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1 Environmental influences on sleep behavior in captive male chimpanzees (*Pan*
2 *troglydtes*)
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8 Running head: Sleep in captive male chimpanzees
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19 Abstract

20 Little is known as to the influence of captivity and stressful events on sleep patterns
21 in primates. We investigated the sleep patterns of 19 male chimpanzees living under
22 similar conditions at the Chimpanzee Sanctuary Uto (CSU) in Kumamoto, Japan, using a
23 behavioral sleep index. We conducted nighttime observations of all subjects during a
24 stable period and then observed three subjects after relocation to an unfamiliar facility at
25 CSU. We estimated length of sleep and non-sleep periods over 13-hr video recordings
26 using instantaneous sampling at 1-min intervals to record sleep, which we defined
27 operationally as an inactive posture with the body lying down with the head on the floor
28 or on nesting materials. The 19 subjects slept for a mean \pm SEM of 11.3 ± 0.26 hr during
29 the stable period, and sleep patterns varied significantly among the subjects. The three
30 relocated subjects all showed temporarily decreased sleep duration in the post-move
31 period but subsequently recovered to the levels observed during the stable period when
32 habituated to the new living quarters. These results suggest that a stressful event may
33 induce temporary sleep shortage lasting for over a week in captive chimpanzees. Sleep
34 patterns may serve as a useful behavioral index of the stress response, as it is less
35 confounded by other behaviors and the actions of human caretakers than other indices.

36 Keywords: sleep, environmental change, stress, chimpanzee, welfare

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38

39 INTRODUCTION

40 Sleep quality, measured in humans (*Homo sapiens*) as the duration and pattern of
41 sleep, has significant effects on physical health and psychological well-being (Anch et al.
42 1988), but no studies have addressed such effects in non-human primates. However, some
43 studies have investigated intrinsic and extrinsic factors influencing sleep patterns in
44 non-human primates, such as abiotic environmental conditions, social status, and rearing
45 history (Campbell and Tobler 1984). For instance, total sleep time decreases in captive
46 chimpanzees (*Pan troglodytes*) as maximum relative humidity increases (Videan 2006);
47 the amount of “relaxed” sleep, defined as sleep where the head is held on the chest, is
48 lower in dominant male and female geladas (*Theropithecus gelada*) compared with
49 lower-ranking group members (Noser et al. 2003), and nursery-reared rhesus macaques
50 (*Macaca mulatta*) have shorter nocturnal sleep durations than mother-reared monkeys
51 (Barrett et al. 2009). Moreover, total sleep duration correlates negatively with age in
52 geladas (Noser et al. 2003) and humans (Carskadon and Dement 2000), but is positively
53 related to age in owl monkeys (*Aotus azarae*) (Suzuki and Sri Kantha 2006) and
54 chimpanzees (Videan 2006). Thus, the length of sleep (Carskadon and Dement 2000)
55 could be useful to evaluate the sleep characteristics of primates.

56 Chimpanzees are a popular primate species for the study of sleep and sleep-related
57 behavior (Anderson 2000). Early studies using both EEG techniques (Adey et al. 1963;
58 McNew et al. 1971) and behavioral observations (Anderson 2000; Riss and Goodall
59 1976) suggested that lying down in a supine position is a common sleep posture in this

60 species. Thus, this posture can serve as a simple behavioral index for sleep. Three EEG
61 studies revealed that unrestrained immature chimpanzees slept for 9.7–11.8 hr
62 nocturnally (Bert et al. 1970; Freemon et al. 1971; McNew et al. 1971). In an
63 observational study that defined an awake state as sitting up and engaging in activities
64 such as defecation, urination, or moving about, six captive chimpanzees retired at around
65 7:05–7:20 p.m. and awoke at around 6:40 a.m. (i.e., 11.2–11.4 hr of nocturnal sleep) (Riss
66 and Goodall 1976). Another study showed that 20 adult captive chimpanzees retired for
67 an average of 10.3 hr and slept for 8.8 hr, based on subjects being reclined and remaining
68 immobile for a minimum of 5 min (Videan 2006). Cross-sectional comparison revealed
69 that age and humidity influence the sleep duration of captive chimpanzees (Videan 2006).
70 Moreover, an observational study reported that the death of a group member also affected
71 the sleep characteristics of group-living captive chimpanzees (Anderson et al. 2010).
72 When one female of the group died, the remaining individuals delayed nesting and
73 changed posture more frequently during the night.

