardized to a mean of zero and a standard deviation of two. ß (CI) = Estimated value (95% Confidence Interval) and RI = Relative Importance. Bold estimates had a confidence interval that did not overlap zero.

Explanatory variables	**A. Ingestion**		**B. Locomotion**		**C. Stationary**		**D. Swimming**		**E. Investigation**		**F. Resting**		**G. Aggression**	
	ß (CI)	RI	ß (CI)	RI	ß (CI)	RI	ß (CI)	RI	ß (CI)	RI	ß (CI)	RI	ß (CI)	RI
Intercept	2.59 (1.92, 3.28)	-	3.42 (2.88, 3.95)	-	3.24 (2.88, 3.60)	-	4.28 (1.62, 6.85)	-	1.77 (0.40, 3.14)	-	5.51 (5.27 5.75)	-	-0.06 (-1.24, 1.13)	-
Sex	0.29 (-0.16, 0.74)	0.34	0.04 (-0.29 0.38)	0.21	0.16 (-0.02, 0.33)	0.47	-0.14 (-1.26, 0.97)	0.14	0.64 (-1.42, 2.72)	0.23	-0.17 (-0.42, 0.08)	0.36	-0.36 (-1.77, 1.03)	0.23
Enclosure type	**0.45 (0.23, 0.67)**	**1.00**	-0.05 (-0.25, 0.14)	0.23	0.02 (-0.09, 0.13)	0.24	**-0.84 (-1.53 - 0.15)**	**0.53**	**0.89 (0.60, 1.17)**	**1.00**	-0.02 (-0.18, 0.13)	0.21	0.16 (-0.47, 0.80)	0.23
Visitor	-0.08 (-0.16, 0.01)	0.55	**-0.19 (-0.28, -0.09)**	**1.00**	**-0.10 (-0.19, -0.02)**	**0.93**	**-0.19 (-0.25, -0.14)**	**1.00**	**-0.07 (-0.13, -0.009)**	**0.82**	**0.09 (0.05, 0.12)**	**1.00**	-0.04 (-0.45, 0.38)	0.21
Humidity	**-0.13 (-0.25, -0.003)**	**0.69**	**0.23 (0.06, 0.40)**	**1.00**	0.05 (-0.076, 0.17)	0.25	**0.43 (0.33, 0.53)**	**1.00**	0.07 (-0.07, 0.23)	0.30	**-0.19 (-0.24, -0.13)**	**1.00**	0.34 (-0.12, 0.81)	0.48

Fixed effects: sex (male = 0; female = 1); Enclosure type (ZN=1; ZM=2; SDA=3; SDB= 4; SDC= 5). Full model: Behavior = glmer (Type of behavior (A-G) ~ (1 | month) + (1 | individual) + sex + enclosure type + humidity + visitor, data = A-G, na.action = na.fail, family = poisson

