

This is a **peer-reviewed manuscript version** of the article:

Úbeda, Y., Ortín, S., Robeck, T.R., Llorente, M. & Almunia, J. Personality of killer whales (*Orcinus orca*) is related to welfare and subjective well-being. *Applied Animal Behaviour Science*, vol. 237 (April 2021), art. 105297. DOI <https://doi.org/10.1016/j.applanim.2021.105297>

The Published Journal Article is available at:

<https://doi.org/10.1016/j.applanim.2021.105297>

© 2021. This manuscript version is made available under the CC-BY-NC-ND 4.0 license <https://creativecommons.org/licenses/by-nc-nd/4.0/>



1 **Cite this article:**

2 Yulán Úbeda, Sara Ortín, Todd R. Robeck, Miquel Llorente, Javier Almunia,
3 Personality of killer whales (*Orcinus orca*) is related to welfare and subjective well-being,
4 *Applied Animal Behaviour Science*, Volume 237, 2021, 105297, ISSN 0168-1591,
5 <https://doi.org/10.1016/j.applanim.2021.105297>.
6 (<https://www.sciencedirect.com/science/article/pii/S0168159121000848>)

7

8 **Personality of killer whales (*Orcinus orca*) is related to welfare and subjective well-being**

9 Yulán Úbeda^a, Sara Ortín^b, Todd R. Robeck^c, Miquel Llorente^a, Javier Almunia^d

10 ^a Facultat d'Educació i Psicologia, Universitat de Girona, Plaça de Sant Domènec, 7. 17004

11 Girona, Spain

12 ^b Fundació Universitat de Girona: Innovació i Formació, Carrer Pic de Peguera, 11. 17003

13 Girona, Spain

14 ^c SeaWorld Parks and Entertainment, 7007 SeaWorld Drive, Orlando FL 32821

15 ^d Loro Parque Fundación, Tenerife, Calle Bencomo, 1. 38400, Puerto de la Cruz, Tenerife, Spain

16

17 Correspondence concerning this article should be addressed to Yulán Úbeda, Facultat

18 d'Educació i Psicologia, Universitat de Girona, Plaça de Sant Domènec, 7. 17004 Girona,

19 Spain. E-mail: yulanubeda@gmail.com

20

21 **Abstract**

22 Questionnaires are very useful tools when it comes to assessing zoo based animal measures and
23 caretakers of these animals (such as keepers, trainers and veterinarians) are in the best position
24 to provide accurate answers to these assessments. Our goal was (a) to empirically demonstrate
25 the utility of a welfare questionnaire and (b) to examine the relationship between personality,
26 subjective well-being and welfare ratings, in a sample of killer whales (*Orcinus orca*) (n=26).
27 For this purpose, we applied the 4-factor personality structure previously applied to the species
28 (Úbeda et al., 2018), a 4-item subjective well-being questionnaire, and we designed and applied
29 a 39-item welfare questionnaire. The welfare questionnaire was composed by positive and
30 negative welfare indicators related to social and environmental interactions, physical health
31 condition, presence of species-typical and stereotypical behaviors, the capacity to accept
32 situations, and relationships with conspecifics and humans, among others. Each killer whale was
33 rated by an average of 12.5 raters. The mean interrater reliability for subjective well-being and
34 welfare questionnaires was high, and the Principal Components Analysis and the Regularized
35 Exploratory Factor Analysis, revealed one and six factors, respectively. We found some
36 correlations among the three constructs, for instance, Extraversion ($r = 0.62$, 95% CI 0.02-0.06)
37 and Dominance ($r = 0.61$, 95% CI 0.03-0.09) were associated to the subjective well-being
38 factor, while subjective well-being was negatively associated with the Abnormal ($r = -0.73$,
39 95% CI -0.13- -0.06) and Nervousness ($r = -0.66$, 95% CI 0.06-0.17) welfare factors, among
40 others. According to the reliability and validity obtained, our research represents the first
41 empirical evidence of the utility of assessing the welfare of cetaceans through the use of a
42 questionnaire. Therefore, facilities housing cetaceans could use welfare questionnaires to
43 gradually monitor welfare and to intervene if needed. Finally, some of the correlations found
44 closely resembled previous correlations found in primates, which could indicate a possible
45 evolutionary convergence between Orders.

