

Behavioral analysis of a captive male Bornean orangutan (*Pongo pygmaeus*) when exposed to environmental changes

Josefine F. Larsen^{1,*}, Karl K. D. Andersen¹, Julia Cupryś¹, Thomas B. Fosgaard¹, Johanne H. Jacobsen¹, Dominika Krysztofiak¹, Silje M. Lund¹, Birgitte Nielsen¹, Maja E. B. Pedersen¹, Matilde J. Pedersen¹, Adam Trige-Esbensen¹, Emilie M. Walther¹, Cino Pertoldi^{1,2}, Trine H. Jensen^{1,2}, Aage K. O. Alstrup^{3,4} and Juan O. Perea-García⁵

¹Department of Chemistry and Bioscience, Aalborg University, Aalborg, Denmark

²Department of Zoology, Aalborg Zoo, Aalborg, Denmark

³Department of Nuclear Medicine PET, Aarhus University Hospital, Aarhus, Denmark

⁴Department of Clinical Medicine, Aarhus University, Aarhus, Denmark

⁵Department of Psychology, Leiden University, Leiden, Netherlands

*Corresponding author: josefine.fly.larsen@gmail.com

Received: August 16, 2023; **Revised:** September 8, 2023; **Accepted:** September 9, 2023; **Published online:** November 16, 2023

Abstract: Understanding the species-specific behavioral needs of Bornean orangutans (*Pongo pygmaeus*) has led zoological gardens to focus on creating more natural and stimulating facilities. Studies have documented enhanced welfare through various methods, including environmental enrichment like mixed-species habitats, which could improve animal welfare. This study aimed to evaluate the behavioral adaptation following the transfer to a new facility and the possible effects of environmental enrichment on an orangutan in captivity at Aalborg Zoo in Denmark. A newly arrived male was observed for analyzing behavioral changes in the weeks after relocation and introducing two small-clawed Asian otters (*Aonyx cinereus*) to the facility. Changes in behavior were analyzed using recorded behavior and an ethogram before and after the introduction of the otters. The expression of behaviors associated with stress and individual plasticity was analyzed, and the results indicated a change in the behavioral phenotype in response to the introduction of the otters. The study shows that behaviors associated with stress decreased after the introduction of small-clawed otters, suggesting that it had a positive effect on the behavior of the orangutan.

Keywords: Bornean orangutan (*Pongo pygmaeus*), facility improvement, mixed species habitat, ethogram

INTRODUCTION

Optimization of animal welfare is an important issue for zoological gardens, and numerous actions have been implemented to address this [1]. Natural behavior and natural stimulation are viable methods to improve the well-being of captive zoo animals [2]. Environmental enrichment can provide the stimuli necessary for an animal's physical and psychological welfare [3]. Enrichment is also essential for all captive primates, including Bornean orangutans (*Pongo pygmaeus*), to ensure their natural behavioral activity. Thus, natural behavioral activity resembling their lifestyle in natural environments can reduce stress and stress-related behaviors by up to 50% [4]. In the

wild, orangutans are a semi-solitary species, with only mother-infant pairs remaining together [5]. In captivity, orangutans will often socialize in larger groups where the opportunity for social learning is greater. Consequently, skills learned by one individual can more easily spread to others [6,7]. Furthermore, orangutans in captivity are less active compared to wild animals. Those in captivity spend more time resting than searching for food or being active since they do not need to spend time foraging [8]. Orangutans in captivity typically spend 10-15% of their day foraging, while wild orangutans spend approximately 43% [8,9]. In the wild, orangutans spend on average 42% of their time resting, 14% in locomotion, and 2% on

other activities, including nest building and socializing [9]. However, the time spent on a given behavior can vary between individuals. The individual variation in behavior is displayed as a response to changes in environmental conditions over a lifespan. This is characterized by individual plasticity, which depicts changes in the behavioral phenotype [10]. Behavioral reaction norms can be used to describe an individual's behavioral responses across an environmental gradient while also revealing how an animal reacts on average [11]. Phenotypic variance in behavior can be used to describe individual personalities within populations. Additionally, their phenotype will evolve in response to environmental changes [12]. To determine how individuals differ in their level of behavioral consistency over a gradient, the individual stability statistic (ISS) can be used. It makes it possible to estimate within-individual behavioral stability [10].

Some specific behaviors can be used as indicators of impaired animal welfare. These behaviors may be expressed as inactivity and reduced foraging and locomotion activity [13]. Some self-directed behaviors, such as grooming and scratching, are associated with stressful, anxious, or frustrating situations [14,15]. Behavioral issues in captivity may be a consequence of differences between their natural environment and the captive environment [16]. Poorly designed facilities without any features of variability or stimulation can lead to low reproductive success, poor body condition, abnormal repetitive behavior, and, in some cases, death [17]. To increase the well-being of captive orangutans, enrichment can be used by improving the facility design. Facility designs that attempt to resemble the recognizable parts of the habitat, such as climbing ropes, nesting places, vegetation, etc., contribute to an increase in species-specific behavior in zoo-housed orangutans [18]. Furthermore, enrichment can be provided by introducing other species to the facility. Mixed-species facilities can offer the animals dynamic interaction between species, like in their natural environments [19]. However, mixed-species facilities can also lead to stress and conflict for the animals involved [20]. Studies have shown that species from different ecological niches can be mixed to provide shelter and isolation for smaller or more vulnerable species [21,19].

In captivity, people can interact with the zoo-housed orangutans in various ways. Their effect on the animal can either be positive in the form of stimulation or

negative in the form of stress or fear [22]. Human presence can act as enrichment if the interaction between humans and animals is considered beneficial to the participating individuals. In this way, positive interactions between humans and animals could increase general animal welfare [23]. A tool used in zoological gardens to establish a series of positive interactions between the zookeeper and the animal is conditioning training with positive reinforcement [24]. This technique has several advantages, such as facilitating care procedures and making veterinary procedures safer for animals and humans [25,26].

This study examined a male Bornean orangutan's behavioral adaptation to a new facility and the potential effects of adding small-clawed otters to the environment as enrichment. It was expected that the orangutan would exhibit fewer behaviors associated with stress when exposed to environmental enrichment. Furthermore, the orangutan would express individual plasticity as a variation in behavior in response to environmental changes, including relocation and the effect of environmental enrichment.

MATERIALS AND METHODS

Ethics statement

This study was conducted in accordance with Aalborg Zoological Gardens' welfare guidelines and was approved by Aalborg Zoological Gardens' institutional ethics committee.

Participants and setting

The study took place at Aalborg Zoo in Denmark. The behavior of a newly arrived male orangutan was observed on selected days over 4 months from June 26 to October 23, 2022. The orangutan (born on July 5, 2010, in Zoo Aquarium de Madrid in Spain) arrived at Aalborg Zoo on June 21, 2022, just five days before the start of the observations. The orangutan facility in Aalborg included an area of approximately 303 m² separated into two large outdoor areas and four smaller indoor areas. The outdoor areas consisted of trees, bushes, ropes, swings, a small stream, concrete platforms, and a frame of wired fence around and between the two areas. The indoor areas comprised trees, ropes,

swings, platforms, nests, steel doors, concrete floor, walls, and ceiling. Windows placed at one side of the indoor areas allowed visitors to observe and interact with the orangutan. The orangutan's diet consisted of vegetables and was not given systemically throughout the day. In addition, the orangutan was given dried fruit and juice when interacting with the zookeepers throughout training sessions.

Data collection

The total observation time for the orangutan throughout the 5-month period was 412.5 h distributed over 25 different observation days. The observed time frame during each session was from 4:30 AM (UTC+1) to 9:00 PM (UTC+1). Throughout the observation period, two Asian small-clawed otters (*Aonyx cinereus*) were introduced to the facility, one on August 24 and the other on August 30, 2022. The observation period was divided into two periods, referred to as BO before the introduction of otters and AO after the introduction of the otters. The orangutan had access to the indoor and outdoor areas on observation days. Construction work outside of the orangutan's enclosures took place from September 5 to October 9, 2022. Data were collected as recordings from cameras covering the outdoor (Milesight Mini PTZ Dome Network Camera) and indoor areas (Milesight AI 360° Panoramic Fisheye Network Camera). The behavioral observations were analyzed using an ethogram (Table 1). The observed behavior was noted at the specific time for how long

the orangutan would spend on the observed behavior. Due to the camera angle, the behavior of the orangutan could not always be determined. Hence, this was noted as 'Out of view'. Also, when the camera switched to night vision, it was noted as 'Out of view'.

Data analysis

Since the data were not normally distributed, non-parametric statistical methods [28] were used for analysis. To ensure representative data, each behavior had to be observed a minimum of 5 times per day in the entire period to be included in the statistical analysis, otherwise it was excluded in the data analysis. Using the macro function in Microsoft Excel version 2210 (Microsoft), the number of seconds during which a given behavior occurred was calculated.