74 We examined the influence of individual identity, age, and a move to unfamiliar
75 housing (a stressful event) on sleep patterns in captive chimpanzees. First, we
76 investigated 19 captive male chimpanzees to compare individual sleep patterns and
77 investigate the effect of age. Second, we observed the sleep behavior of 3 chimpanzees
78 after they were moved to an unfamiliar facility at CSU to elucidate whether this
79 presumably stressful event affected behavioral sleep patterns.

80

81 METHODS

82 Study Subjects and Sites

83 We studied chimpanzees housed at the Chimpanzee Sanctuary Uto (CSU; a former
84 laboratory facility) in Kumamoto, Japan (Morimura et al. 2010). All subjects (N=19)
85 were males aged 12–37 years at the beginning of the study. We studied all 19
86 chimpanzees during a stable period (October 2007–April 2008) when all individuals lived
87 in three independent, all-male groups. The outdoor compounds of these three groups were
88 128 m² (W: D: H = 10.0: 12.8: 3.8 m, one group) or 117 m² (W: D: H = 8.5: 12.8: 3.8 m,
89 the other two groups) in area. The compounds were surrounded by iron mesh fences and
90 contained vegetation, climbing structures made of logs, fire hoses, hammocks made of
91 burlap sacks, and several feeding devices, for environmental enrichment. Indoor rooms
92 were small chambers of 4 m² (W: D: H = 2.0: 2.0: 2.7 m). The subjects remained isolated
93 in indoor rooms from evening until the next morning, but were able to communicate with
94 neighboring individuals visually and physically through iron bars. Indoor rooms were
95 bright from 7:00 a.m.–7:00 p.m., giving a light–dark condition (L:D) of 12:12 each day,
96 with daylight reaching interior rooms through windows on the roof. The indoor rooms
97 were temperature controlled to 20–28 °C; outside air blew into the rooms through a gap in
98 the door, so seasonal changes in the outdoor environment may have influenced indoor
99 conditions.

100 We also studied three of the chimpanzees, aged 21–25 yr, during a post-move period
101 (February–March 2009). We isolated one male (Takashi) from other chimpanzees during

102 the night immediately after the move. The other two males (Kazuya and Kenji) spent the
103 night as a pair. All three males were able to access an outdoor compound with different
104 females during daytime hours in their new housing. Their new outdoor compound and
105 indoor rooms were 150 m² (W: D: H = 9.0: 15.6: 6.0 m) and 3.6 m² (W: D: H = 2.0: 1.8:
106 3.5 m) in area, respectively, and were similar to the facility described above.

107 Food and water were available ad libitum in this study. The care and use of the
108 chimpanzees complied with the Guide for the Care and Use of Great Apes of the
109 Chimpanzee Sanctuary Uto. This experiment was approved by the CSU and was
110 conducted in a manner commensurate with the ethical policy of the Wildlife Research
111 Center and the Primate Research Institute, Kyoto University, as well as domestic laws
112 related to the welfare and management of animals.

113

114 Data Collection

115 We recorded nocturnal behavior among chimpanzees kept in their indoor rooms
116 using a digital video camera (DCR-SR300; Sony Corp.) equipped with enhanced
117 low-light recording capability (Night Shot; Sony Corp.). We used an infrared LED
118 illuminator (LIR-CA60; Surveillance Tech) to light the space without the subjects'
119 awareness. We recorded images continuously for 13 hr, from 5:00 p.m. until 6:00 a.m. the
120 next morning. We recorded the behavior of each subject once per month (i.e. six times)
121 during the stable period. In the post-move period, we recorded behavior once every two
122 days for three weeks. We observed Kazuya and Takashi for 11 days and Kenji for 10 days

123 in the post-move period.

