

Does behaviour predict weight gain during adulthood in captive group-living rhesus macaques?

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ABSTRACT

Many non-human primates (NHPs) in captivity become overweight. Individual variation in adiposity may result from differences in behaviour related to energy intake, energy expenditure and dominance rank. Understanding how behaviour contributes to becoming overweight may provide opportunities to improve housing and husbandry of captive group-living NHPs. This study therefore investigated whether behaviour predicts weight gain during adulthood in captive female rhesus macaques (*Macaca mulatta*) housed in three social groups at the Biomedical Primate Research Centre in Rijswijk, the Netherlands. Relative adiposity was quantified with a species-specific weight-for-height index (WHI) during three consecutive annual health checks. Behavioural data were collected at baseline on food intake, activity budgets and dominance rank. We examined which factors were associated with WHI at baseline and whether behaviour predicted the subsequent change in WHI over time, while controlling for individual characteristics. At baseline, a high WHI was associated with low activity levels, but not related to food intake, age or dominance rank. WHI did not differ from baseline after one year but had significantly increased after the second year. This increase in WHI was independent of food intake and activity budgets, while higher-ranking females had a higher increase in WHI compared to lower-ranking monkeys. This suggests that captive NHPs with a high dominance rank are more prone to becoming overweight, whereas differences in activity budgets are merely a consequence and not a cause. Thus, dominance rank, but not behaviour, likely predicts weight gain during adulthood in captive group-living NHPs.

1. Introduction

Non-human primates (NHPs) in captivity are susceptible to becoming overweight, characterized by excessive amounts of body fat resulting from an imbalance between energy intake and expenditure (Chen et al., 2002; Kemnitz, 1984). Although overweight NHPs do not naturally occur in the wild (Altmann et al., 1993; Dittus, 2013), a considerable proportion of captive NHPs become overweight during their life (Sterck et al., 2019; West and York, 1998). The welfare of these animals may be compromised as being overweight is associated with a higher risk of several health problems, such as diabetes and cardiovascular disease (Kemnitz and Francken, 1986; Shively and Clarkson, 1988). Besides, overweight NHPs may be restricted in performing natural, species-specific behaviour due to their size and condition (Bauer

et al., 2011, 2012). The prevalence of overweight individuals in captive group-living NHPs has been reported to range between 10 % and 30 % (Crumley and Raleigh, 1995; Hamada et al., 2003; Sterck et al., 2019; Yue et al., 2017, 2016). This high prevalence in captivity may be caused by differences in energy intake and/or energy expenditure compared to the wild, since captive housing conditions differ from wild conditions in the type and availability of food and the amount of space.

Energy intake and expenditure of wild primates depend on the distribution, seasonality and abundance of food, as well as habitat quality (Dasilva, 1992; Murray et al., 2006; van Schaik, 1986). In the wild, food availability is seasonally variable and food is typically widespread, while in captivity high-quality and nutritionally balanced diets are easily accessible and often provided ad libitum all year round (Bauer et al., 2010). As a result, food may be more abundant and easier to

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obtain for captive than wild NHPs. In addition, activity budgets generally differ between wild and captive NHPs, with more resting and less foraging and moving in captivity (Melfi and Feistner, 2002). Wild NHPs spend up to 60 % of their waking hours foraging and feeding and 10–30 % resting (Altmann and Muruthi, 1988; Kurup and Kumar, 1993). In contrast, captive NHPs generally spend less than 20 % of their waking hours foraging and feeding and may spend up to 50 % resting (Beisner and Isbell, 2008; Jaman and Huffman, 2008). Captive enclosures are also restricted in space, which may further reduce activity. Thus, captive NHPs are likely more at risk for becoming overweight due to limited motivation for physical activity associated with foraging in an environment where food is abundant (Bauer et al., 2011).

Captive NHPs living in the same group experience the same housing conditions, yet not every individual in a group becomes overweight (Sterck et al., 2019). Some group members become relatively heavy, while others stay lean. Middle-aged NHPs are most likely to be overweight (Ramsey et al., 2000; Schwartz and Kemnitz, 1992). Variation in relative adiposity is likely related to individual differences in energy intake and expenditure. In squirrel monkeys (*Saimiri sciureus*) housed under similar conditions, overweight individuals had significantly higher caloric intake compared to normal weight individuals (Ausman et al., 1981). Furthermore, overweight individuals were more likely to be inactive in group-housed long-tailed (*Macaca fascicularis*) and rhesus macaques (*Macaca mulatta*) (Bauer et al., 2012; Wolden-Hanson et al., 1993). Behaviour related to energy intake and expenditure may potentially play an important role in captive NHPs becoming overweight.