Testing the differences between the period with and without otters

Median, interquartile range (IQR), skewness, and kurtosis were calculated for both periods, BO and AO, for each behavior using Microsoft Excel version 2210. Differences between medians, skewness, and kurtosis were tested with a Mann-Whitney U-test using Past version 4.03 (Palaeontologia Electronica) to determine if the behaviors were significantly different between conditions. Bonferroni correction was used for multiple testing due to the high number of tests. The application of Bonferroni correction led to the derivation of a new

Table 1. Ethogram with the ten behaviors and their descriptions used in this study [14,22,27].

Behavior	Description
Locomotion	Walking, crawling, or climbing, also with objects in hands or feet. Thinking breaks in movement should only be set as continued locomotion if there is less than 2 min when it is unclear whether he is standing up or not. If he stands up and is making arrangements to walk, locomotion should be continued if the walking arrangements last less than 2 min.
Inactive	Sitting or lying down without a cover.
Inactive covered	Sitting or lying down under a cover.
Foraging/Feeding	Manipulating or ingesting freely available food or drinking.
Positive social interaction	Interacting with each other in a positive manner, e.g., playing, grooming, or mating. Interaction with zookeepers was also included.
Self-directed behavior	Cleaning or combing their hair and body with hands, feet, or mouth, e.g., scratching or licking on parts of their body, studying hands and feet. Eating own feces. Interacting with straw or licking gates.
Interaction with enrichment	Using objects introduced to the environment for enrichment purposes, e.g., smoothies, food boxes.
Yawning	Yawning is characterized by a powerful gaping of the jaw with deep inspiration, followed by a temporary period of peak muscle contraction with a passive closure of the jaw during expiration.
Out of view	When the animal is out of view or it is too dark to observe its behavior (night vision).
Other	Urinating, defecating, or vocalizing.

confidence interval (CI) to account for multiple tests due to the high number of tests performed. A similar approach was used for skewness and kurtosis to test if BO and AO are different based on symmetry [28,29].

Reaction norms

For each behavior, a reaction norm was computed with medians, IQR, skewness, and kurtosis between the BO and AO periods. Slopes were calculated and compared across behaviors using χ^2 tests to examine whether the behaviors were independent of each other [28]. Bonferroni correction was used to account for multiple testing [30]. The reaction norms, slopes, and χ^2 were calculated in R-studio version 2022.07.2 (R Foundation for Statistical Computing) and Microsoft Excel version 2210 (Microsoft). Furthermore, the individual stability statistic (ISS) was calculated for the reaction norms for each behavior. This was done to describe the behavioral stability between t1 and t2, which correspond to BO and AO, as well as to describe the average behavior across all behaviors [12].

Time budget

By dividing the total time observed in BO and AO by the total amount of time spent on behavior in the given period, a time budget was compiled for the two periods based on the observed behaviors. Thus, the behavior is expressed as a percentage of each period [22]. The behavior 'Out of view' was excluded before data analysis.

Daily cumulative distribution

The cumulative values were calculated from the intervals for each behavior for each day, and then cumulative graphs were produced for each behavior in BO and AO. In addition, cumulative graphs were created for each behavior where all days in BO and AO were compared in one graph. This was done to compare the times as well as the intervals for a given performed behavior [29].

Rolling correlation

For each behavior, the correlation between all days in BO and AO for each behavior was examined using Rolling Correlation (Statology). This was done by

dividing all intervals for the given behavior into half-hour intervals for the given days. Here, six half-hours for a behavior from one day were compared with six half-hours for the same behavior from another day. A Rolling correlation was then created, where the six half-hours being compared were moved forward by half an hour. For this, R-studio version 2022.07.2 zoo package, rollapply function (R Core Team), was used. Since the time interval during the day was from 4:30 AM to 9:00 PM, there are 33 half hours in a day's observations. With a Rolling correlation of 6, this gives 28 correlation coefficients for each day compared. All days were compared to each other, yielding 21 comparisons in BO and 152 comparisons in AO. A graph of the correlation coefficients for each behavior in BO and each behavior in AO was then made using Microsoft Excel version 2210 (Microsoft). In this way, the correlations of all the days with each other within a behavior were examined to see if there was a pattern for the behaviors during the day [28]. If the correlation coefficient is $>\pm 0.8$, there is a very high association and thus very high repeatability. If the correlation coefficient is $>\pm 0.6 - \pm 0.8$, there is a high association and, therefore, high repeatability. If the correlation coefficient is $>\pm 0.4 - \pm 0.6$, there is a moderate association and hence moderate repeatability. If the correlation coefficient is $<\pm 0.4$ there is a low association and thus low repeatability [29].

RESULTS

Comparison between the period with otters and without otters

For most behaviors, no significant difference was found in the medians, skewness, or kurtosis between BO and AO ($P > 0.002$). However, the results show that skewness in AO is significantly higher than in BO ($P \leq 0.002$) for the behavior 'Interaction with enrichment' (Table 2).

Reaction norms testing for differences in behaviors between periods

Reaction norms for each behavior were established between BO and AO for median, IQR, skewness, and kurtosis (Fig. 1). Lines without slopes indicate that no individual plasticity and, thus, no variation in behavior in response to environmental change is present. Lines

Table 2. Results of the Mann-Whitney U test.

Behavior	No. of tests	Median	Skewness	Kurtosis
Locomotion	1	ns	ns	ns
Inactive	1	ns	ns	ns
Inactive covered	1	ns	ns	ns
Foraging/Feeding	1	ns	ns	ns
Positive social interaction	0	-	-	-
Self-directed behavior	1	ns	ns	ns
Interaction with enrichment	1	ns	(BO<AO)*	ns
Yawning	1	ns	-	-
Out of view	1	ns	ns	ns
Other	0	-	-	-

The Mann-Whitney U test for medians, skewness (99.8% CI), and kurtosis (99.8% CI) between the period before the introduction of otters (BO) and the period after the introduction of otters (AO). ‘No. of tests’ showed the possible number of tests to calculate for each behavior in each statistical test. ‘ns’ indicates that there is no significance in the tested groups. ‘-’ indicates few observations and therefore no possibility to make statistical tests. In groups with significant differences, angle brackets indicate which of the periods has the highest value. Asterisk indicates different levels of significance. ‘*’ indicates P<0.002.

with slope indicate individual plasticity in the orangutan [12, 28].

AO shows a decrease in reaction norms for median relative to BO for the behaviors ‘Inactive’, ‘Inactive covered’, ‘Self-directed behavior’, ‘Interaction with enrichment’, ‘Yawning’, and ‘Other’. However, the following behaviors show an increase in activity between BO and AO: ‘Locomotion’, ‘Foraging/Feeding’, ‘Positive social interaction’, and ‘Out of view’ (Fig. 1A).

The results for the reaction norms for IQR show that there was a decrease in the 50% middle values between BO and AO for the behaviors ‘Locomotion’, ‘Inactive’, ‘Inactive covered’, ‘Foraging/Feeding’, ‘Self-directed behavior’ and ‘Interaction with enrichment’. However, an increase is observed in the behaviors ‘Positive social interaction’, ‘Out of