46

47 **Keywords:** welfare, personality, subjective well-being, killer whales, orcas, cetaceans

48 **Highlights**

- 49 • An evaluation of a questionnaire for killer whale welfare assessment.
- 50 • Ratings of personality, welfare and subjective well-being were highly correlated.
- 51 • Questionnaires are a reliable and valid tool for assessing killer whale welfare.
- 52 • Similarities to primates' correlations were probably due to convergence.
- 53

54 **1. Introduction**

55 The psychological approach of the trait rating method has a number of psychometric and
56 pragmatic advantages over the behavior coding method. These advantages include among
57 others: higher reliability than the coding method, control of variability due to changes in an
58 animal's situation or environment, aggregation of measures across time, a quicker and more
59 efficient data collection and finally a rating method can capture a broader set of states (see
60 Freeman et al., 2011 and Vazire et al., 2007 for a review). These psychometric and pragmatic
61 advantages promote the use of rating method when behavioral characteristics of animals can be
62 transferred into descriptor items (Meagher, 2009; Whitham and Wielebnowski, 2009).
63 Consequently, the rating method has been used to assess a wider range of different traits in
64 animals, such as: personality (Stevenson-Hinde and Zunz, 1978), subjective well-being (King
65 and Landau, 2003), welfare (Robinson et al., 2017), emotions (Morris et al., 2008), social
66 behavior (Rousing and Wemelsfelder, 2006) or psychopathology (Úbeda et al., 2020), among
67 others.

68 Most of the animal rating studies have been conducted within personality research on a wide
69 range of species, with the Primate order being one of the most commonly studied (see Carere
70 and Maestriperi, 2013 and Gosling, 2001 for a review). Associations have been found between
71 animal personality studies and biology, health, psychometrics or behavior, among others (see
72 Freeman and Gosling, 2010; Gartner and Weiss, 2013a; Weinstein et al., 2008; or Weiss et al.,
73 2011c for a review), as well as with conservation, welfare and management (Carere and
74 Maestriperi, 2013; Gartner and Weiss, 2013a).

75 The use of the subjective well-being questionnaire (SWB) (King and Landau, 2003), which was
76 based on a human happiness measure (Sandvik et al., 1993), is also commonly used in rating
77 animal studies. The studies, which have primarily focused on detecting associations between
78 SWB and personality, have been conducted in six primates species (King and Landau, 2003;
79 Robinson et al., 2016; Schaefer and Steklis, 2014; Simpson et al., 2019; Weiss et al., 2020,
80 2006) and in four felids species to date (Gartner et al., 2016; Gartner and Weiss, 2013b).

81 Furthermore, it has been found that SWB is related to longevity (Weiss et al., 2011a), has a
82 genetic overlap with personality (Adams et al., 2012; Weiss et al., 2002) and is associated with
83 cortisol levels (Inoue-Murayama et al., 2018), among others.

84 Animal welfare is another research topic that is receiving increasing amounts of interest.
85 Historically, this topic has been mainly assessed by using physiological, behavioral and health
86 indicators (Hill and Broom, 2009; Melfi, 2009; Whitham and Wielebnowski, 2013). However,
87 due to the aforementioned psychometric and pragmatic arguments, the use of questionnaires has
88 also been transferred to the study of animal welfare (Meagher, 2009; Whitham and
89 Wielebnowski, 2009). Through this method, rating approach tools have been applied, such as:
90 the *Quality of Life* (QoL), in farm and domestic animals (Wemelsfelder, 2007; Wojciechowska
91 et al., 2005); the *Animal Welfare Assessment Grid* (AWAG), in birds and primates (Justice et
92 al., 2017; Wolfensohn et al., 2015) or versions of the “*Five Domains*” which were recently
93 added to “The World Zoo and Aquarium Animal Welfare Strategy” of the World Association of
94 Zoos and Aquariums (WAZA) (Mellor et al., 2015), among others.