In addition, dominance rank may be related to relative adiposity in captive group-living NHPs. Dominant individuals typically have priority of access and can monopolize preferred resources such as food (Barton, 1993; Boccia et al., 1988; Overduin-de Vries et al., 2020; Whitten, 1983). High-ranking individuals generally have greater access to food and are interrupted less during feeding (Altmann and Alberts, 2005; Deutsch and Lee, 1991; Smuts and Nicolson, 1989). Dominant individuals were also more likely to be engaged in eating behaviour in group-housed long-tailed macaques (Bauer et al., 2012). In contrast, low-ranking individuals cannot monopolize food. As a result, high-ranking individuals may have a higher body weight and body fat levels compared to low-ranking monkeys (Michopoulos and Wilson, 2011; Schwartz et al., 1993; Small, 1981).

Identifying risk factors for becoming overweight in captive group-living NHPs may yield opportunities to improve animal husbandry and reduce weight gain during adulthood, thereby increasing animal welfare. This study therefore investigates whether behaviour related to energy intake and expenditure predicts weight gain during adulthood in captive group-living rhesus macaques. Relative adiposity was quantified with a species-specific weight-for-height index (WHI) during three consecutive annual health checks (2015–2017), while behavioural data on food intake, activity budgets and dominance rank were collected at baseline (i.e. 2015). Our study encompasses a two-year period during adulthood, which is a relatively short period in relation to the average lifespan for captive rhesus macaques of approximately 25 years (Chiou et al., 2020). Linear mixed models were used to determine which factors were associated with relative adiposity at baseline, and whether behaviour predicted the change in WHI after one and two years, while controlling for individual characteristics.

2. Material and methods

2.1. Animals and housing

Subjects of this study were 31 sexually mature (i.e. 3 years and older) non-pregnant female rhesus macaques of Indian origin housed in three social groups at the Biomedical Primate Research Centre (BPRC) in Rijswijk, the Netherlands. The animals were on average 8.0 ± 0.8 (range: 3.5 – 18.8) years old and weighed 8.2 ± 0.4 (range: 4.8 – 12.5) kg at the start of the study. The groups contained 20–40 individuals per

group that were managed by adhering to natural group dynamics. The groups consisted of several multigenerational matrilineal, encompassing adult females with their offspring, and one group contained an adult breeding male temporarily. We refer to the three groups by using the names of the dominant females: Macaroni, Avocado and Calimero. The number of subjects per group was 12 (Macaroni), 12 (Avocado) and 7 (Calimero). These groups were selected for this study as they contained both normal- and overweight individuals. The groups also contained two elderly females (> 25 years old), but these females were not included in the study as aging likely affected their behaviour, physiology and body measures (Ramsey et al., 2000; Veenema et al., 1997).

Each social group had access to an enriched indoor ($\pm 72 \text{ m}^2$ and 2.85 m high) and outdoor ($\pm 250 \text{ m}^2$ and 3.1 m high) enclosure. The indoor enclosure contained sawdust bedding, while the outdoor enclosure had a sand bedding with natural plant growth. The enclosures were divided into several compartments and contained several climbing structures, fire hoses, beams, sitting platforms and an outside swimming pool (Vernes and Louwerse, 2010). In the morning, the macaques were provided with monkey chow (Ssniff, Soest, Germany). The amount of monkey chow fed to each group consisted of the sum of all individual's energetic requirements, which was based on their basal metabolic rate and depended on their age, sex and body weight (National Research Council, 2003). Rhesus macaques can store food in their cheek pouches and retrieve this at a later moment. Monkey chow was provided in several (i.e. four to seven) feeding trays to prevent monopolization. In addition, fresh fruit, vegetables, bread or a grain mixture were presented in the afternoon. Fruit and vegetables included apple, banana, bell pepper, cabbage, cauliflower, chicory, cucumber, endive, leek, lettuce, maize, orange, pear, sweet potato and tomato. Most of these items were handed to the animals by a caretaker. Water was available ad libitum.

2.2. Measuring relative adiposity

Relative adiposity was measured using a species-specific weight-for-height index (WHI), which was calculated as body weight (kg) divided by the third power of height (m) (Sterck et al., 2019). WHI is independent of height and highly correlated with other relative adiposity measures, e.g. abdominal circumference and skinfold thicknesses (Sterck et al., 2019). Body weight and height were measured following a standard procedure during three consecutive annual health checks (2015–2017).

Although measured by different people, height of skeletally matured females (i.e. females ≥ 6 years old; (Schwartz and Kemnitz, 1992) was highly correlated between the three health checks ($r_p > 0.856$, $p < 0.0005$), indicating high inter-observer reliability. Baseline WHI was measured in 2015, while the WHI measured in 2016 and 2017 was used to determine the change in relative adiposity after one and two years. The change in relative adiposity was calculated by subtracting the WHIs in 2016 and 2017 from the baseline WHI in 2015. WHI ideally ranges between 42 and 67 kg/m^3 , so individuals with a WHI exceeding the upper boundary were considered to be overweight (Sterck et al., 2019).