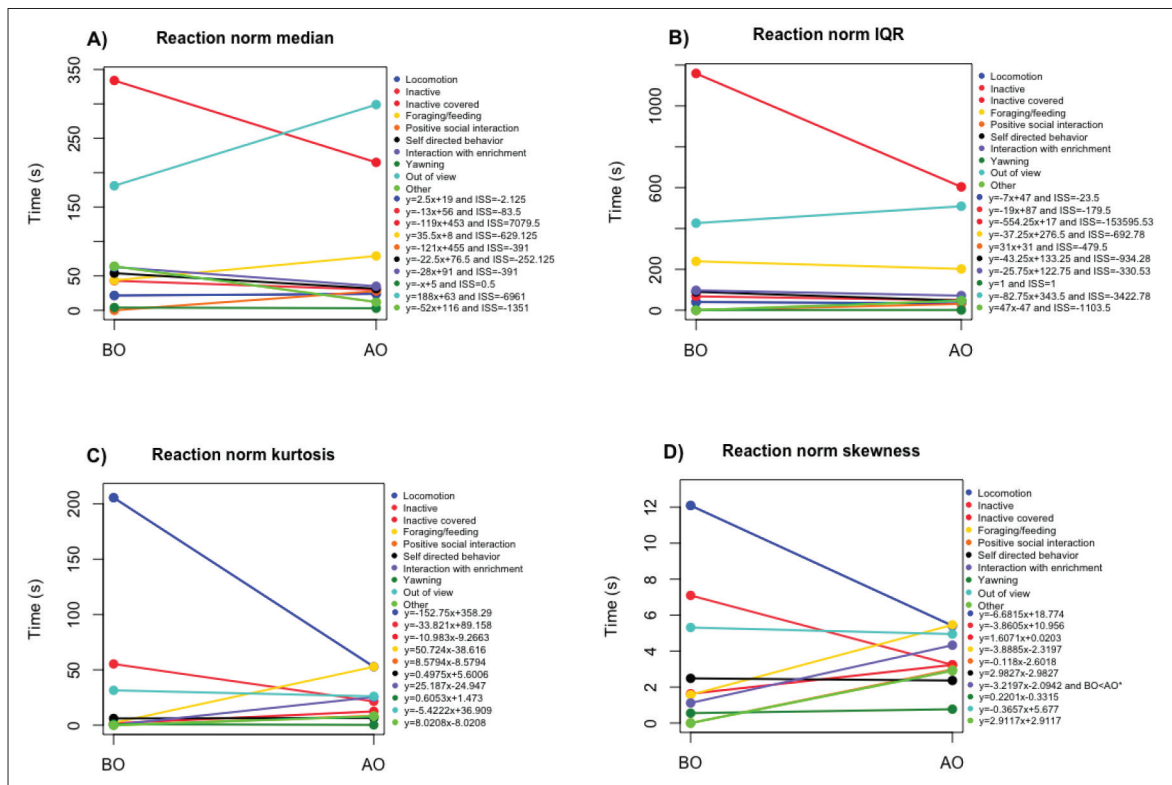


Fig. 1. Slopes for reaction norms between BO and AO for A – median, B – IQR, C – kurtosis, and D – skewness. The x-axis shows BO and AO, while the y-axis shows the time in seconds. For A) and B), the individual stability statistic (ISS) for each slope is shown. BO refers to the period before the introduction of otters, and AO refers to the period after the introduction of otters.

Table 3. Matrix of independence.

Behavior	Locomotion	Inactive	Inactive covered	Foraging/ Feeding	Positive social interaction	Self-directed behavior	Interaction with enrichment	Yawning	Out of view	Other
Locomotion		ns	**	**	**	ns	**	ns	**	**
Inactive	ns		**	ns	ns	ns	ns	ns	**	*
Inactive covered	**	**		**	**	**	**	**	ns	**
Foraging/Feeding	**	ns	**		ns	ns	ns	**	**	ns
Positive social interaction	**	ns	**	ns		ns	ns	ns	**	ns
Self-directed behavior	ns	ns	**	ns	ns		ns	ns	**	**
Interaction with enrichment	**	ns	**	ns	ns	ns		*	**	ns
Yawning	ns	ns	**	**	ns	ns	*		**	**
Out of view	**	**	ns	**	**	**	**	**		**
Other	**	*	**	ns	ns	**	ns	**	**	

The table shows vertically and horizontally a matrix of P values for slopes from the reaction norms with medians. 'ns' – non-significant. The P values above and below the diagonal are equal. Asterisks indicate different levels of significance. The levels are '**' when $P < 0.001$, '*' when $P < 0.002$.

view', and 'Other' between BO and AO. There is no slope in the behavior 'Yawning' (Fig. 1B) [28].

Kurtosis describes the degree of peakedness and the height of the distribution. All kurtosis values are positive, and therefore all data are mesokurtic or leptokurtic [28]. The results for the reaction norms for kurtosis show that there is a decrease in kurtosis between BO and AO for the behaviors 'Locomotion', 'Inactive', 'Yawning', and 'Out of view'. There is an increase in kurtosis between BO and AO for the behaviors 'Inactive covered', 'Foraging', 'Positive social interaction', 'Self-directed behavior', 'Interaction with enrichment', and 'Other' (Fig. 1C).

Skewness describes the degree and direction of a tail in a distribution. All skewness values are positive; thus, all behaviors between BO and AO are skewed to the right. Distributions that have no skewness are symmetric [28]. The results from the skewness reaction norms show a decrease in skewness between BO and AO for the behaviors 'Locomotion', 'Inactive', 'Self-directed behavior', and 'Out of view'. However, there is an increase in skewness between BO and AO for the behaviors 'Inactive covered', 'Foraging/Feeding', 'Positive social interaction', 'Interaction with enrichment' ($P < 0.002$) and 'Other' (Fig. 1D).

The χ^2 -test tests whether the behaviors were independent of each other, and the results, therefore,

indicated either the rejection or the acceptance of the null hypothesis. This means that if the P value was below 0.05, the null hypothesis could be rejected, and the behaviors were dependent on each other. In most of the results, the null hypothesis was therefore rejected, and behaviors were therefore dependent on each other (Table 3).

ISS values were calculated for the reaction norms for median and IQR. ISS is measured on the phenotypic behavior of an individual at times t1 and t2. Values below -500 are observed for the median reaction norms for the behaviors 'Inactive covered', 'Foraging/Feeding', 'Out of view', and 'Other'. In addition, values below -500 are observed for the IQR reaction norms for the behaviors 'Inactive covered', 'Foraging/Feeding', 'Self-directed behavior', 'Out of view', and 'Other'.

From the slopes of the median obtained by the reaction norms, a matrix was constructed to test the independence between all behaviors using χ^2 tests. A confidence level of 0.002 was used, whereby values below this are not independent but rather dependent on each other [28, 30]. A significance $P < 0.001$ and $P < 0.002$ is observed between various behaviors (Table 3).

Time budget

The percentage time spent on each of the behaviors varied between the two periods, BO and AO. The orangutan used more time (expressed in %) on the behavior 'Inactive covered' than on the behavior 'Inactive' in both periods. Hence, the behavior inactive is decreasing, and the behavior inactive covered is increasing between BO and AO. Nevertheless, inactive covered is still the most exhibited behavior in both periods. Other behaviors that show a decrease in time spent (%) from BO to AO are 'Locomotion', 'Self-directed behavior', and 'Yawning'. On the other hand, behaviors that show an increase in time spent (%) from BO to AO are 'Foraging/feeding', 'Positive social interaction', 'Interaction with enrichment', and 'Other' (Fig. 2).

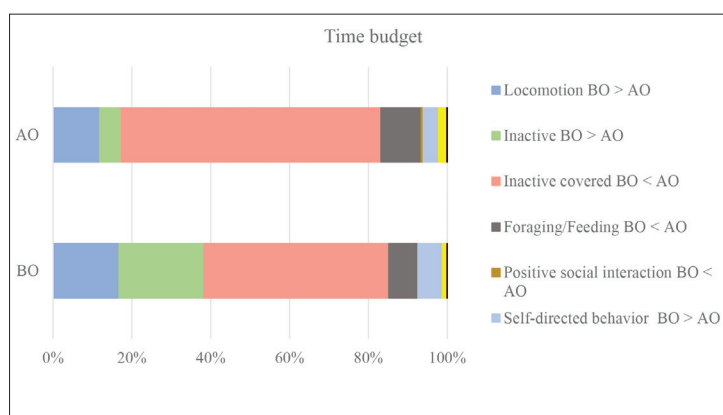


Fig. 2. Time budget of the behavioral proportion. The figure shows how the orangutan's time is distributed between the behaviors. Each behavior is individually colored and shown as a percentage in each of the bars. The x-axis indicates the amount of time in percent each of the behaviors is observed throughout the whole BO or AO. The y-axis indicates BO and AO. BO refers to the period before the introduction of otters, and AO refers to the period after the introduction of otters.

Daily cumulative distribution of the behaviors

Cumulative curves of the distribution of behavior across days were constructed (Figs. 3 and 4). This was done with all days for a behavior in BO and all days with a behavior in AO (Fig. 3). Here, all days are shown with their respective colors on a graph. This is done to examine if there is a pattern between the days for each behavior in BO and AO respectively, and to see if any days stand out (Fig. 3). When the intervals were interpreted, the individual days were considered, not the intervals combined. For 'Locomotion' in BO, there is a single day where more time was spent on this behavior than on the other days in BO. For 'Inactive' in BO, there is again a single day where more inactivity is observed than on the other days. This is the same day as in 'Locomotion' BO. For 'Inactive covered' in BO and AO, there is a single day in each period where less 'Inactive covered' is observed than the other days. For 'Foraging/Feeding' in BO and AO no clear pattern is observed. For 'Self-directed behavior' in BO and AO there is no clear pattern either. 'Yawning' was only observed in BO on one day. Therefore, no pattern can be seen. For 'Out of view' two patterns can be seen in both BO and AO. 'Other' was only observed in BO on day one, so no pattern is visible. No 'Positive social interaction' was observed in BO (Fig. 3).

Cumulative graphs have also been made where each behavior is shown with all days from BO and AO

combined. This has been done to examine the similarity in a pattern between the two periods (Fig. 4).