95 As previously mentioned, most of the research on personality, SWB and welfare on zoo-housed
96 animals have been carried out on primates. The focus on this order could be due to its
97 phylogenetic proximity to humans (Prado-Martinez et al., 2013), and to its cognitive and
98 emotional complexity (de Waal, 2007; Tomasello and Call, 1997; Whiten, 2000). However, the
99 cetacean order, despite the phylogenetic distance (Kumar and Hedges, 1998), shares cognitive
100 and emotional complexity with primates (Marino, 2017; Rendell and Whitehead, 2001), which
101 make the research on these topics for cetaceans in zoological parks relevant (Lott and
102 Williamson, 2017). Nevertheless, research on these cetacean constructs is still really scarce.
103 Regarding personality, few studies have been carried out on bottlenose dolphins (*Tursiops*
104 *truncatus*), Atlantic spotted dolphins (*Stenella frontalis*) and Killer whales (*Orcinus orca*) (see
105 Úbeda et al., 2018). However, as previously mentioned, there is still no research on SWB on
106 cetacean species.

107 In relation to welfare, very little research has been carried out on cetaceans (see Brando et al.,
108 2018; and Clegg and Butterworth, 2017 for a review). More specifically, only two publications
109 used the rating approaches to assess welfare: the WelfareQuality[®] rating (Blokhuis, 2008),
110 which has been adapted to create a welfare assessment index for bottlenose dolphins (Clegg et
111 al., 2015) and the Willingness to Participate (WtP) rating which is related to health (Clegg et al.,
112 2019). Nonetheless, to our knowledge there is no systematic study on the validity and reliability
113 of a multi-trait rating welfare questionnaire in cetaceans. Further, except for two primate species
114 [brown capuchins (*Sapajus apella*) and chimpanzees (*Pan troglodytes*): Robinson et al., 2017,
115 2016], there are no studies in any species that search for correlations between personality, SWB
116 and welfare constructs.

117 Therefore, our goals were to: (1) test the reliability and validity of a 39-item welfare
118 questionnaire; and (2) determine the associations between personality, SWB and welfare factors
119 in a group of killer whales. Since there are no similar studies on cetaceans to compare it to, our
120 hypothesis is that associations among the three constructs will be similar to those found in
121 primates. Thus, among others, we would expect to find positive associations between
122 Extraversion and Dominance with subjective well-being and the obtained welfare factors related
123 to positive welfare.

124 **2. Methods**

125 **2.1. Subjects and study site**

126 This research was reviewed and approved by Loro Parque's and Sea World's Institutional
127 Animal Care and Use Committee and was performed in accordance to the Animal Welfare Act
128 for the care of marine mammals. For this research, we studied 26 killer whales (14 females and
129 12 males) housed at Loro Parque (Tenerife, Spain), SeaWorld Orlando (Florida), SeaWorld San
130 Diego (California) and SeaWorld San Antonio (Texas). Four of the killer whales were caught in
131 the wild before 80s, while the remaining twenty-two were born within one of the facilities and
132 ranged in age from 5.33 to 31.54 years (mean=17.38 ± SD = 9.73 years).

133 The whales are housed in interconnected pools with a mean total volume of 22.845 m³ (SD =
134 571.77 m³) either manufactured or natural salt water filtered systems. Training sessions
135 including public presentations occur six to eight times daily and vary in time, duration, and
136 focus. The total diet is distributed across six to eight feedings daily. The diet comprises herring,
137 sardines, capelin, sprat, mackerel, squid, and salmon fed at 2 to 3% of the body weight per
138 animal per day. Animal groupings and pool access are variable throughout the day.

139 **2.2. Questionnaires**

140 *2.2.1. Personality Questionnaire*

141 We included twenty-one of the killer whales (housed at Loro Parque, SeaWorld Orlando and
142 SeaWorld San Diego) that were rated in our previous research according to a 38-item
143 questionnaire which revealed four personality factors: Extraversion, Conscience-Agreeableness,
144 Dominance and Careful (Úbeda et al., 2018). Five additional killer whales (from SeaWorld San
145 Antonio) were rated with the same 38-item questionnaire, according to a 7-point Likert rating
146 scale (Likert, 1932). Thus unit-weighted factor scores for the four factors described in our study
147 were constructed for the San Antonio sample.