2.3. Behavioural observations

All behavioural observations were performed at baseline in 2015. Food intake was observed using video recordings. First, behaviour around the feeding trays with monkey chow was recorded between 8.30 h and 16.00 h with two video cameras (JVC Everio GZ-R15BE, JVC, Yokohama, Japan) for two days per group with roughly one month between the two recordings. At the end of each recording, the monkeys had consumed all the food in the feeding trays, and leftover monkey chow pieces on the ground outside of the enclosure were counted. The number of monkey chow pieces consumed per individual was counted from the videos. A piece was considered eaten when an individual put this into its mouth or when an individual disappeared out of view with the piece(s) in hand. A hand full counted as four pieces. The error factor

on total monkey chow intake, i.e. relative difference between the observed and expected total number of monkey chow pieces, was on average 10 % (range: 0 – 27 %). The expected number of monkey chow pieces was calculated by dividing the total weight of the chow provided to the group by the average weight of one chow piece. Second, the afternoon feeding of apples and bread, handed to the animals by a caretaker, was observed by video recordings. These items were chosen, because bread was fed three times a week and apples were the most commonly fed type of fruit during the study period. Apple and bread feedings were both filmed five times per group and always in the presence of the same caretaker. Apple and bread feedings were performed opportunistically whenever apples or bread were fed, and the principal caretaker of the building was present to perform the feeding.

Food intake of individual monkeys is generally consistent over time (Sullivan et al., 2006). However, monkey chow intake per individual did not correlate between the two days in the groups (Macaroni group: $r_p = 0.231$, $n = 12$, $p = 0.469$; Avocado group: $r_p = 0.121$, $n = 12$, $p = 0.707$; Calimero group $r_p = 0.593$, $n = 7$, $p = 0.161$). In contrast, both individual apple and bread intake correlated well between the five sessions of each item in all three groups, so intake of these food items was consistent over time (Appendix A). The average monkey chow intake of the two days and the average apple and bread intake of the five sessions per individual were used in further analyses. The average amount of monkey chow, apples and bread per individual was converted into a measure of energy intake in kcal/day using the average weight per piece and information regarding the energy content of each food item (i.e. 3.28 kcal/gram monkey chow, 0.61 kcal/gram apple and 1.98 kcal/gram bread). Total daily food intake per individual was calculated by proportionally adding mean apple (4times/7days) and bread (3times/7days) intake per day to the mean monkey chow intake per day. Total food intake relative to body weight per individual was calculated as the total food intake divided by body weight.

Activity budgets were observed by focal animal sampling during 15-minute periods for a total of three hours per animal (Altmann, 1974). Data were collected by DGMZ using The Observer XT version 11 (Noldus Information Technology, Wageningen, the Netherlands) according to a predetermined balanced randomized observation schedule. Animals had free access to both indoor and outdoor enclosures during the observations, which took place between 9.00 h and 16.00 h. Focal animals were scored continuously for the duration of activity-related behaviour (see ethogram: Appendix B). Behavioural data were categorized in resting, moving, foraging, grooming and other behaviour. Each category was expressed as a percentage of time from the total observation time per individual. Moving combined all behaviour in which the body was not stationary, i.e. walking, running, climbing, aggressive behaviour and playing, while resting consisted of lying, sitting and standing. Foraging is defined as “searching for and investigating (potential) food items such as sifting through bedding”, which is considered a searching activity and not related to food intake.

Finally, all occurrence sampling was used to score submissive behaviour during the live observations and video analyses (Altmann, 1974). Submissive behaviour concerned bared teeth, give ground and make room (Appendix B). These behaviours were used to construct a dominance hierarchy for each group using MatMan (Netto et al., 1993). All three dominance hierarchies were significantly linear and highly consistent (Macaroni: $h' = 0.88$, $DCI = 0.99$, $p < 0.0005$; Avocado: $h' = 0.95$, $DCI = 0.99$, $p < 0.0005$, Calimero: $h' = 0.79$, $DCI = 0.99$, $p < 0.0005$). For the data analyses, absolute dominance rank was rescaled to a relative measure (ranging from zero to one) to correct for the different number of subjects per group. The higher the dominance rank, the closer the score is to zero. Dominance rank of all three groups remained stable over the study period (2015–2017).

2.4. Data analyses

Behaviour related to energy intake and expenditure, i.e. food intake

and activity budgets, at baseline were analyzed first. Spearman correlations were used to determine whether the intake of different food items (i.e. monkey chow, apples and bread) and the percentage of time spent on several behavioural categories (i.e. moving, resting, foraging and grooming) were correlated. Linear mixed models were used to test whether age (in years) and dominance rank were related to the variation in food intake and activity-related behaviour. The parametric paired samples t-test was used to compare WHI at baseline with WHI after one year, because both were normally distributed. The non-parametric Wilcoxon signed ranks test was used to compare baseline WHI with WHI after two years, as WHI after two years was not normally distributed. The Shapiro-Wilk test was used to test normal distribution.