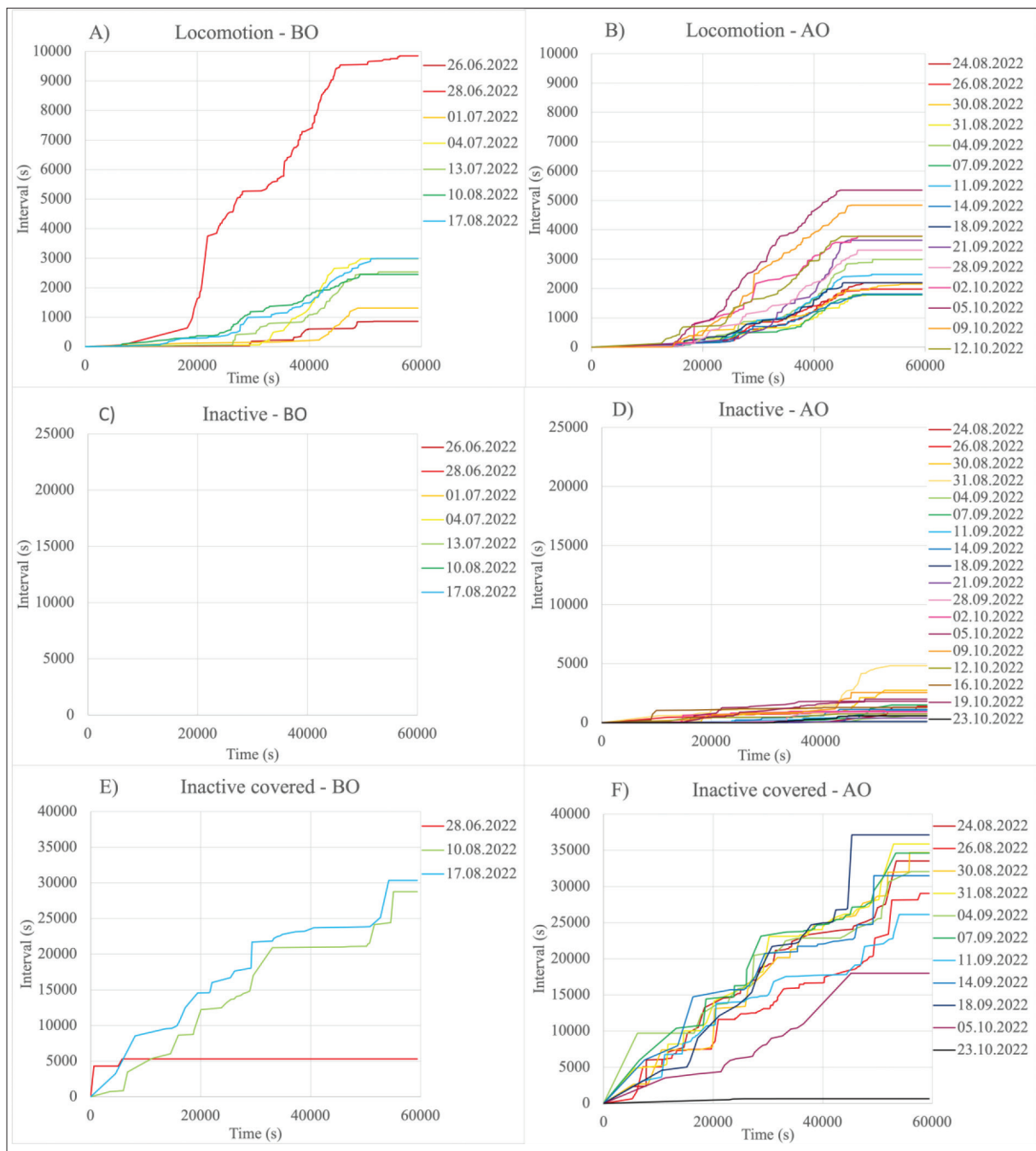
Rolling correlation

Graphs of the correlation values for each behavior in BO and AO have been computed (Fig. 5). For 'Locomotion' in AO, there are two clear patterns, one of which has high repeatability after 20,000 s. For the second pattern, high repeatability is seen at the beginning of the day and again at 33,000 s. A further peak is seen at 40,000 s with a correlation coefficient of ≥ -0.6 . For 'Foraging/Feeding' in AO, the graph shows a pattern indicating a given diurnal rhythm. After 35,000 s, high repeatability is observed extending over the whole day, with a correlation coefficient of ≥ 0.6 .

The time spent on 'Interaction with enrichment' in BO is all observed in the last half of the day, but no general pattern is seen for the correlation. For this behavior in AO, no pattern is observed, but high reliability is seen for some of the regressions between 35,000 s and 45,000 s. For 'Out of view' in AO, there are two clear patterns. The first is consistent at high repeatability with a correlation coefficient of ≥ 0.6 after 13,000 s. In contrast, the second pattern is variable in repeatability, but there is a high repeatability at 1,000 s, 36,000 s, and 42,000 s. For BO, a pattern is observed with a correlation coefficient of ≥ 0.6 between 22,000 s and 45,000 s. Generally, a pattern with a very high association and thus repeatability is observed throughout 'Inactive covered' in AO. Around 37,000 s to 42,000 s, there is a slight drop in many of the lines < 0.8 and some < 0.6 . For 'Locomotion' in BO, 'Inactive' in BO and AO, 'Inactive covered' in BO, 'Foraging/Feeding' in BO, 'Positive social interaction' in AO, 'Self-directed behavior' in BO and AO, 'Yawning' in AO, and 'Other' in AO, no patterns are seen (Fig. 5).

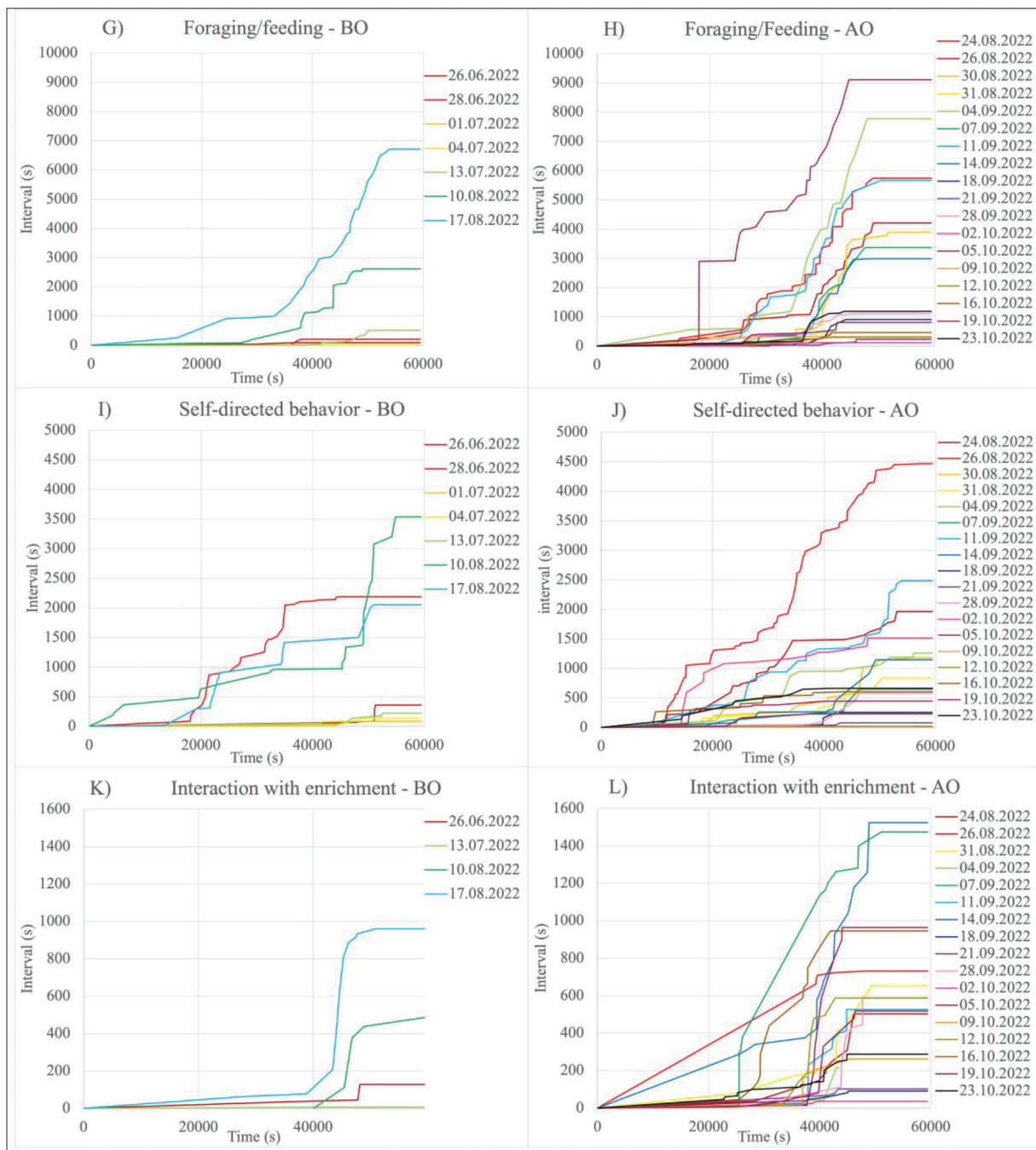
DISCUSSION

Environmental changes in and around the facility could be reflected in the behavioral plasticity of the orangutan. For example, any behavior change caused by the integration of sensory inputs from environmental enrichment can be attributed to behavioral plasticity