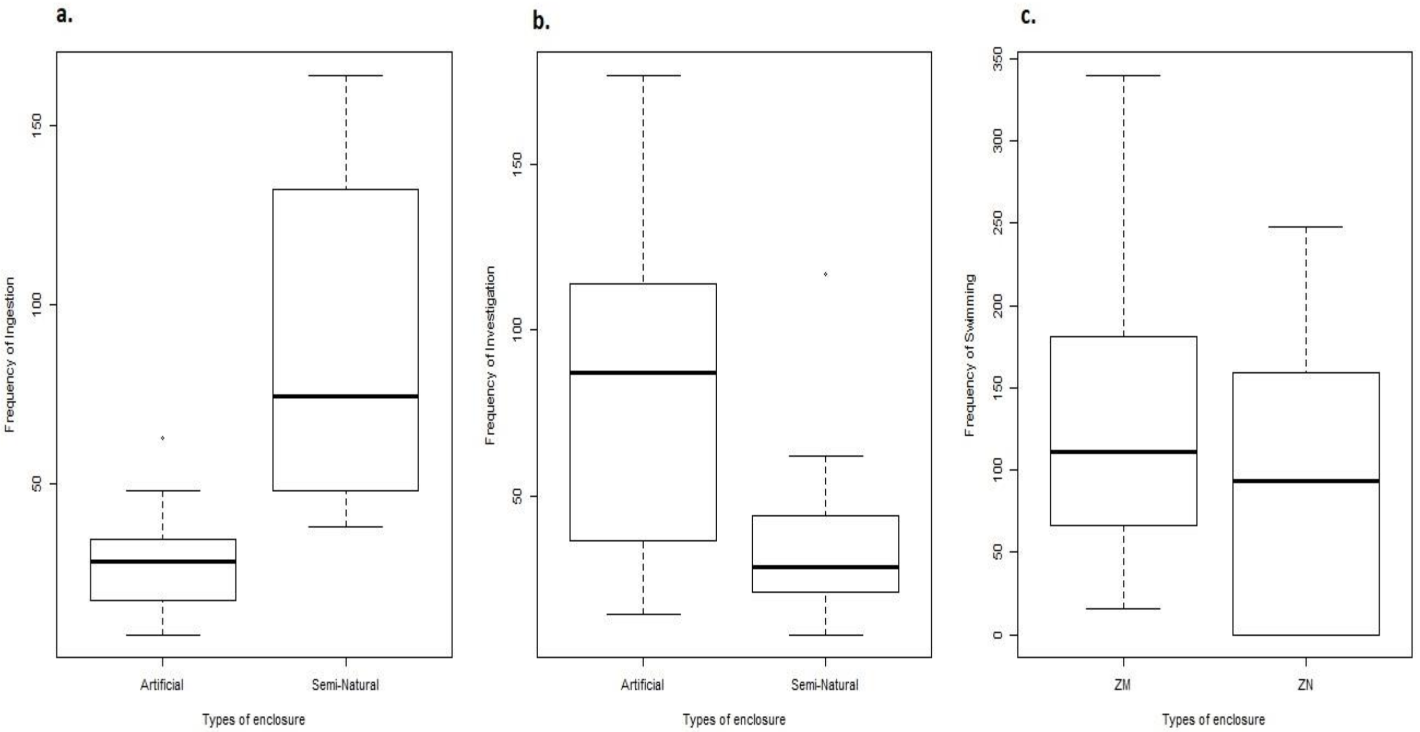


Figure 2: The relationship between (a) ingestion behavior, (b) investigation behavior, (c) swimming behavior and type of enclosures.