Linear mixed models were used to check whether behaviour and individual characteristics were related to baseline WHI. The behavioural categories, age and dominance rank were included in the models as covariates, while the social group in which the individual was housed was included as a random factor. Two separate models were run, as there was high collinearity between resting and the other behavioural categories, i.e. moving, foraging and grooming. In the results section, we report the outcomes for the models including moving, foraging and grooming. The models with only resting provided similar outcomes (Appendix C). Finally, we examined which variables were predictive of the change in WHI after one and two years. The behavioural categories, age, dominance rank and baseline WHI were included as covariates, while social group was included as a random factor. Three individuals were omitted from this final analysis as one individual developed chronic diarrhea and two animals passed away during the two-year study period. The models were visually checked for normal distribution and homoscedasticity of the residuals and the variance inflation factor did not exceed 3.62. Descriptive statistics in the results are reported as mean \pm SE.

Statistical analyses and figure editing were performed in SPSS Statistics version 28 and R studio version 1.2.5 using the packages *car*, *lmerTest*, *jtools* and *ggplot2*. All tests were two-tailed and the level of significance was set at $\alpha = 0.05$, but trends ($0.05 < p < 0.10$) are reported as well.

2.5. Ethical statement

BPRC is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AAALAC International). Ethical review and approval for this study were waived as the annual health checks are a routine veterinary procedure related to the regular health management of the colony (cf. Balansard et al., 2019). This study performed no experimental procedures that would require ethical approval according to the European Directive 2010/63 or the Dutch law. All applicable international, national, and institutional guidelines and laws for the care and ethical use of animals were followed.

3. Results

3.1. Energy intake

Total food intake was derived from an individual's daily consumption of monkey chow, apples and bread. Monkey chow intake was not correlated with apple ($r_s = -0.016$, $n = 31$, $p = 0.933$) or bread intake ($r_s = -0.030$, $n = 31$, $p = 0.871$). In contrast, there was a highly significant positive correlation between apple and bread intake ($r_s = 0.893$, $n = 31$, $p < 0.0005$). Monkey chow intake was independent of age ($F(1,26) = 1.796$, $p = 0.192$) and dominance rank ($F(1,26) = 0.899$, $p = 0.352$). Apple intake was independent of dominance rank ($F(1,26) = 0.877$, $p = 0.358$), while older individuals tended to have a higher apple intake than younger monkeys ($F(1,26) = 3.378$, $p = 0.078$). Bread intake was not related to age ($F(1,26) = 2.505$, $p = 0.126$) or dominance rank ($F(1,26) = 0.076$, $p = 0.785$).

Total food intake, combining the three measured food items, was on

average 679 ± 31 kcal/day. There was a 2.6-fold difference in the number of calories consumed between individuals with the highest and lowest total food intake (range: 394 – 1028 kcal/day). Total food intake was independent of dominance rank ($F(1,26) = 0.530$, $p = 0.473$), while older individuals had higher total food intake compared to younger individuals ($F(1,26) = 4.310$, $p = 0.048$). Total food intake relative to body weight was on average 87 ± 4 kcal/kg. There was also considerable variation in food intake per kilogram body weight between monkeys (range: 44 – 146 kcal/kg). Total food intake relative to body weight was higher in younger individuals compared to older monkeys ($F(1,26) = 5.411$, $p = 0.028$), while dominance rank ($F(1,26) = 0.413$, $p = 0.526$) had no significant influence.

3.2. Energy expenditure

Energy expenditure was estimated using activity budgets. Females spent on average 9.3 ± 0.9 % of the time moving, 54.6 ± 2.1 % resting, 11.5 ± 1.2 % foraging, 21.6 ± 1.5 % grooming and 3.0 ± 0.4 % on other behaviour. The most and least active monkeys differed more than tenfold in their percentage of time spent moving (range: 1.8 – 19.2 %), while resting differed only 2.1-fold (range: 39.3 – 82.2 %). Time spent resting was negatively correlated with time spent moving ($r_s = -0.776$, $n = 31$, $p < 0.0005$) and foraging ($r_s = -0.642$, $n = 31$, $p < 0.0005$), but not related to grooming ($r_s = -0.154$, $n = 31$, $p = 0.407$). Moving and foraging were positively correlated ($r_s = 0.736$, $n = 31$, $p < 0.0005$), while moving was not related to grooming ($r_s = -0.269$, $n = 31$, $p = 0.144$). There was a significant negative association between foraging and grooming ($r_s = -0.427$, $n = 31$, $p = 0.016$).