[31]. The orangutan's behavioral reaction norm changed from BO to AO by either an increase or a decrease in specific behaviors. Studies have shown that a stimulating environment alters animal behavior, improves complex cognitive functions, including memory and learning, and impacts the central nervous system [32]. Furthermore, environmental enrichment can positively influence the emotional and stress response of animals [33]. An increase in 'Inactive covered' from BO to AO

could indicate impaired animal welfare, as increased inactivity and the use of objects to hide could indicate this [13]. In zoological gardens, blankets can also be used for enrichment by replacing big leaves and other plant materials from the wild. Blankets can stimulate the natural behavior of orangutans, where they can be used for nest building, bedding, and rain or sun cover [13]. Nesting provides shelter from predators and helps thermoregulation when the weather is harsh, or the



temperature is low [34]. As the AO period was in the autumn, temperatures were lower than for the BO period, and the weather could therefore be a reason for the increase in covered inactive [13]. Although there was an increase in 'Inactive covered', a decrease in 'Inactive' was observed from BO to AO, which could be a sign of improved welfare as increased inactivity is an indicator for impaired welfare [13]. The larger amount of time spent on self-directed behavior in BO could be

a sign of frustration or anxiety and a measure of stress, which may be an indication of impaired animal welfare [14,15]. An indication of improved animal welfare is increased time spent on positive social interaction because orangutans develop through social learning and positive social interaction [6,7]. The increase in 'Positive social interaction' is considered beneficial, but it is unknown if this development was due to the introduction of otters to the enclosure [23].

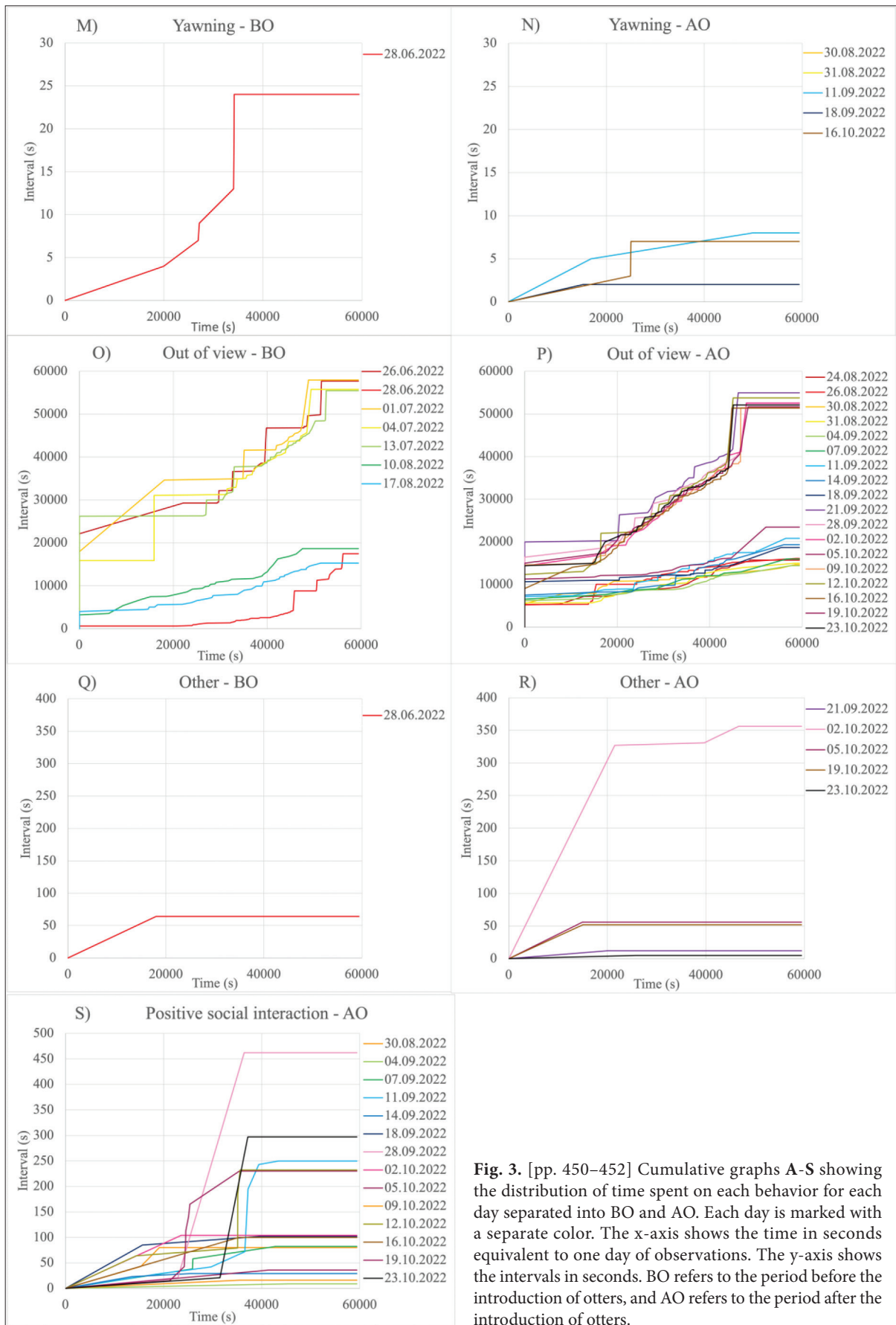
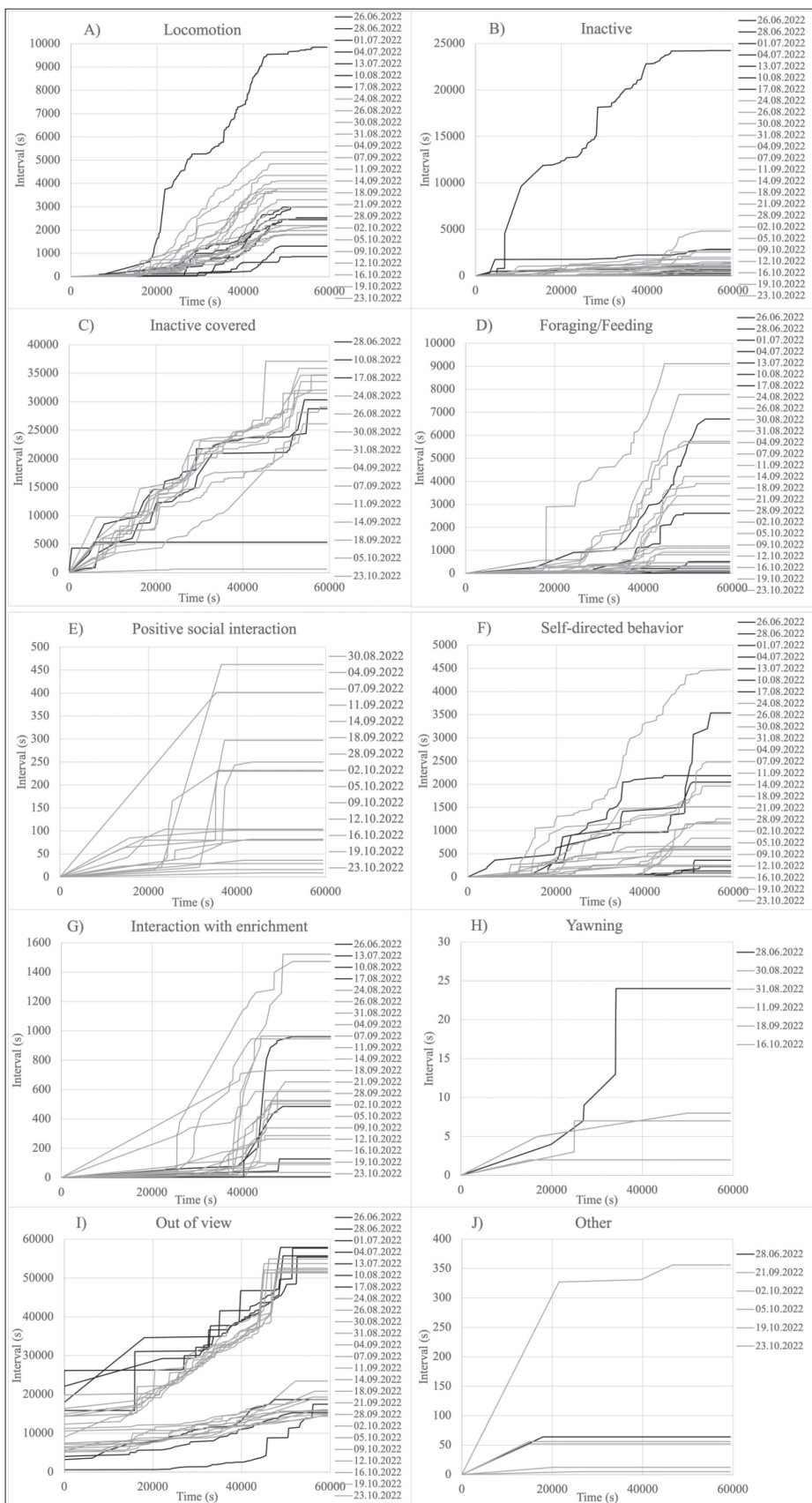
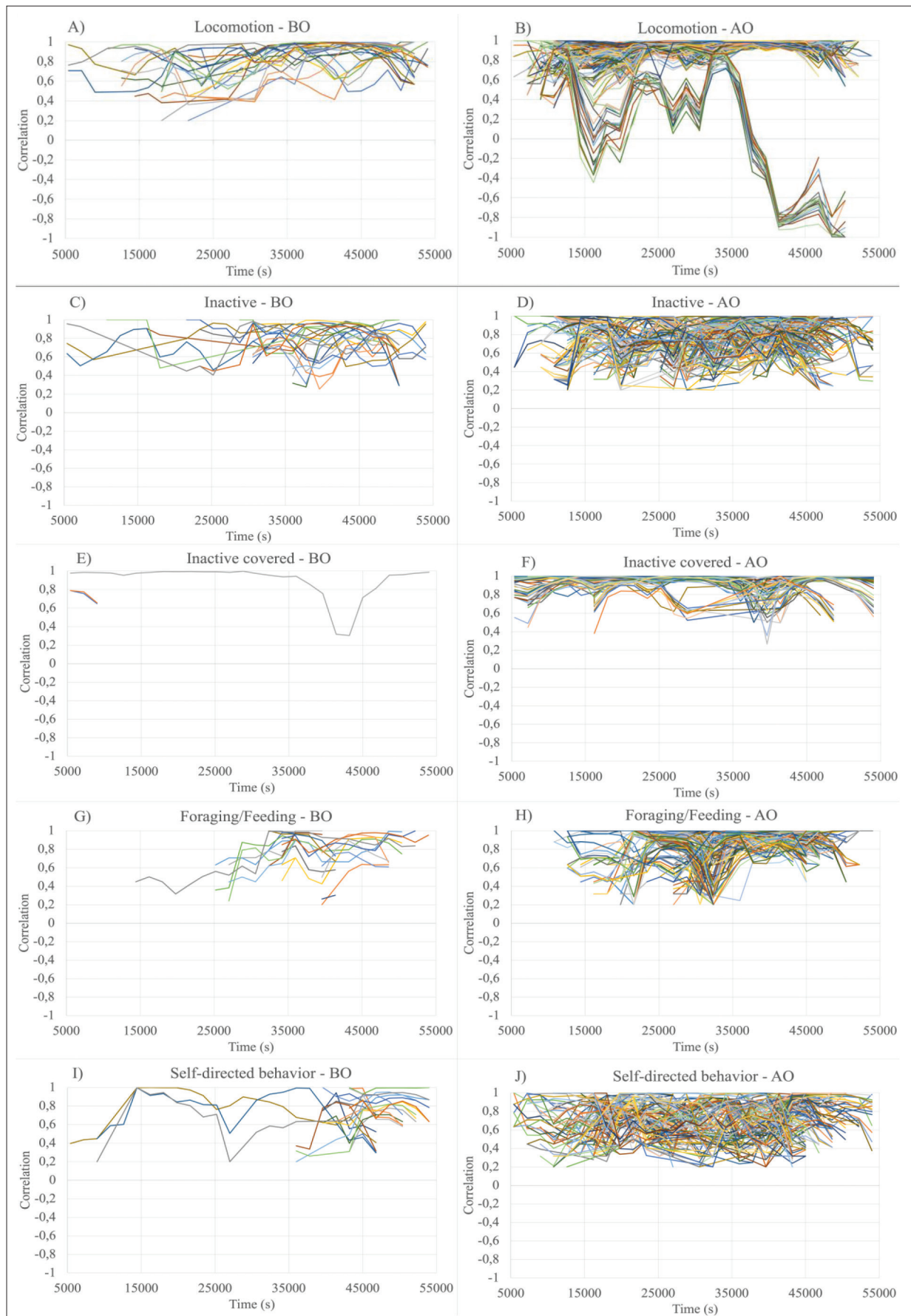