124 We used instantaneous sampling at 1 min intervals through the 13 hr period to record
125 sleep, which we defined operationally as an inactive posture with the body lying down
126 with the head on the floor or on nesting materials. We assumed that if an animal was
127 asleep or awake at two consecutive points, then the animal was in that state for the
128 intervening period. The total sleep duration was assumed to be the sum total of the length
129 of sleep bouts for each observation of 13 hr.

130

131 Statistical Analysis

132 To examine influences on length and continuity of sleep behavior, we calculated four
133 variables: total sleep duration as the total length of sleep bouts for each 13 hr observation
134 period; the maximum length of sleep and non-sleep bouts; and the number of sleep bouts
135 per night for each subject. Day length and external temperatures varied during the study
136 period, so we compared the four dependent variables over time (in months) as well as
137 among subjects using two-way analysis of variance (ANOVA) followed by Bonferroni's
138 *post hoc* tests using the R computer program (R Development Core Team, 2007). We also
139 examined the relationship between age and the four dependent variables using Pearson's
140 product-moment correlation. Finally, we compared the four variables between the stable
141 and post-move periods and among moved subjects using a two-way ANOVA with
142 Bonferroni's *post hoc* test. We considered values of $p < 0.05$ as statistically significant.

143

144 RESULTS

145 The 19 male chimpanzees slept for a mean (\pm SEM) of 11.3 ± 0.26 hr during the
146 stable period and showed individual differences in total sleep duration ($F(5,18) = 11.28$, p
147 < 0.01). Norihei, Shiro, Kanao, and Mikota slept for shorter durations than the rest of the
148 subjects (Fig 1a).

149 <<<Fig. 1 around here>>>

150 The mean maximum length of a sleep bout per night was 3.1 ± 0.17 hr., and this
151 differed among the 19 chimpanzees ($F(5, 18) = 1.83$, $p = 0.03$; Fig. 1b), although there
152 were no significant differences in *post hoc* pairwise comparisons among the subjects. The
153 maximum length of non-sleep bouts per night (0.5 ± 0.07 hr) also differed among the 19
154 individuals ($F(5, 18) = 6.78$, $p < 0.01$). Six individuals showed longer maximum
155 non-sleep bouts per night than the other subjects (Fig 1c). The number of sleep bouts per
156 night (24.4 ± 0.72) differed among the 19 subjects ($F(5, 18) = 3.86$, $p < 0.01$) and was
157 higher in nine individuals than in the others (Fig. 1d).

158 The four dependent variables did not vary significantly between months in the stable
159 period (Table I). We found a significant relationship between age and the number of sleep
160 bouts but not between age and the other three sleep variables (Table II).

161 <<<Tables I & II around here>>>

162 In the post-move period, the three chimpanzees slept for a mean duration of $10.0 \pm$
163 0.37 hr. The change in housing influenced total sleep duration ($F(2, 3) = 5.17$, $p < 0.01$),
164 but not the mean maximum length of a sleep bout per night ($F(2, 3) = 0.19$, $p = 0.90$), the

165 maximum non-sleep bout length per night (mean \pm SEM: 0.5 ± 0.07 hr, $F(2, 3) = 2.37$, $p =$
166 0.09), or the number of sleep bouts per night ($F(2, 3) = 1.55$, $p = 0.22$). Total sleep
167 duration decreased after changing facilities but then increased over time (Fig. 2), reaching
168 the mean total sleep duration of the stable period on the 11th, 9th, and 21st days after the
169 move for Kazuya, Kenji, and Takashi, respectively.