Time spent moving and foraging were independent of dominance rank ($F(1,26) = 1.748$, $p = 0.198$; $F(1,26) = 2.659$, $p = 0.115$), while younger individuals moved and foraged more than older monkeys ($F(1,26) = 16.013$, $p < 0.0005$; $F(1,26) = 8.678$, $p = 0.007$). Similarly, resting was not related to dominance rank ($F(1,27) = 0.778$, $p = 0.386$), but older animals spent more time resting compared to younger individuals ($F(1,26) = 15.152$, $p < 0.0005$). Time spent grooming was independent of age ($F(1,26) = 0.106$, $p = 0.924$) and dominance rank ($F(1,26) = 0.395$, $p = 0.535$).

3.3. Baseline and change in relative adiposity

At baseline, mean WHI was 61.1 ± 1.4 kg/m³ and 9 of 31 individuals (29 %) exceeded the upper boundary for a healthy relative adiposity and were considered to be overweight. Baseline WHI was independent of age ($F(1,24) = 0.144$, $p = 0.708$), dominance rank ($F(1,24) = 0.124$, $p = 0.728$), total food intake ($F(1,24) = 0.004$, $p = 0.953$) and grooming ($F(1,24) = 0.029$, $p = 0.866$). Baseline WHI was negatively correlated with the time spent moving ($F(1,24) = 6.415$, $p = 0.018$) and tended to be

negatively correlated with time spent foraging ($F(1,24) = 3.557$, $p = 0.071$), meaning individuals with low activity levels had a higher relative adiposity (Fig. 1ab). Similarly, resting was significantly related to baseline WHI with more resting in relatively heavy individuals (Appendix C; Fig. 1c).

The baseline data were employed to determine whether behaviour, age or dominance rank affected the change in WHI after one and two years. One year after the baseline period, mean WHI was 62.4 ± 1.7 kg/m³, which is roughly comparable to the baseline WHI ($t = -1.673$, $n = 31$, $p = 0.105$), and 10 out of 31 individuals (32 %) were overweight (Fig. 2a). Change in WHI after one year was independent of age ($F(1,23) = 0.057$, $p = 0.814$), dominance rank ($F(1,23) = 1.019$, $p = 0.324$), baseline WHI ($F(1,23) = 0.260$, $p = 0.616$), food intake ($F(1,23) < 0.0005$, $p = 0.989$), moving ($F(1,23) = 0.229$, $p = 0.637$), foraging ($F(1,23) = 0.054$, $p = 0.819$) and grooming ($F(1,23) = 1.314$, $p = 0.265$). When only resting was used in the model instead of moving, foraging and grooming, this resulted in similar non-significant outcomes (Appendix C).

Two years after the baseline period, mean WHI was 70.4 ± 1.7 kg/m³, which is significantly higher compared to the baseline WHI ($Z = -4.463$, $n = 28$, $p < 0.0005$; Fig. 2b). WHI increased in 86 % of the animals and more than two-third (20 of 28 individuals, 71 %) of the individuals was overweight in 2017. Change in WHI after two years was independent of age ($F(1,20) = 2.869$, $p = 0.107$), baseline WHI ($F(1,20) = 0.936$, $p = 0.346$), food intake ($F(1,20) = 1.356$, $p = 0.258$), moving ($F(1,20) = 0.557$, $p = 0.465$), foraging ($F(1,20) = 0.479$, $p = 0.497$) and grooming ($F(1,20) = 0.017$, $p = 0.897$). However, change in WHI was significantly related to dominance rank, as high-ranking individuals had a higher increase in WHI compared to low-ranking monkeys ($F(1,20) = 11.481$, $p = 0.003$; Fig. 3). A similar result was obtained when only resting was used instead of moving, foraging and grooming (Appendix C).

4. Discussion

This study aimed to identify risk factors for becoming overweight in captive group-living NHPs. First, we checked whether behaviour related to energy intake and expenditure was associated with relative adiposity, measured using a weight-for-height index (WHI), at baseline. Second, we determined whether behaviour at baseline predicted the subsequent change in relative adiposity, while controlling for individual characteristics. A high WHI was associated with low activity levels at baseline, but was not related to food intake, age or dominance rank. WHI did not differ from baseline after one year but had significantly increased after the second year. This increase in WHI was independent of food intake and activity budgets, while higher-ranking females had a higher increase in WHI compared to lower-ranking monkeys.