Fig. 3. [pp. 450–452] Cumulative graphs A-S showing the distribution of time spent on each behavior for each day separated into BO and AO. Each day is marked with a separate color. The x-axis shows the time in seconds equivalent to one day of observations. The y-axis shows the intervals in seconds. BO refers to the period before the introduction of otters, and AO refers to the period after the introduction of otters.



A routine was observed in the afternoon in AO for 'Foraging/Feeding', which may indicate that the orangutan either spent more or less time feeding at the end of the day. The orangutan was observed returning to the nesting place with browse to eat the leaves and chew on the branches. One study found that fresh browse increases activity and foraging, as the branches can be used for object manipulation [22]. To this end, the orangutan was observed manipulating browse to get food from enrichment items around the facility. This may indicate that the facility design stimulated the orangutan's behavior [18]. A significant increase in locomotion could be an indicator of stress [35,14]. However, locomotion is not a clear indicator of welfare because most animals exhibit locomotion, but the level of locomotion can be used to analyze the change over a gradient [36]. Studies indicate that captive orangutans show an increase in locomotion when small food items are provided and objects like robes, swings, and platforms are present in the facility [22]. Orangutans are arboreal and have a need for climbing and resting high up; hence, the design of the facility is important for their well-being. The facility

Fig. 4. Cumulative graphs A-J showing the distribution of time spent on each behavior for each day from both BO and AO. The BO days are black, and the AO days are grey. The x-axis shows the time in seconds equivalent to 1 day of observations. The y-axis shows the intervals in seconds. BO refers to the period before the introduction of otters, and AO refers to the period after the introduction of otters.