148 *2.2.2. Welfare Questionnaire*

149 The welfare questionnaire was designed by the researchers, so as to include a large amount of
150 both positive and negative welfare indicators, related to: social and environmental interactions,
151 physical health condition, presence of species-typical and stereotypical behaviors, the capacity
152 to accept situations, and relationships with conspecifics and humans, among others. The
153 questionnaire was composed by 39 items, which were rated on a 7-point Likert scale (Likert,
154 1932) ranging from least to most expression of the trait. The welfare questionnaire is available
155 in supplementary materials.

156 *2.2.3. Subjective Well-being Questionnaire*

157 The subjective well-being questionnaire was identical to the King and Landau's 4-item
158 questionnaire (2003). The first item asked raters to assess the amount of time the killer whale
159 spends happy, the second item asked the degree to which the killer whale enjoyed social
160 interactions, the third one, the ability of the killer whale to achieve goals, and the fourth asked
161 raters to identify themselves with the killer whales and imagine how happy they would feel for a
162 week. Raters were also asked to use a 7-point Likert scale (Likert, 1932) ranging from least to
163 most expression of the trait.

164 **2.3. Raters**

165 Questionnaires were evaluated by 17 raters from Loro Parque (14 trainers and 4 show audio-
166 visual staff), 12 raters from Sea World San Diego (8 trainers, 3 supervisors and 1 curator) 11
167 raters from SeaWorld Orlando (10 trainers and 1 veterinarian) and 10 raters from SeaWorld San
168 Antonio (7 trainers, 2 supervisors and 1 curator). Raters all had a high level of contact with the
169 animals. Trainers were in contact with the animals for a mean of over 66.11 months (SD =
170 49.67), audio-visual staff a mean of 74 months (SD = 42.79), supervisors a mean of 157 months
171 (SD=125.75), curators a mean of 282 months (SD = 59.40) and the veterinarian 96 months. All
172 of the raters evaluated all the subjects and all the three questionnaires. Raters were instructed to
173 base their judgments on general impressions of the killer whales, not on frequency estimates of
174 past behaviors. Evaluators were cautioned to avoid discussing their ratings with other raters.
175 None of the researchers rated any of the questionnaires.

176 **2.4. Data analysis**

177 *2.4.1. Intraclass correlations*

178 The observer agreement of the 50 raters was assessed by using two intraclass correlation
179 coefficients (ICC; Shrout and Fleiss, 1979). To compute ICCs, the mean squares scores for
180 killer whales and Rater x Killer whales were obtained using a general linear model with Type III
181 sums of squares. The first ICC (3, 1) indicates the reliability of the scores for a single evaluator.
182 The second ICC (3, k) indicates the reliability for the mean scores of the evaluators, in our case,

183 based on an average of 12.5 raters per killer whale ($SD = 3.11$). Due to our small sample size,
184 and further to ensure a high degree of interrater reliability, we chose to be conservative and to
185 omit items with an ICC (3, k) < 0.60.

186 *2.4.2. Data Reduction: Principal component analyses and regularized exploratory factor*
187 *analyses*

188 To determine the welfare trait domains, we first transformed our data into z-scores using
189 a principal-components analysis (PCA) to identify the dimensions underlying the mean ratings.
190 To determine the number of factor components to extract (only the factors that exceeded the 95th
191 percentile of the values derived from random matrices were extracted), we examined the scree
192 plot and used parallel analysis (Horn, 1965; O’connor, 2000). After determining the number of
193 components, we subjected those components to an orthogonal (varimax) and oblique (promax)
194 rotation. For the purpose of interpreting and scoring factors, we defined absolute loadings
195 greater than or equal to 0.40 as salient. The component scores were unit-weighted, thus the z-
196 scores of items with salient primary loadings were assigned weights of +1 or -1, depending on
197 the direction of the loading. Items with non-salient loadings were assigned weights of 0. Unit-
198 weighted scores are more generalizable across studies and are highly correlated with
199 differentially weighted scores (Gorsuch, 1983). If an item had a loading greater than or equal to
200 .40 on more than one component, we assigned the item to the component on which it had the
201 highest loading. Due to the small sample, we used regularized exploratory factor analysis
202 (REFA), a technique specifically designed to derive factors when the sample size is small (Jung
203 and Lee, 2011; Jung and Takane, 2008). For this analysis, we used quartimax rotation and
204 specified unweighted least squares for factor extraction. As REFA loadings are shrunk toward
205 zero (Jung and Lee, 2011), they are more conservative than loadings obtained via PCA. We
206 therefore defined loadings greater than or equal to 0.30 as salient. In the event that an item had a
207 loading greater than or equal to 0.30 on more than one component, we assigned the item to the
208 component on which it had the highest loading. The same procedure was used to determine the
209 subjective well-being domains. To calculate personality factor scores, we combined the results