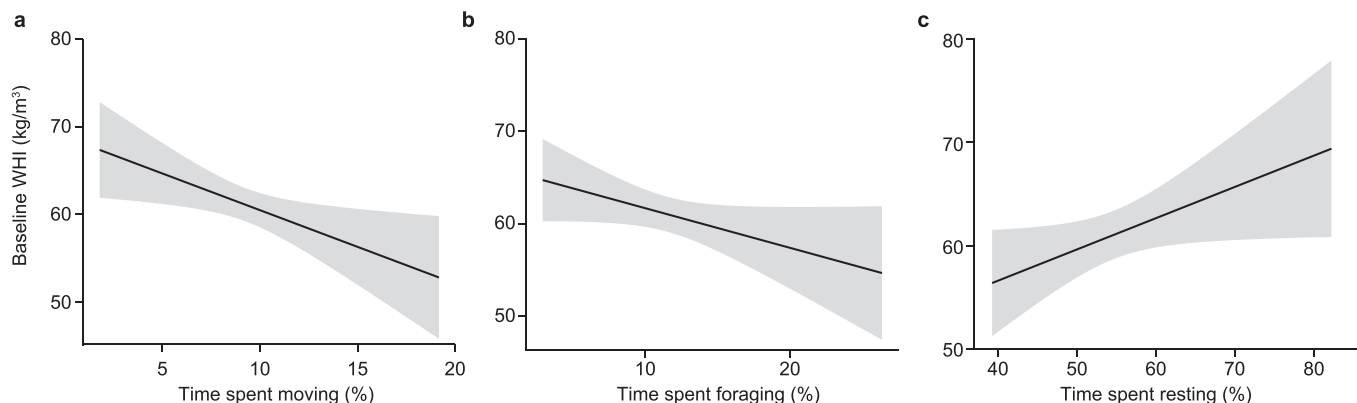


Fig. 1. Females that spent less time moving (a), less time foraging (b) and more time resting (c) had a higher baseline weight-for-height index (baseline WHI; mean + 95 % confidence interval).

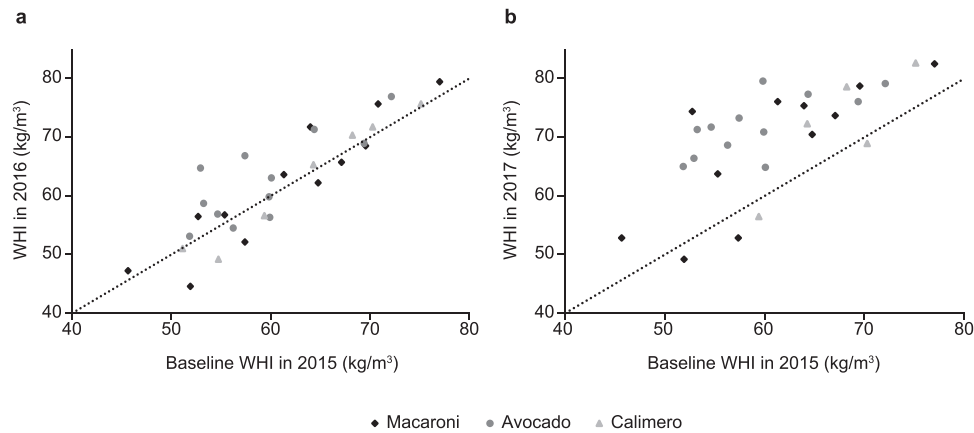


Fig. 2. Baseline WHI in 2015 plotted against WHI in 2016 (a) and 2017 (b) per group. The black dotted line separates the individuals that increased (top-left) or decreased (bottom-right) their relative adiposity compared to baseline.

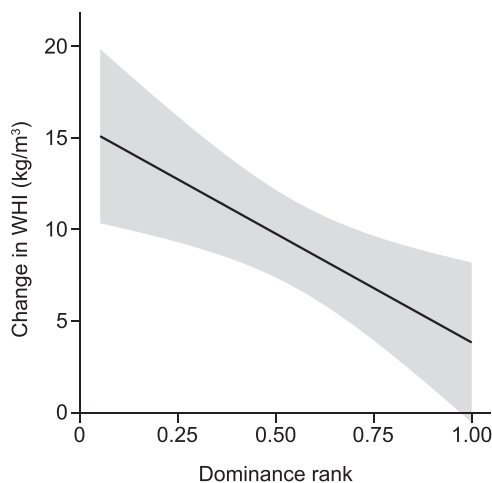


Fig. 3. Dominance rank plotted against the change in weight-for-height index after the second year (change in WHI; mean + 95 % confidence interval). A higher dominance rank is indicated by a score closer to zero.

4.1. Energy intake

This study used behavioural observations to quantify energy intake, yet accurate measurements of food intake are notoriously difficult to obtain in a group setting (Chivers, 1998; Wilson et al., 2008). Observations have previously been used to quantify food intake in individually housed NHPs (e.g. Hannah and Hansen, 1990; Hansen et al., 1995; Wolden-Hanson et al., 1993). In these studies, the error factor is usually less than 5 % (Hansen et al., 1995). Our average error factor on the monkey chow pellets was 10 % (range 0 – 27 %) and the observed number of pellets was always lower than the expected number of pellets, which likely resulted in an underestimation of the actual food intake. Similarly, human observers underestimate food intake compared to an automated feeding system by 12.9 % (Wilson et al., 2008). These automated feeders release one pellet upon activation by a microchip in the wrist, which is then recorded by a computer (Wilson et al., 2008). Besides, individuals could take a piece of food, put it in their cheek pouches and disappear out of view from the camera. So, whether they actually ate the food could not be observed. More accurate ways to quantify energy intake of group-housed NHPs are needed.