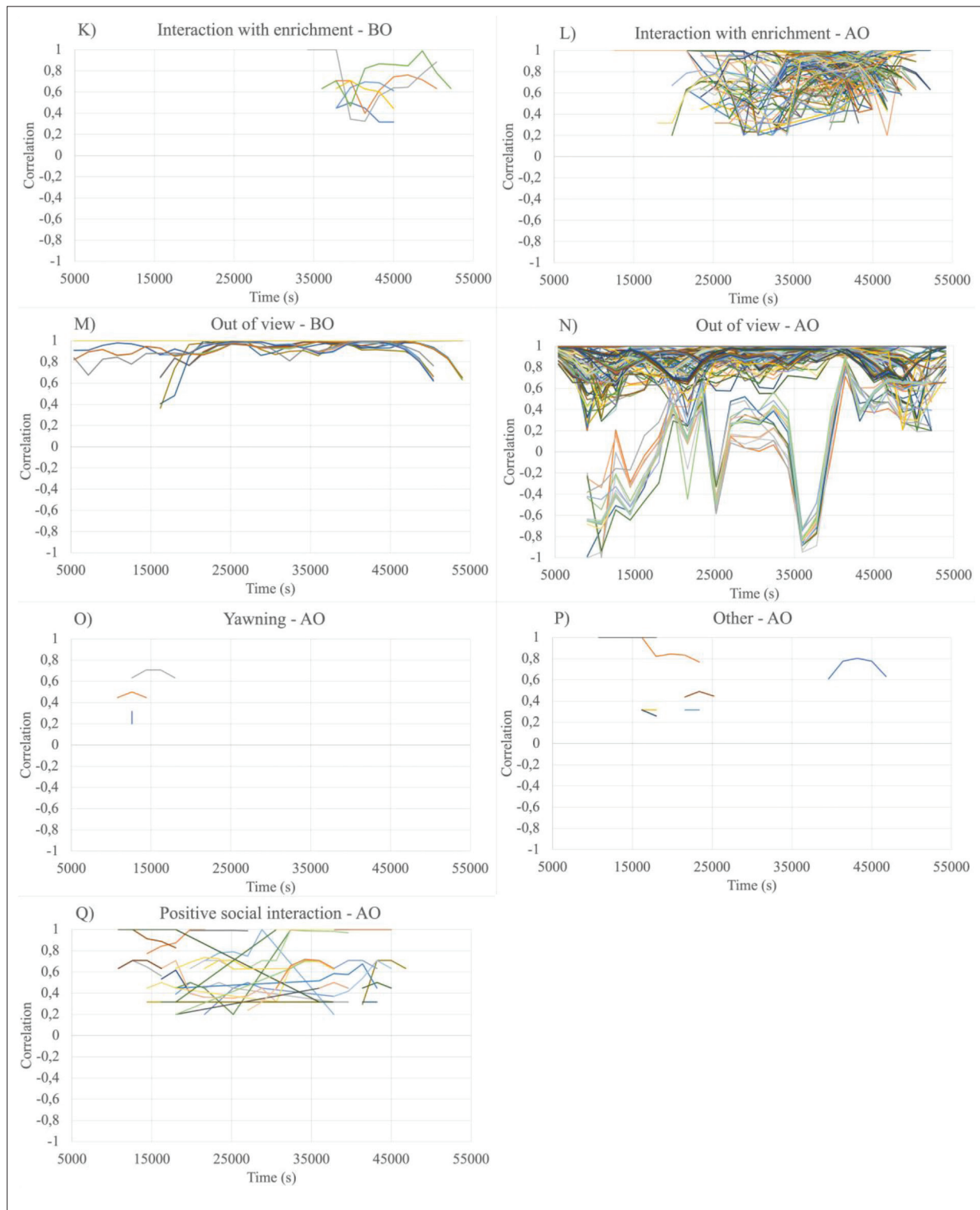


Fig. 5. Graphs A-Q present the rolling window correlation values for each behavior separated into BO and AO. BO refers to the period before the introduction of otters, and AO refers to the period after the introduction of otters. The x-axis shows time in seconds, and the y-axis shows the correlation value.

should be designed to resemble orangutans' natural habitat as closely as possible [25]. The orangutan spent more time interacting with provided enrichment in the facility from BO to AO. Therefore, a change in the orangutan's behavioral plasticity ranging from BO to AO could be indicated, whereby a behavioral adaptation to the stimulating environment could have occurred. Providing enrichment is important as the lack of enrichment can promote bad psychological health and be shown as aggression or abnormal behaviors [25].

The circadian rhythm shows how the orangutan reacts on average during the day, which can be used to describe the personality of an individual [12]. Personality as a behavioral aspect of an animal can be observed as differences in the average level of a given behavior and the maintenance of that level over a gradient [37,38]. However, this does not imply that individuals are completely consistent in their behavior; they may differ across the gradient and thus exhibit plasticity [38,39]. Therefore, the orangutan's personality can be seen in an unchanged circadian rhythm between the BO and AO periods, where the variations between these periods can be described as plasticity and, consequently, a change in the behavioral phenotype in response to environmental changes. In addition, the height of the reaction norms can be used to describe plasticity, with the slope describing personality [39]. When looking at an individual, the variation within a behavior can be used to describe behavioral stability, and the average behavior over all other behaviors examined is used as an index of personality. Low values of ISS describe a high instability in personality, and this may indicate that there has been a change in phenotype, and thus a plastic response, of the orangutan between BO and AO, for which a personality cannot be described from these values. This is because the link between personality and individual plasticity cannot be described in an obvious parameter, as these can develop independently of each other [38,12]. Nevertheless, it is important to be careful when construing some of these behaviors because a large part of an animal's behavioral pattern is likely to involve behaviors with no obvious welfare consequences [36]. The significant difference between interaction with enrichment in BO and AO may suggest that the orangutan has adapted better to the facility, which could lead to improved animal welfare [18]. No significant difference in the remaining behaviors could be found, as the orangutan did not change behavior

significantly between the two periods. This could be interpreted as positive and negative as it may imply that the orangutan has not adapted to the facility over the period or that it has not been adversely affected by the mixed-species facility [18,21]. Although the addition of otters to the facility is not seen to affect the orangutan, it can still be assumed to be successful simply because the species tolerate each other [19]. Behaviors that could indicate impaired animal welfare were decreased in most statistical analyses from BO to AO [14,15]. However, other statistical analyses showed conflicting results for behaviors associated with stress. This may be because some of the tests used median, IQR, skewness, and kurtosis, whereas others used the total intervals for each behavior in BO and AO.

CONCLUSIONS

This paper addresses the behavioral adaptation of a male Bornean orangutan upon translocation to a new facility, as well as the impact of environmental enrichment. Behavioral adaptation was examined before and after the addition of otters as environmental enrichment. The study documented some variation in behaviors between these two periods. Less stress-related behavior and more behavior associated with welfare were observed after the introduction of the otters, suggesting that adaptation to the new facility and the introduction of otters to the facility may have had a positive effect on the orangutan. To thoroughly investigate orangutans' adaptation to the new facility and the influence of enrichment, further studies are needed. These studies should provide a greater opportunity for observation throughout the facility, and the possibility to observe the orangutan in the facility before relocation and in an environment with less enrichment.

Acknowledgments and funding: Sincere thanks to Aalborg Zoological Garden for their cooperation and support (AZCF Grant 2022-3).

Author contributions: Josefine F. Larsen, Karl K. D. Andersen, Julia Cuprys, Thomas B. Fosgaard, Johanne H. Jacobsen, Dominika Krysztofiak, Silje M. Lund, Birgitte Nielsen, Maja E. B. Pedersen, Matilde J. Pedersen, Adam Trige-Esbensen and Emilie M. Walther performed the study, the analysis and wrote the manuscript. Cino Pertoldi, Trine H. Jensen and Juan O. Perea-García conceived the study and contributed to the manuscript. Cino Pertoldi conceived the statistical analysis. Aage K. O. Alstrup contributed to the analysis and manuscript.

Conflict of interest disclosure: The authors declare no conflict of interest.

Data availability: The data are not publicly available due to the preservation of privacy regarding work-related footage from the Aalborg Zoological Garden. The data presented in this study are available on request from the corresponding author.