210 for the five killer whales included in this study to those previously assessed on Úbeda et al
211 (2018), in order to generate the factor scores for the personality factors obtained for this sample.

212 *2.4.3. Pearson correlations*

213 To examine the correlations among the factors obtained for personality, welfare and subjective
214 well-being, we standardize the variables of the factor scores and used Pearson correlation.

215 **3. Results**

216 *3.1. Intraclass correlations*

217 There were no items with negative ICC values or with ICC (3,k) estimates below 0.60 to be
218 excluded from further analyses from any of the questionnaires. The reliabilities of individual
219 ratings, ICC (3, 1) for the 39 welfare items ranged from 0.07 to 0.79 with a mean reliability of
220 0.41, while the reliabilities of mean ratings, ICC (3, k) ranged from 0.79 to 0.99 with a mean
221 reliability of .95 (Table 1). The reliabilities of individual ratings, ICC (3, 1) for the four SWB
222 items ranged from 0.35 to 0.55 with a mean reliability of 0.43, while the reliabilities of mean
223 ratings, ICC (3, k) ranged from .96 to .98 with a mean reliability of 0.97 (Table 2). The
224 reliabilities of individual ratings, ICC (3, 1) for the 38 personality adjectives for San Antonio
225 sample ranged from 0.16 to 0.89 with a mean reliability of 0.54, while the reliabilities of mean
226 ratings, ICC (3, k) ranged from 0.69 to 0.99 with a mean reliability of 0.91.

227 — place Table 1 and 2 here —

228 *3.2. Data reduction of Welfare questionnaire and Subjective well-being questionnaire*

229 *3.2.1. Welfare Questionnaire*

230 An examination of the scree plot suggested six components and the Parallel analysis (Horn,
231 1965; O’connor, 2000) indicated that the eigenvalues of the first six components exceeded the
232 95th percentile of eigenvalues expected by chance. Therefore, a PCA with varimax rotation
233 (K.M.O = .78) was used to extract six components, accounting for 52.98 % of the total variance.
234 We extracted six factors from the 26 mean ratings using REFA and subjected these factors to a

235 quartimax rotation. The dimensions extracted by REFA and those extracted by PCA were
236 comparable (see Table 3). Correlations obtained between the same labelled factors for PCA and
237 REFA show statistical concordance, whereas correlations obtained between some of the other
238 factors show statistical similarities that could be due to the sample size (Table 4). With little
239 exception, none of the extractions led to differences in how the dimensions were interpreted.
240 From the six components extracted, the promax rotation produced moderately high correlations,
241 with a mean absolute intercorrelation value of 0.19 (see Table 5).

242 On the first factor positively loaded items related to environment inspection, enrichment
243 interaction, enclosure exploration and routine acceptance, among others, and negatively loaded
244 items related to motionless behavior and attachment to objects. Therefore, we labelled this
245 factor as Confidence. The second factor is negatively related to isolation and contact avoidance
246 with conspecifics, and positively related to playful and affiliative interactions, among others.
247 For this reason, we labelled this factor as Sociability. The third factor is positively associated
248 with items related to stereotypes, abnormal and self-directed behaviors, among others, and
249 negatively associated with species-typical behaviors. Thus, we labelled this factor as
250 Abnormality. The fourth factor is characterized by items related to good physical condition and
251 health, good alimentary habit, normal sexual response, as well as overall welfare and happiness.
252 We labelled this factor as Overall welfare. The fifth factor is associated with items related to
253 attack, dominance displays, frustration and breaching behaviors, among others. We labelled this
254 factor as Nervousness. The sixth factor is mainly defined by items related to dependence and
255 interaction with humans. Therefore, we labelled this factor as Self-sufficiency.