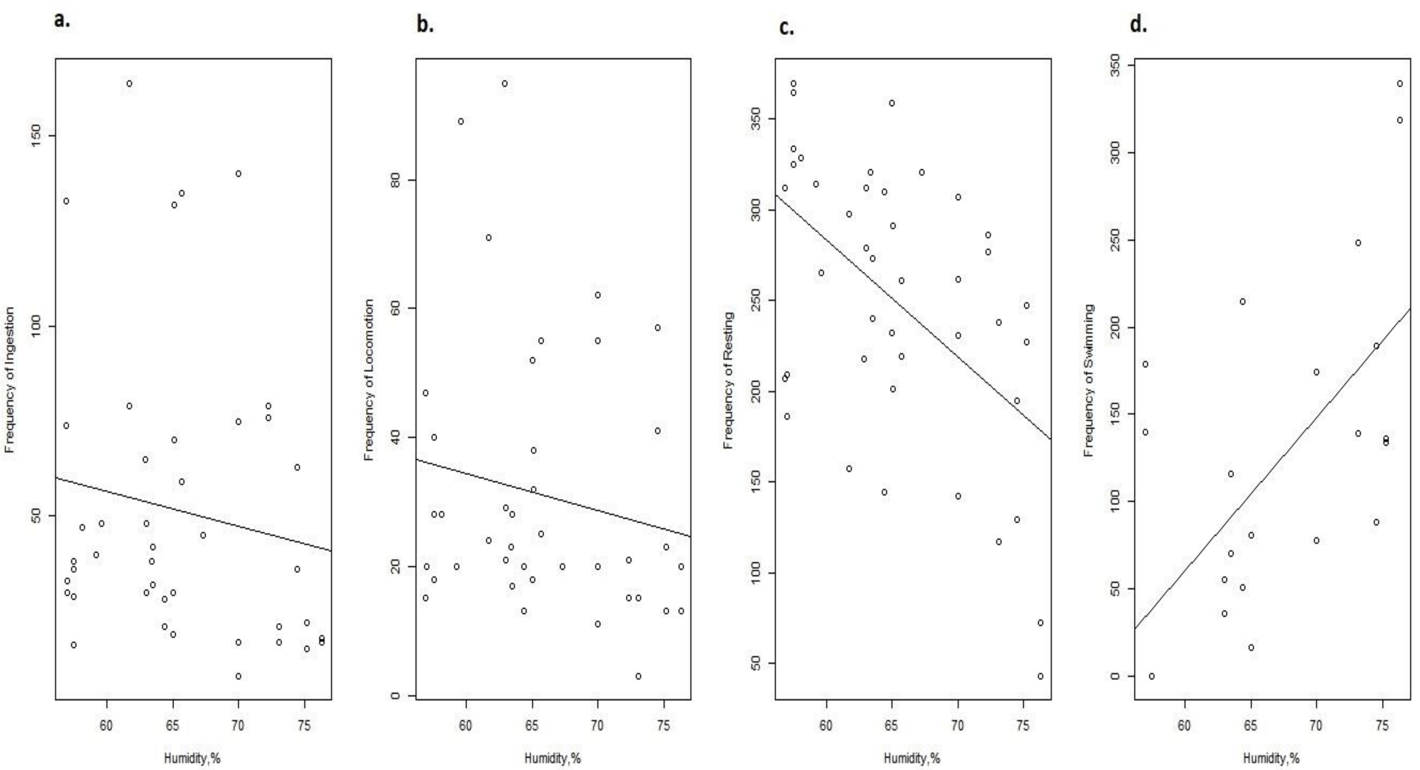


Figure 3: The relationship between (a) ingestion behavior, (b) locomotion behavior, (c) resting behavior, (d) swimming behavior and humidity, %.

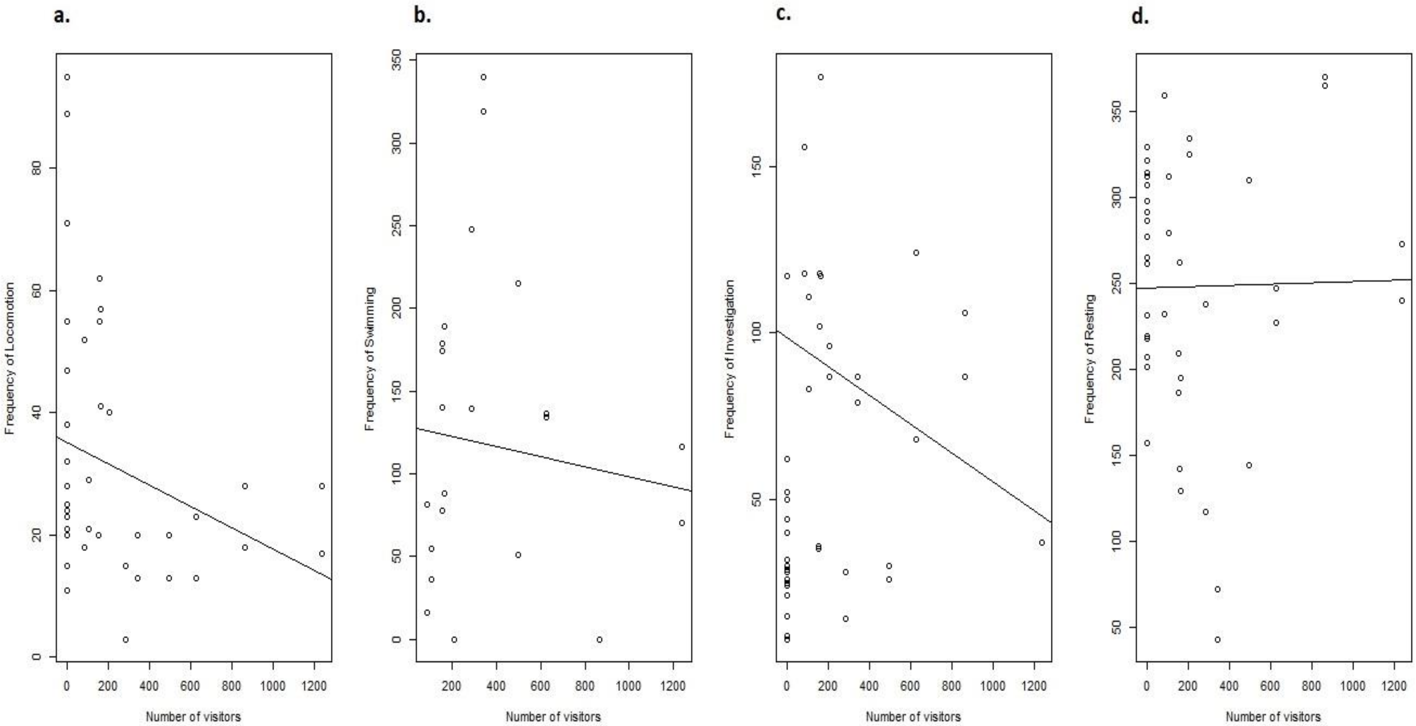


Figure 4: The relationship between (a) locomotion behavior, (b) swimming behavior, (c) investigation behavior, (d) resting behavior and numbers of visitors.