REFERENCES

- Olsen, AM, Kristensen HG, Iversen KW, Pedersen NH, Pertoldi C, Alstrup AK, Jensen TH, Pagh S. Assessment of Abnormal Behaviour and the Effect of Enrichment on Captive Chimpanzees in Aalborg Zoo. *Genet Biodivers J.* 2020;4(2):73-91. <https://doi.org/10.46325/gabj.v4i2.99>
- Ottosen MP, Kjaer JW, Andersen M, Bach LA, Pagh S. Chimpanzees Behavioral Response to a Hift in Number of Visitors during Autumn Holiday in Aalborg Zoo. *Genet Biodivers J.* 2020;4(2):1-60. <https://doi.org/10.46325/gabj.v4i2.97>
- Mellen J, MacPhee MS. Philosophy of Environmental Enrichment: Past, Present, and Future. *Zoo Biol.* 2001;20(3):211-26. <https://doi.org/10.1002/zoo.1021>
- Puteri S, Ruppert N. Effect of Environmental Enrichment on Activities of Captive Orangutans at Taiping Zoo, Malaysia. *Malayan Nat J.* 2017;69(4):327-35.
- Spillmann B, Van Noordwijk MA, Willems E, Mitra Setia T, Wipfli U, Van Schaik CP. Validation of an Acoustic Location System to Monitor Bornean Orangutan (*Pongo pygmaeus wurmbii*) Long Calls. *Am J Primatol.* 2015;77(7):767-76. <https://doi.org/10.1002/ajp.22398>
- Russon AE. The Nature and Evolution of Intelligence in Orangutans (*Pongo pygmaeus*). *Primates.* 1998;39(4):485-503. <https://doi.org/10.1007/BF02557571>
- Russon AE, van Schaik VO, Kuncoro P, Ferisa, A, Handayani DP, van Noordwijk MA. Innovation and Intelligence in Orangutans. In: Wich AS, Atmoko SU, Setia TM, van Schaik CP, editors. *Orangutans: Geographic Variation in Behavioral Ecology and Conservation.* New York: Oxford UP; 2010. p. 279-98.
- Bucken SM, Gürtler W-D. Vergesellschaftung als Verhaltensbereicherung im Zoo - Soziale Interaktion und Raumnutzung bei Orang-Utans, Hulmans und Kurzkralotten in der Zoom Erlebniswelt Gelsenkirchen. *Zool Garten.* 2013;82(1-2):40-59. <https://doi.org/10.1016/j.zoolgart.2013.04.004>
- Delgado RA, Van Schaik CP. The Behavioral Ecology and Conservation of the Orangutan (*Pongo pygmaeus*): A Tale of two Islands. *Evol Anthropol.* 2000;9(5):201-18. [https://doi.org/10.1002/1520-6505\(2000\)9:5<201::AID-EVAN2>3.0.CO;2-Y](https://doi.org/10.1002/1520-6505(2000)9:5<201::AID-EVAN2>3.0.CO;2-Y)
- Dingemans NJ, Wolf M. Between-Individual Differences in Behavioural Plasticity within Populations: Causes and Consequences. *Anim Behav.* 2013;85(5):1031-9. <https://doi.org/10.1016/j.anbehav.2012.12.032>
- Fröhlich M, van Schaik CP, van Noordwijk MA, Knief U. Individual Variation and Plasticity in the Infant-Directed Communication of Orangutan Mothers. *Roc R Soc B: Biol Sci.* 2022;289(1975):1-10. <https://doi.org/10.1098/rspb.2022.0200>
- Dingemans NJ, Kazem AJ, Réale D, Wright J. Behavioural Reaction Norms: Animal Personality meets Individual Plasticity. *Trends Ecol Evol.* 2010;25(2):81-9. <https://doi.org/10.1016/j.tree.2009.07.013>
- Condon E, Wehnelt S. The Effect of an Enriched Environment on Behavioural and Hormonal Indicators of Welfare in Oran-utans at Chester Zoo. In: Gilbert TC, editor. *Proceedings of The Fifth Annual Symposium on Zoo Research.* UK: Federation of Zoological Gardens of Great Britain and Ireland; 2003. p. 53-8.
- Elder CM, Menzel CR. Dissociation of Cortisol and Behavioral Indicators of Stress in an Orangutan (*Pongo pygmaeus*) During a Computerized Task. *Primates.* 2001;42(4):345-57. <https://doi.org/10.1007/BF02629625>
- Amrein M, Heistermann M, Weingrill T. The Effect of Fission-Fusion Zoo Housing on Hormonal and Behavioral Indicators of Stress in Bornean Orangutans (*Pongo pygmaeus*). *Int J Primatol.* 2014;35(2):509-28. <https://doi.org/10.1007/s10764-014-9765-5>
- Claxton AM. The Potential of the Human-animal Relationship as an Environmental Enrichment for the Welfare of Zoo-housed Animals. *Appl Anim Behav Sci.* 2011;133(1-2):1-10. <https://doi.org/10.1016/j.applanim.2011.03.002>
- Finch K, Waterman JO, Cowl VB, Marshall A, Underwood L, Williams LJ, Davis N, Holmes L. Island Life: Use of Activity Budgets and Visibility to Evaluate a Multi-Species Within-Zoo Exhibit Move. *Animals.* 2022;12(16):2123. <https://doi.org/10.3390/ani12162123>
- Ross SR, Wagner KE, Schapiro SJ, Hau J, Lukas KE. Transfer and Acclimatization Effects on the Behavior of Two Species of African Great Ape (*Pan troglodytes* and *Gorilla gorilla gorilla*) Moved to a Novel and Naturalistic Zoo Environment. *Int J Primatol.* 2011;32(1):99-117. <https://doi.org/10.1007/s10764-010-9441-3>
- Pearson EL, Davis JM, Litchfield CA. A Case Study of Orangutan and Siamang Behavior Within a Mixed-Species Zoo Exhibit. *J Appl Anim Welf Sci.* 2010;13(4):330-46. <https://doi.org/10.1080/10888705.2010.507125>
- Probst C, Matschei C. Mixed-species Exhibits With Mammals in Central European Zoos. *Int Zoo News.* 2008;55(6):324-47.
- Hardie SM. Exhibiting Mixed-species Groups of Sympatric Tamarins *Saguinus* spp at Belfast Zoo. *Int Zoo Yearb.* 1997;35(1):261-6. <https://doi.org/10.1111/j.1748-1090.1997.tb01218.x>
- Birke L. Effects of Browse, Human Visitors and Noise on the Behaviour of Captive Orangutans. *Anim Welf.* 2002;11(2):189-202. <https://doi.org/10.1017/S0962728600028141>
- Hosey G. A Preliminary Model of Human-animal Relationships in the Zoo. *Appl Anim Behav Sci.* 2008;109(2-4):105-27. <https://doi.org/10.1016/j.applanim.2007.04.013>
- Schapiro SJ, Bloomsmith MA, Laule GE. Positive Reinforcement Training as a Technique to Alter Nonhuman Primate Behavior: Quantitative Assessments of Effectiveness. *J Appl Anim Welf Sci.* 2003;6(3):175-87. https://doi.org/10.1207/S15327604JAWS0603_03
- Maggioncalda AN, Weber B, Lester B, Schaefer B, Sodaro C, Cassella CM, Mallar C, Cossaboon C, Demitros C, Fogarty

- D, Schmidt D, Bredahl D, Frank E, Lyon E, Watts E, Singleton I, Porton I, Rafert JW, Franklin JA, Mellen J, Smith J, Killmar KS, Mayo LK, Cocks L, Perkins L, MacPhee M, Fernandez M, Elder M, Bond M, Bastian M, Sahw M, Czekala N, Lung N, Greenbaltt N, Boutelle S, Walker S, Husband S. Orangutan (Pongo) Care Manual [Internet]. Silver Spring; Assn Zoos Aq; 2017 [cited 2023]. 141 p. Available from: <https://ams.aza.org/iweb/upload/Orangutan%20Care%20Manual%20DRAFT-0a71e9d2.pdf>
26. Dezechache G, Bourgeois A, Bazin C, Schlenker P, Chemla E, Maille A. Orangutans' Comprehension of Zoo Keepers Communicative Signals. *Animals*. 2019;9(6):300. <https://doi.org/10.3390/ani9060300>
 27. Perea-García JO, Miani A, Alstrup AK, Malmkvist J, Pertoldi C, Jensen TH, Nielsen RK, Hansen DW, Bach LA. Orangulas: Effect of Scheduled Visual Enrichment on Behavioral and Endocrine Aspects of a Captive Orangutan (*Pongo pygmaeus*). *J Zoo Aquac Res*. 2020;8(1):67-72. <https://doi.org/10.19227/jzar.v8i1.416>
 28. Zar JH. *Biostatistical Analysis*. 5th ed. New Jersey: Pearson; 2010. 944 p.
 29. Gerstman BB. *Basic Biostatistics*. 2nd ed. Burlington: Jones & Bartlett Learning; 2014. 648 p.
 30. Hastie T, Tibshirani R, Friedman J. *The Elements of Statistical Learning: Data Mining, Inference, and Prediction*. New York: Springer; 2009. 745 p.
 31. Mery F, Burns JG. Behavioural Plasticity: An Interaction Between Evolution and Experience. *Evol Ecol*. 2009;24(3):571-83. <https://doi.org/10.1007/s10682-009-9336-y>
 32. Rampon C, Tsien JZ. Genetic Analysis of Learning Behavior-Induced Structural Plasticity. *Hippocampus*. 2000;10(5):605-9. [https://doi.org/10.1002/1098-1063\(2000\)10:5<605::AID-HIPO11>3.0.CO;2-3](https://doi.org/10.1002/1098-1063(2000)10:5<605::AID-HIPO11>3.0.CO;2-3)
 33. Chapillon P, Patin V, Roy V, Vincent A, Caston J. Effects of Pre- and Postnatal Stimulation on Developmental, Emotional, and Cognitive Aspects in Rodents: A Review. *Dev Psychobiol*. 2002;41(4):373-87. <https://doi.org/10.1002/dev.10066>
 34. Anderson JR, Ang MY, Lock LC, Weiche I. Nesting, Sleeping and Nighttime Behaviors in Wild and Captive Great Apes. *Primates*. 2019;60(4):321-32. <https://doi.org/10.1007/s10329-019-00723-2>
 35. Dunn AJ, Berridge CW. Physiological and Behavioral Responses to Corticotropin-Releasing Factor Administration: is CRF a Mediator of Anxiety or Stress Responses? *Brain Res Rev*. 1990;15(2):71-100. [https://doi.org/10.1016/0165-0173\(90\)90012-D](https://doi.org/10.1016/0165-0173(90)90012-D)
 36. Sherwen SL, Hemsworth PH. The Visitor Effect on Zoo Animals: Implications and Opportunities for Zoo Animal Welfare. *Animals*. 2019;19(6):366. <https://doi.org/10.3390/ani9060366>
 37. Dall SR, Houston AI, McNamara JM. The Behavioural Ecology of Personality: Consistent Individual Differences from an Adaptive Perspective. *Ecol Lett*. 2004;7(8):734-9. <https://doi.org/10.1111/j.1461-0248.2004.00618.x>
 38. Sih A, Bell A, Johnsen JC. Behavioral Syndromes: An Ecological and Evolutionary Overview. *Trends Ecol Evol*. 2004;19(7):372-8. <https://doi.org/10.1016/j.tree.2004.04.009>
 39. Réale D, Dingemanse NJ. Personality and Individual Social Specialisation. In: Székely T, Moore AJ, Komdeur J, editors. *Social Behaviour: Genes, Ecology and Evolution*. UK: Cambridge UP; 2010. p. 417-40.