Furthermore, apple and bread intake may have been influenced by the feeding and scoring method. Apples and bread were handed to the animals by a caretaker, and were thus monopolizable, while monkey chow was distributed over multiple feeding trays. Apple and bread

intake were highly correlated, while intake of monkey chow was not correlated with the intake of apples or bread. Apple and bread intake were independent of dominance rank though. The intake of these food items is likely more related to personality and the quality of the animal-keeper relationship. In stump-tailed macaques (*Macaca arctoides*), individuals with a “friendly” personality are more likely to approach and accept food offered by caretakers (Waitt et al., 2002). In our study, the intake of apples and bread was unequally distributed, with some individuals receiving several pieces while others received none. However, individuals that did not accept food from the caretaker still managed to obtain some food as they scavenged the ground for leftovers or stole pieces from other animals (personal observation). As a result, our method likely overestimated apple and bread intake for some individuals, while underestimating it for others. Thus, also this estimate of food intake may be less accurate than the observations suggest.

Although the estimated energy intake based on monkey chow, apples and bread should be interpreted with caution, some interesting results were found. Total food intake was highly variable between individuals, ranging between 394 and 1028 kcal/day. Such individual differences may be due to different energetic requirements based on individual characteristics, such as age. For example, young animals generally require more energy to enable growth (Draper, 1966). Indeed, in our study, food intake relative to body weight was higher in younger individuals compared to older monkeys. Thus, the relatively high energetic demands of younger individuals were reflected in their food intake.

Dominance rank is a second possible factor to affect food intake as dominant individuals typically have priority of access to food (Barton, 1993; Boccia et al., 1988; Whitten, 1983). However, none of the food intake measures were related to dominance rank, implying that low-ranking individuals were able to somehow compensate for this. In the wild, low-ranking individuals travel more to find food, forage away from the main group or compensate by switching to other, lower-quality food items (Saito, 1996; Soumah and Yokota, 1991; Tsuji and Takatsuki, 2012; van Schaik and van Noordwijk, 1988). In captivity, low-ranking females store food in their cheek pouches and then move away from the group to eat it (Brennan and Anderson, 1988; Deutsch and Lee, 1991). NHPs thus adjust their foraging and eating behaviour according to their dominance rank (Bauer et al., 2012; Soumah and Yokota, 1991). As a result, food intake probably does not differ systematically between high- and low-ranking individuals (cf. Michopoulos et al., 2012; van Noordwijk and van Schaik, 1987).

All in all, some measures of food intake were related to age, but food intake was independent of dominance rank. The method of feeding and observations may have affected the accuracy of our food intake measures and more accurate ways to measure energy intake in group-housed NHPs are needed to verify our results.

4.2. Energy expenditure

Similar to energy intake, energy expenditure may vary depending on individual characteristics. There was a tenfold difference in time spent moving between the most and least active monkeys, whereas this difference is eightfold in individually housed female rhesus macaques (Sullivan et al., 2006). Younger animals spent more time moving and foraging and less time resting compared to older monkeys, which complies with previous studies (Jaman and Huffman, 2008; Melfi and Feistner, 2002; Ramsey et al., 2000; Veenema et al., 1997). Furthermore, dominance rank had no effect on the time spent moving, foraging, grooming or resting. Similarly, in group-housed long-tailed macaques dominance rank has no effect on the level of moving or resting (Bauer et al., 2012). Activity budgets of captive group-housed female rhesus macaques thus vary depending on age, but not dominance rank.

The enclosure environment plays an important role in shaping activity budgets. In captive Sulawesi crested macaques (*Macaca nigra*), resting increases and moving and feeding behaviour decrease with smaller enclosure sizes (Melfi and Feistner, 2002). Larger enclosures with natural substrate and vegetation increase foraging behaviour and lead to activity budgets that are more similar to activity budgets of wild NHPs (Beisner and Isbell, 2008; Jaman and Huffman, 2008). In our study, the macaques had 24 h access to relatively spacious indoor and outdoor enclosures with environmental enrichment. However, space and foraging opportunities were still restricted, which likely affected their activity budgets. Animals spent on average 9.3 % of the time moving, 54.6 % resting, 11.5 % foraging and 21.6 % grooming. Captive group-living Japanese (*Macaca fuscata*) and rhesus macaques on a similar diet, but with larger outside enclosures (500–6400 m²), also spend more time resting compared to other activities (Beisner and Isbell, 2008; Jaman and Huffman, 2008). However, their activity budgets are comprised of 10–15 % moving, 35–50 % resting, 15–30 % foraging and feeding and 10–15 % grooming (Beisner and Isbell, 2008; Jaman and Huffman, 2008). In our study, resting and grooming were thus higher, while moving and foraging were lower. Differences in housing conditions likely explain why activity budgets differ between captive studies.