IV. DISCUSSIONS

A. Enclosure Condition

We found that Malayan tapirs in *artificial* fed less often compared to those kept in *semi-natural* enclosures. Previous study on Malayan tapirs' feeding behavior in *artificial* enclosures showed that Malayan tapirs fed comparatively lower than other captive animals such as horse and elephant with evidence of a low defecation frequency, which linked to their low food intake [31]. In addition, all subjects in this study did not feed with the same diet. At *artificial* enclosure (ZN and ZM), tapirs were fed with *Mallothus biaceae* and *Artocarpus heterophyllus*, respectively, and the same plant species were provided every day throughout the study period. In contrast, *semi-natural* tapirs consumed several types of plants such as *Melastoma* spp., *Artocarpus heterophyllus*, *Mallothus biaceae* and *Macaranga* spp. Therefore, limited food choice could be another possible reason. In the wild, Malayan tapirs are known to be selective browsers [32] and therefore, in environments with a higher variety of food choices, the anticipatory behavior of animals increased; concomitantly they were also willing to exert more energy and effort to search for food items if diet was varied. However, when variation in their diet was kept low, anticipation was also low, resulting not only in reduced feeding behaviors [33, 34] but potentially also in nutritional stress and behavioral abnormalities [35].

Investigative behaviors were strongly affected by the enclosure conditions. Investigation through sniffing, general alertness or observation of their surroundings either while standing (stationary), or sitting/ lying down (resting) were observed to be higher in *artificial* than in *semi-natural* environments. These could be explained by the likelihood of tapirs in *artificial* expose to loud noises from the surrounding area, such as building renovation, traffic and noises from visitors. All other tapirs in SDA, SDB and SDC engaged with investigative behavior only when they were exposed to noise, for example, during the monthly grass cutting activity in their enclosure. Irrespective of enclosure type, we observed that tapirs became more frightened (tensing, alert, flee to hide) by loud noises, which often resulted in trembling. In addition, the low fences in ZM made tapirs more susceptible to bullying by visitors such as poking using sticks and pouring water onto them in order to wake the animal. Consequently, tapirs in ZM were more alert and more vigilant to their surroundings compared to tapirs in ZN and they preferred to spend more time hiding inside the pool as a defensive mechanism. Higher fences and accumulation of stones along the fence at observation areas prevented the tapirs in ZN from resting near the fence, and thus helped them to avoid the disturbance from visitors (Fig. 1a). High exposure to noise and the associated elevated stress levels likely result in potential adverse psychological and physiological effects that may alter their habitat use, courtship and mating behavior [36, 37]. Therefore, appropriate plans for enclosure design and location are crucial for tapir welfare.

Wallows or pools are essential elements during the dry season because access to water is important for tapirs to regulate their body temperature [11]. Typically, air humidity was high (70-75%) in the morning between 0900 to 1000hr both in *artificial* and in the *semi-natural* enclosures, and drier (55-69%) from 1100 to 1700hr. Nevertheless, higher frequency of swimming in high humidity (70-

75%) showed that tapirs in *artificial* enclosures were still suffering from the dryness although the suggested outdoor temperature was not exceeded 35°C (humidity of 50%) [38]. This was also supported with increase in locomotion (moving) behavior looking for shaded area to rest and ingestion (drinking) during lower humidity in both *artificial* and *semi-natural* enclosures showing tapirs were seriously affected by the extreme heat. Lack of a pool, water and wallow are the major welfare issues that need immediate action in these ex situ breeding facilities. Further, increasing the amounts of shade and a concurrent decrease to the exposure of light could also help to control temperature [21] and prevent over-heating that would lead to heat stress in tapirs.

B. Visitors

Tapirs in ZM and ZN were negatively affected by the number of visitors: Tapirs showed significantly more locomotion, swimming and investigation when visitor numbers were low and became more passive (resting) during periods of high numbers of visitors. This could be explained by the amount of noise and disturbance caused by large crowds causing tapirs to reduce their activity and to ignore the presence of visitors (personal observation).