256 From the 39 items analyzed, three of them (“4. *The killer whale often shows visible*
257 *physical injuries*”, “32. *The killer whale tends to vocalize*” and “33. *The killer whale seeks the*
258 *attention of his/her trainer*”) did not have salient loadings in any factor in PCA, although they
259 loaded in a REFA factor.

260 — place Table 3, 4 and 5 here —

261 3.2.2. Subjective Well-being Questionnaire

262 We conducted a principal-components analysis of the mean ratings of the four subjective well-
263 being items. Only the first factor, designated as *Subjective well-being*, had an eigenvalue greater
264 than 1.00 (2.66), accounting for 66.39% of the variance. Factor loadings of the four items
265 ranged from .80 to .84. Therefore, each killer whale's subjective well-being score was defined
266 as the sum of the mean ratings for all four items.

267 3.3. *Correlations of personality, welfare and subjective well-being*

268 We found correlations between personality and welfare factors (Table 6), personality
269 factors and the subjective well-being factor (Table 7), and between welfare factors and the
270 subjective well-being factor (Table 8). The personality factor of *Extraversion* was positively
271 associated to the welfare *Confidence* factor ($r = 0.82$, $P < 0.001$) and to the *subjective well-being*
272 factor ($r = 0.62$, $P = 0.001$). The personality factor of *Dominance* was positively associated to the
273 *subjective well-being* factor ($r = 0.61$, $P = 0.001$) and to the welfare *Confidence* factor ($r = 0.64$,
274 $P < 0.001$), and negatively associated to *Abnormality* ($r = -0.60$, $P = 0.001$) and *Nervousness*
275 welfare factors ($r = -0.57$, $P = 0.003$). The personality factor of *Conscientiousness* was
276 negatively associated to the *Nervousness* welfare factor ($r = -0.55$, $P = 0.003$). The *Careful*
277 personality factor was negatively associated to the *Sociability* welfare factor ($r = -0.73$,
278 $P < 0.001$). Finally, the *subjective well-being* factor was positively associated to the *Confidence*
279 welfare factor ($r = 0.71$, $P < 0.001$) and negatively to the *Abnormality* ($r = -0.73$, $P < 0.001$) and
280 *Nervousness* ($r = -0.66$, $P < 0.001$) welfare factors.

281 — place Tables 6, 7 and 8 here —

282 **4. Discussion**

283 Our study presented two main results. First, the welfare questionnaire revealed six
284 factors with reliability and validity. Second, the correlations found between personality, welfare,
285 and subjective well-being, are similar to those found in primates, indicating a possible
286 convergence among species, and perhaps orders.