4.3. Baseline and change in relative adiposity

This study aimed to identify risk factors for becoming overweight in captive group-living NHPs by testing whether behaviour was related to the baseline adiposity and to change in relative adiposity, while controlling for individual characteristics. Baseline WHI was independent of food intake, age and dominance rank, while a higher baseline WHI was associated with less moving, less foraging and more resting. Less active monkeys were thus more likely to be overweight, which complies with previous studies (Bauer et al., 2012; Wolden-Hanson et al., 1993). Similar to our findings, food intake was not related to body weight in individually housed rhesus macaques (Hannah and Hansen, 1990; Wolden-Hanson et al., 1993). In contrast, high-ranking female NHPs generally have higher body fat levels compared to low-ranking females (Schwartz et al., 1993; Small, 1981). Altogether, our results largely replicate previous findings from cross-sectional studies, but our aim was to identify risk factors instead of studying associations.

We therefore determined whether age, dominance rank, WHI and behaviour at baseline predicted the change in WHI. WHI did not differ from baseline after one year, but significantly increased after the second year. This increase in WHI was independent of behaviour related to energy intake and expenditure, i.e. food intake and activity budgets, at baseline. Food intake neither correlates with weight gain in individually housed female rhesus macaques (Sullivan et al., 2006). In contrast, total caloric intake is significantly correlated with weight gain when feeding high-fat diets in group-housed female rhesus macaques (Wilson et al., 2008). When monkeys are maintained on a standard laboratory (low-fat) diet, body weight does not change (Wilson et al., 2008). Even though food intake was not predictive of change in WHI and commercial

monkey chow was provided to the monkeys in our study, relative adiposity increased during the study period in the majority (86 %) of individuals. This indicates that the animals consumed more energy than required. The standard feeding routine at BPRC, i.e. providing 100 % of the required energy in monkey chow and providing other food items in addition, may have led to a higher prevalence of overweight individuals and this should therefore be critically evaluated.

The time spent moving, foraging and resting were significantly correlated with baseline WHI, but it did not predict the change in WHI. This suggests that the time spent on these activities is merely a consequence and not a cause of captive NHPs being overweight. Yet, activity is a risk factor of weight gain in individually housed female rhesus macaques maintained on a high-fat diet: more active individuals gain less body weight compared to less active monkeys (Sullivan et al., 2006). These contradicting findings may result from differences in housing and diet and call for more studies on risk factors of weight gain in captive group-living NHPs. Nevertheless, dominance rank was a significant predictor of change in WHI: higher-ranking individuals had a higher increase in WHI than lower-ranking monkeys. Similarly, juvenile rhesus macaques with a high dominance rank gain more body weight between one and three years of age compared to low-ranking juveniles (Bastian et al., 2003). Thus, dominance rank likely predicts weight gain during adulthood in captive group-living NHPs.

A potential mechanism behind this relationship between dominance rank and weight gain may lie in the role of physiology and circulating hormones in the deposition of fat tissue. Glucocorticoids, such as cortisol, are produced by the hypothalamic-pituitary-adrenal axis during stress and have been linked to alterations in fat deposition (Shively et al., 2009). Several studies found that dominance rank was related to cortisol levels with low-ranking female NHPs generally having higher levels compared to high-ranking females (Cavigelli and Caruso, 2015). These findings indicate a possible relationship between dominance rank of an individual and glucocorticoid-mediated accumulation of adipose tissue. Contrasting with this proposal, hair cortisol concentrations did not differ between high- and low-ranking female rhesus macaques from the BPRC colony, suggesting that cortisol levels did not play a role in the weight gain during our study (Zijlmans et al., 2021). However, further studies are needed to assess the role of hormones in weight gain in group-housed NHPs.

5. Conclusion

This study aimed to identify risk factors for becoming overweight in captive group-living rhesus macaques. Although it seems plausible that the provisioning of food and housing conditions in captivity both contribute to the problem (Bauer et al., 2012), this study found no evidence for a link between behaviour related to energy intake and expenditure and weight gain. More accurate ways to measure energy intake in group-housed NHPs are needed to verify this. Thus, not individual differences in behaviour, but dominance rank seems to predict weight gain during adulthood in captive group-living NHPs.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.applanim.2022.105748](https://doi.org/10.1016/j.applanim.2022.105748).

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