V. CONCLUSION

Findings of this study showed that Malayan tapir behaviors were affected significantly by the enclosure conditions (enclosure type and humidity) and number of visitors. Enclosure type caused differences in their feeding behavior and the environment surrounding them had affected their investigative and resting behaviors. As a suggestion a wide variety of plants need to be provided and the leaves should be spread around the enclosure rather than piled in a fixed placed to enhance anticipation in foraging and feeding behavior. This step will help to introduce tapirs to finding their own food. As independent foraging is vital for their survival in the wild, gaining experience in finding their own food is particularly important for tapirs in ex-situ breeding programs to enable them to be released successfully into wild. Moreover, tapir enclosures need to be placed away from exposure to loud noises such as road traffic, and if any renovation takes place in, or in the vicinity of, any tapir enclosure, the animals should be removed temporarily or a sound absorbent barrier should be put in place to reduce the detrimental effects on their welfare due to prolong investigation to the surrounding and lack of resting.

When the air humidity was low, and no swimming pool or water hole was provided within enclosure, tapirs were observed suffered from over-heating, thus engaged in more drinking and moving behavior to find shaded area. When air humidity was high, and despite being within the suggested outdoor temperature of 35°C, tapirs still engaged in swimming behavior. Therefore, further analysis is needed to suggest a suitable outdoor temperature. Furthermore, plenty of shade trees should be planted, and a pool with clean water as well as a mud wallow should always be provided for tapirs to allow them to regulate their body temperature and prevent heat stress.

ACKNOWLEDGEMENTS

We are grateful to the Department of Wildlife and National Parks (PERHILITAN) well as the Zoo Negara and Zoo Melaka for permitting us to study the behavior of their Malayan tapir populations. We thank Dr. Mat Naim Bin Haji Ramli, Dr. Kavita, CEO of Zoo Melaka, the zoo staffs, keepers and veterinarians for their kind support in this study. We also profoundly thankful to the Malaysia Nature Society (MNS) for funding this project under Tapir Project Grant and Mr. Balu Perumal and Mr. Sony for allowing us to borrow their camera traps. During this study, CDB held a Poleberry Foundation Research Fellowship.

ETHICAL APPROVAL

All animal handling procedures were approved by the University of Putra Malaysia ethics committee (Reference: UPM/IACUC/AUP-R033/2016).

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AUTHORS

First Author – Kalai Arasi Arumugam, MSc Student, Biology Department, Faculty of Science, Universiti Putra Malaysia
Second Author – Lim Qi Luan, MSc Student, Biology Department, Faculty of Science, Universiti Putra Malaysia
Third Author – Wan Norhamidah Binti Wan Ibrahim (Dr.), Biology Department, Faculty of Science, Universiti Putra Malaysia
Fourth Author – Marina Binti Mohd. Toh @ Mohd. Tah (Dr.), Biology Department, Faculty of Science, Universiti Putra Malaysia
Fifth Author – Christina D. Buesching (Dr.), Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, United Kingdom
Sixth Author – Geetha Annavi (Dr.), Biology Department, Faculty of Science, Universiti Putra Malaysia

Correspondence Author – Geetha Annavi, Email: geetha@upm.edu.my.

SUPPORTING INFORMATIONS

Table S1: Models with Delta Akaike's Information Criterion (ΔAICc) < 7 for ingestion behavior, df = degree of freedom, Δ=delta, ω= weight.

Variable	df	Loglike	AICc	Δ	ω
Enclosure type, Humidity, Visitor	6	-196.54	407.47	0.00	0.23
Enclosure type, Humidity	5	-197.96	407.59	0.12	0.22
Enclosure type, Visitor	5	-198.42	408.52	1.04	0.14
Enclosure type, Sex, Humidity, Visitor	7	-195.76	408.81	1.34	0.12
Enclosure type, Sex, Humidity	6	-197.21	408.82	1.35	0.12
Enclosure type	4	-200.32	409.73	2.26	0.07
Enclosure type, Sex, Visitor	7	-197.81	410.02	2.55	0.06
Enclosure type, Sex,	5	-199.72	411.12	3.64	0.04

Table S2: Models with Delta Akaike's Information Criterion (ΔAICc) < 7 for locomotion behavior, df = degree of freedom, Δ=delta, ω= weight.