287 The utility of a welfare questionnaire is valuable only if it produces reliable and valid data
288 (Meagher, 2009). The reliability measures the agreement among raters (Shrout and Fleiss,
289 1979), and in our case the value was high (0.95) and in line with the ones previously obtained
290 from the welfare questionnaires applied to chimpanzees (0.92; Robinson et al., 2017) and
291 capuchin brown monkeys (0.72; Robinson et al., 2016). The validity is obtained from the
292 convergent and discriminant validity of the factors (Campbell and Fiske, 1959). On one hand,
293 convergent validity is valued by the presence of correlations between different measures of the
294 same construct (Campbell and Fiske, 1959), as well as by the values of the item loadings onto
295 the factors to which they are assigned (Ferketich et al., 1991; Figueredo et al., 1991). In our
296 case, some of the welfare factors were related to some of the personality factors (Table 6) and
297 with the subjective well-being factor (Table 8). Likewise, from the 39 items of the PCA, 30
298 items were loaded with values superior to 0.50, 6 loaded with values between 0.50 and 0.40, and
299 3 did not have salient loadings (Table 3). On the other hand, discriminant validity is valued by
300 the absence of unexpected correlations (Campbell and Fiske, 1959), as well as by the factorial
301 independence obtained from the low intercorrelation values of the oblique factors (King and
302 Figueredo, 1997). In our case, there were no unexpected correlations between welfare and
303 personality factors (Table 6) and between welfare and Subjective well-being factor (Table 8).
304 Likewise, the mean absolute factor intercorrelation value was 0.19 (Table 5). Thus, the welfare
305 reliabilities and validities suggest that welfare ratings produced by the people in close contact to
306 the animals are reliable, valid, and valuable (Meagher, 2009; Whitham and Wielebnowski,
307 2009). Moreover, the questionnaire covers a wide range of aspects related to positive and
308 negative welfare, by obtaining six factors related to: basic welfare (*Overall Welfare* factor),
309 social aspects (*Sociability* factor), extraverted behaviors (*Confidence* factor), abnormal and non-
310 desirable behaviors (*Abnormality* factor), excitability (*Nervousness* factor) and relationship with
311 humans (*Self-sufficiency* factor). Therefore, facilities housing animals can assess the welfare of
312 the animals by using welfare questionnaires as pragmatic and trustworthy assessment tools.

313 As mentioned above, because of the lack of any systematic study that assesses the
314 relationship between personality, subjective well-being and welfare on cetaceans, any
315 comparison to previous results with cetaceans is not possible. Thus, on one hand, our results can
316 only be compared to the studies on the six species of nonhuman primates and on the four
317 species of felids that assessed the relationships between personality and subjective well-being.
318 On the other, it can also be compared to the studies on chimpanzees and brown capuchins that
319 assessed the relationship between personality, subjective well-being and welfare (which data
320 reduction in the welfare questionnaire revealed a single combined factor of welfare-SWB). One
321 of the most common association found among these constructs, is the positive correlation
322 between *subjective well-being* and *Extraversion* found in humans (Steel et al., 2008),
323 chimpanzees (King and Landau, 2003; Robinson et al., 2017; Weiss et al., 2009), orangutans
324 (Weiss et al., 2006), and gorillas (Schaefer and Steklis, 2014). Similarly, other correlations have
325 been found between the *subjective well-being* factor and the *Openness* factor for chimpanzees
326 (Weiss et al., 2009) and rhesus macaques (Simpson et al., 2019), the *Sociability* factor for
327 brown capuchins (Robinson et al., 2016) and common marmoset (Inoue-Murayama et al.,
328 2018), and the *Friendliness* factor for rhesus macaques (Weiss et al., 2011b). In our study, we
329 have also found a positive correlation between *subjective well-being* and *Extraversion* for killer
330 whales. Additionally, we have found a correlation between the *subjective well-being* and the
331 *Confidence* welfare factor, which reflects an aspect of welfare related to extraversion and
332 openness (in fact, we have also found a correlation between *Extraversion* and the *Confidence*
333 welfare factor). These associations demonstrate the importance of social relationships among
334 intensively social cetaceans as the killer whales, which in the wild present complex social
335 organizations (Baird, 2000; de Bruyn et al., 2013). Moreover, in captive settings, those
336 relationships could explain the social buffering, a term related to the ability of a social partner to
337 reduce stress responses (Hennessy et al., 2009; Kikusui et al., 2006). Another association found
338 in killer whales is the negative correlation between *subjective well-being* and both *Abnormality*
339 and *Nervousness* welfare factors. This finding does not come as a surprise, since abnormal
340 behaviors, as well as those behaviors related to stress and anxiety, may indicate psychological