170 <<<Fig. 2 around here>>>

171 The individual males showed no difference in total sleep duration ($F(2, 3) = 2.27$, $p =$
172 0.12), the mean maximum length of a sleep bout ($F(2, 3) = 1.46$, $p = 0.25$), or the
173 maximum non-sleep bout length ($F(2, 3) = 2.27$, $p = 0.12$). However, the mean number of
174 bouts was different among the three subjects ($F(2, 3) = 6.63$, $p < 0.01$). Takashi's sleep
175 was more fragmented than that of the other two subjects (*post hoc* tests: Takashi–Kazuya,
176 $p < 0.01$; Takashi–Kenji, $p = 0.04$, Kazuya–Kenji; $p = 1.00$).

177

178 DISCUSSION

179 Mean sleep duration during the stable period was 11.3 hr, ranging from 8.7–12.6 hr,
180 similar to the results of previous studies (Bert et al. 1970; Freemon et al. 1971; Videan
181 2006). Age influenced the number of sleep bouts but not the other patterns of these adult
182 male chimpanzees. A longitudinal comparison of sleep patterns between the stable and
183 the post-move period revealed a temporary sleep shortage in chimpanzees moved from
184 one facility to the other. Total sleep duration in the post-move period was significantly
185 less than the shortest sleep duration of subjects during the stable period. However, total

186 sleep duration increased gradually during the post-move period and reached a level
187 comparable to that observed during the stable period. Therefore, a stressful event (a
188 change of housing) disturbed the sleep of captive chimpanzees in the present study,
189 supporting the results of a study on the effects of the death of a group member on sleep
190 (Anderson et al. 2010).

191 We also identified individual differences in sleep patterns. In particular, Norihei had
192 the shortest total sleep duration and shortest maximum-length sleep bout per night as well
193 as the longest maximum-length non-sleep bout per night during the stable period. A
194 questionnaire study for caretakers suggests that traumatic experiences can cause
195 behavioral abnormalities in captive chimpanzees similar to those observed in
196 post-traumatic stress disorder and depression in humans (Ferdowsian et al. 2010). Sleep
197 shortages and sleep fragmentation in non-human primates are also similar to disturbances
198 observed in human sleep disorders (Adachi et al. 2003; Lévy and Pépin 2003).
199 Chimpanzees might share negative outcomes (e.g., illness or pathology) with humans as a
200 result of sleep disturbances (Averina et al. 2005; Barraud et al. 2009). More intensive
201 studies using behavioral sleep indices should elucidate the relationship between sleep
202 shortages and poor health outcomes in non-human primates.

203 Abnormal daytime behaviors such as yawning and scratching are commonly used as a
204 proxy for stress responses (Baker and Aureli 1997; Brent 2001; Chamove 1989). However,
205 given that these behaviors are measured during the day, their use as indices may be
206 confounded by other behaviors and the actions of human caretakers. In contrast, sleep is

207 less influenced by caretakers. Therefore, sleep patterns may serve as an alternative
208 behavioral index of the stress. Further study is necessary to examine the sleep
209 characteristics of captive non-human primates using large samples that include both sexes.
210 A comparative perspective that includes both health problems in captive animals and sleep
211 disorders in humans will aid our understanding of how sleep and stress are related to health
212 and well-being in primates.

213

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225

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292

293 Table I. Results of ANOVAs testing the influence of time on four measures of sleep over
294 the six months of the stable period for 19 adult male chimpanzees.

Variables	<i>F</i> (5,18)	P-value
Total sleep duration	1.13	0.35
Maximum duration of sleep bout	0.28	0.93
Maximum duration of awake bout	1.41	0.23
Number of sleep bouts	0.64	0.67

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299 Table II. Results of Pearson's product-moment correlation tests comparing four sleep
300 variables and age during the stable period for 19 adult male chimpanzees

Variables	<i>r</i>	<i>t</i>	P-value
Total sleep duration	0.14	1.49	0.14
Maximum duration of sleep bout	-0.14	-1.49	0.14
Maximum duration of awake bout	-0.17	-1.86	0.07
Number of sleep bouts	0.20	2.63	0.01