Variable	df	Loglike	AICc	Δ	ω
Humidity, Visitor	5	-227.89	467.44	0.00	0.61
Enclosure type, Humidity, Visitor	6	-227.71	469.81	2.37	0.19
Sex, Humidity, Visitor	6	-227.85	470.10	5.26	0.16
Enclosure type, Sex, Humidity, Visitor	6	-227.70	472.70	2.66	0.04

Table S3: Models with Delta Akaike's Information Criterion (ΔAICc) < 7 for stationary behavior, df = degree of freedom, Δ=delta, ω= weight.

Variable	df	Loglike	AICc	Δ	ω
Visitor	4	-176.38	361.83	0.00	0.28
Sex, Visitor	5	-175.18	362.03	0.19	0.25
Humidity, Visitor	5	-175.96	363.59	1.75	0.12
Sex, Humidity, Visitor	6	-175.00	364.40	2.57	0.08
Enclosure type, Visitor	5	-176.38	364.42	2.58	0.08
Enclosure type, Sex, Visitor	6	-175.10	364.60	2.77	0.07
Enclosure type, Humidity , Visitor	6	-175.96	366.31	4.48	0.03
Enclosure type, Sex	5	-177.44	366.55	4.72	0.03
Enclosure type, Sex, Humidity, Visitor	7	-174.91	367.11	5.28	0.02
Null	3	-180.47	367.57	5.74	0.02
Sex	4	-179.51	368.10	6.26	0.01
Enclosure type	4	-179.55	368.18	6.34	0.01
Enclosure type, Sex, Humidity	6	-177.20	368.81	6.97	0.01

Table S4: Models with Delta Akaike's Information Criterion (ΔAICc) < 7 for swimming behavior in captivity, df = degree of freedom, Δ=delta, ω= weight.

Variable	df	Loglike	AICc	Δ	ω
Enclosure type, Humidity, Visitor	6	-224.76	466.46	0.00	0.45
Humidity, Visitor	5	-226.66	466.65	1.19	0.41
Sex, Humidity, Visitor	7	-226.62	470.18	3.73	0.07
Enclosure type ,Sex, Humidity, Visitor	7	-224.64	470.28	3.82	0.07

Table S5: Models with Delta Akaike's Information Criterion (ΔAICc) < 7 for investigation behavior, df = degree of freedom, Δ=delta, ω= weight.

Variable	df	Loglike	AICc	Δ	ω
Enclosure type, Visitor	5	-258.45	528.56	0.00	0.42
Enclosure type, Humidity,	6	-257.81	530.02	1.45	0.20
Enclosure type, Sex, Visitor	6	-258.25	530.91	2.34	0.13
Enclosure type	4	-261.05	531.19	2.63	0.11
Enclosure type, Sex, Humidity, Visitor	7	-257.61	532.51	3.95	0.06
Enclosure type, Sex	5	-260.86	533.38	4.82	0.04
Enclosure type, Humidity	5	-261.01	533.70	5.13	0.03

Table S6: Models with Delta Akaike's Information Criterion (ΔAICc) < 7 for resting behavior, df = degree of freedom, Δ=delta, ω= weight.

Variable	df	Loglike	AICc	Δ	ω
Humidity, Visitor	7	-473.53	958.72	0.00	0.50
Sex, Humidity, Visitor	6	-472.72	959.83	2.11	0.29
Humidity, Visitor	5	-473.53	961.32	2.61	0.14
Enclosure type, Humidity, Visitor	6	-473.46	959.99	5.84	0.04

Table S7: Models with Delta Akaike's Information Criterion (ΔAICc) < 7 for aggression behavior, df = degree of freedom, Δ=delta, ω= weight.

Variable	df	Loglike	AICc	Δ	ω
Null	3	-69.97	146.58	0.00	0.23
Humidity	4	-69.79	146.67	0.09	0.22
Sex	4	-69.84	148.76	2.18	0.08
Enclosure type	4	-69.84	148.77	2.19	0.08
Enclosure type, Humidity	4	-68.63	148.92	2.34	0.07
Sex, Humidity	5	-68.65	148.96	2.38	0.07
Visitor	4	-69.97	149.03	2.45	0.07
Enclosure type, Sex	5	-69.77	151.20	4.62	0.02
Enclosure type, Visitor	5	-69.84	151.34	4.76	0.02

Sex, Visitor	5	-69.84	151.35	4.77	0.02
Enclosure type, Sex, Humidity	6	-68.55	151.50	4.92	0.02
Sex, Humidity, Visitor	6	-68.56	151.52	4.94	0.02
Enclosure type, Humidity , Visitor	6	-68.59	151.58	5.00	0.02