301

302

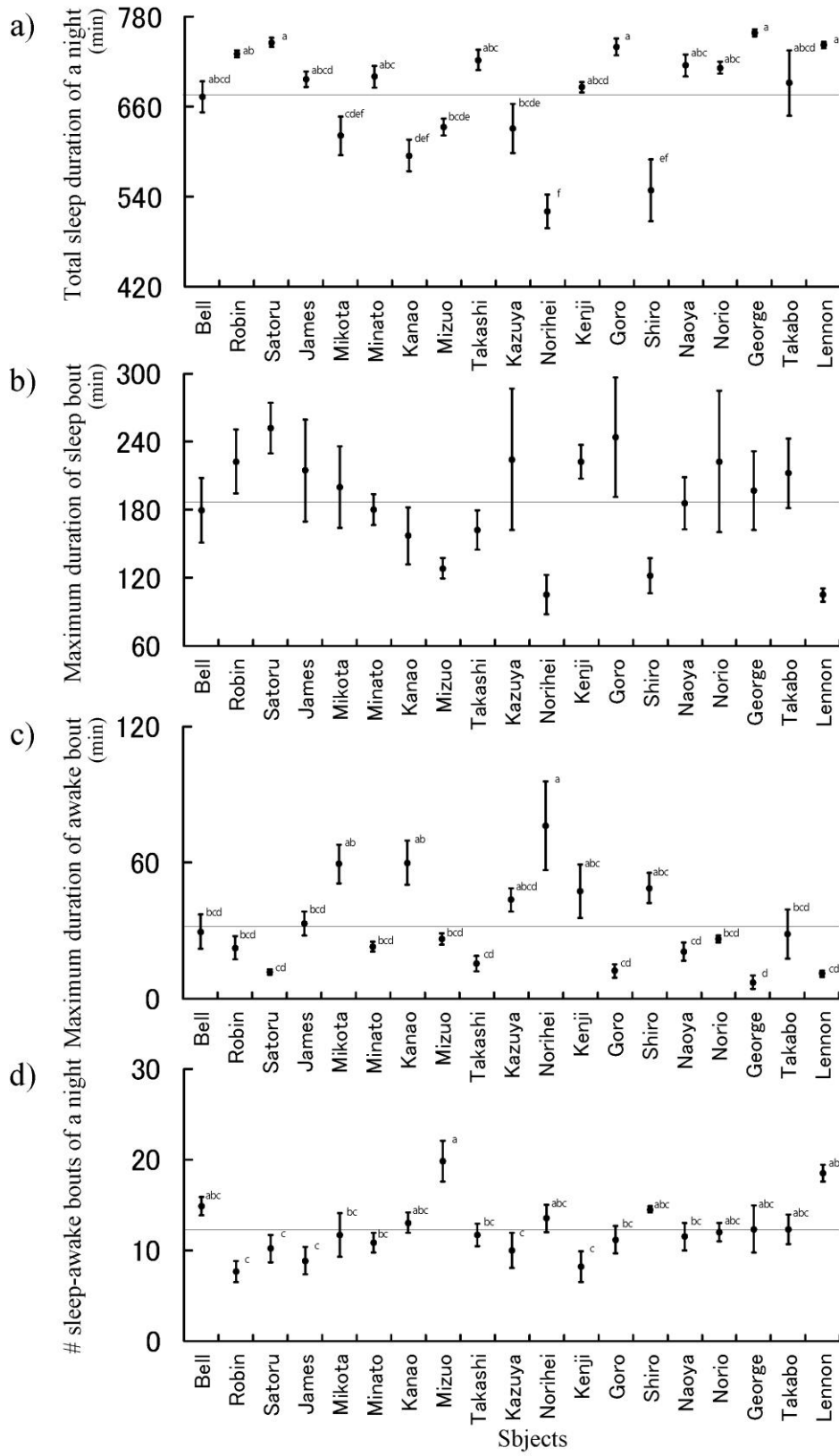
303 Figure legends

304 Figure 1: Mean \pm SEM (a) total sleep duration, b) maximum length of sleep bout, c)
305 maximum length of non-sleep bout, and d) number of sleep bouts per night for
306 individual chimpanzees during the stable period. Individuals are shown by age in
307 ascending order, from left to right. The dotted line indicates the overall mean for each
308 variable. Significant differences in *post hoc* pairwise comparisons are indicated by
309 small letters.

310

311 Figure 2: Mean \pm SEM sleep duration during the stable period and three-week blocks
312 during the post-move period for three chimpanzees. Significant differences in *post*
313 *hoc* pairwise comparisons are marked by connecting lines.

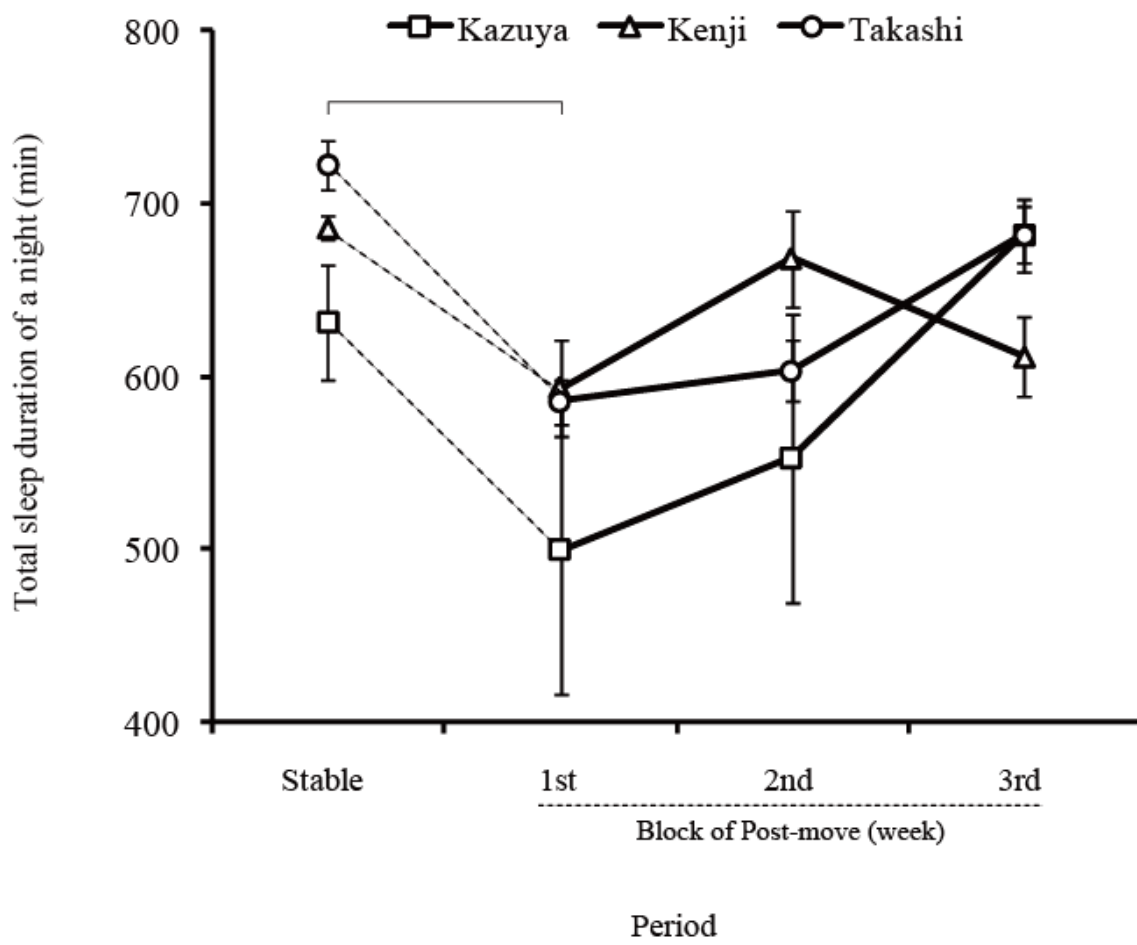
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316

Figure 1



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318

Figure 2