341 suffering and are known to have a negative impact on health outcomes in animals (Capitanio,
342 2011; Deary et al., 2010; Rollin, 2006). Thus, it would make sense that these results would
343 spread across multiple species. Our results are in concordance with the negative correlation
344 obtained between *subjective well-being* and abnormal behaviors (Robinson et al., 2017) and
345 generalized anxiety (O'Connor et al., 2001) for chimpanzees, and are in accord with the
346 negative correlation obtained between *subjective well-being* and *Neuroticism* found in humans
347 (DeNeve and Cooper, 1998; Steel et al., 2008), chimpanzees (Robinson et al., 2017; Weiss et
348 al., 2009), orangutans (Weiss et al., 2006), brown capuchins (Robinson et al., 2016), common
349 marmosets (Inoue-Murayama et al., 2018), clouded leopards, snow leopards and African lions
350 (Gartner et al., 2016). Another association found in our study with killer whales is the one
351 between *subjective well-being* and *Dominance*, and the same correlation has been found in
352 chimpanzees (King and Landau, 2003; Weiss et al., 2009). While in orangutans (Weiss et al.,
353 2006) and gorillas (Schaefer and Steklis, 2014), *Dominance* was positively associated with the
354 item related to the ability to achieve goals from the SWB questionnaire. The link between
355 *Dominance* and *subjective well-being* could be due to the fact that dominance confers
356 advantages that may lead to better welfare, including primary access to food, being less likely to
357 be intimidated, more assertive and decisive, more adept at tactical deception and better at
358 making allies (Weiss et al., 2002). We have also found a negative correlation between
359 *Dominance* and both *Abnormality* and *Nervousness* welfare factors, as well as a positive
360 correlation between *Dominance* and *Confidence* welfare factor. This is a logical correlation,
361 since as previously mentioned, same correlations were found between those three welfare
362 factors and the *subjective well-being* factor, and moreover the *subjective well-being* factor was
363 related to *Dominance*. Finally, we have found a negative correlation between the *Conscien-*
364 *Agreeableness* personality factor and the *Nervousness* welfare factor, and a negative correlation
365 between the *Careful* personality factor with the *Sociability* welfare factor. We have not found
366 similar correlations in the other studied species. However, the first correlation could be
367 interpreted by the fact that those killer whales with higher conscientiousness and agreeableness

368 personalities are naturally calmer and more confident, while the second correlation may reflect
369 that cautious individuals tend to be less extroverted so as to avoid possible social conflicts.

370 Since there are no similar psychometric studies on cetaceans to serve as comparison to
371 our findings, in many respects' killer whales seem to have evolved associations among
372 personality, welfare and subjective well-being constructs, resembling closely to those found in
373 primates. Those results could be explained as evolutionary convergences, taking in
374 consideration that previous studies on social organization (Bearzi and Stanford, 2007; Connor et
375 al., 1998; Pearson, 2011), cognition (Marino, 2011, 2002; Reiss and Marino, 2001) or
376 personality (Úbeda et al., 2018), among others, indicated possible evolutionary convergences
377 due to the similarities shared between cetaceans and primates.

378 While welfare science itself is a rapidly evolving discipline that is still embroiled in
379 debate concerning the most effective methods for evaluating animal welfare, zoo and aquariums
380 associations are encouraging the development of studies and assessment tools to identify,
381 address and monitor welfare (Kagan et al., 2015; Whitham and Wielebnowski, 2013). Despite
382 this push, and unexpectantly due to the novelty of the science itself, to date very little behavioral
383 based research has focused on assessing and improving welfare on cetaceans in zoological parks
384 (see Brando et al., 2018 and Clegg and Butterworth, 2017 for a review). As a consequence of
385 the keeper's holistic knowledge of an animal's welfare, the use of the rating method is being
386 transferred to the assessment of animal welfare (Whitham and Wielebnowski, 2009). Being a
387 relatively new science, only a few studies related to cetacean welfare to date have used rating
388 methods (Clegg et al., 2019, 2015; Clegg and Butterworth, 2017; Joblon et al., 2014). However,
389 and to our knowledge, only Clegg and colleagues' study (2015) used multiple variables to
390 assess welfare in a cetacean, by applying 36 welfare measures to bottlenose dolphins, 58% of
391 them being animal-based measures (Whitham and Wielebnowski, 2013, 2009). Nevertheless,
392 this assessment needs more work to fully validate the measures, which are also currently
393 unweighted (Clegg and Delfour, 2018). Despite that, Clegg and colleagues' study represented
394 an important first step in the development of comprehensive and practical welfare assessment

395 tools for cetaceans. Our study in contrast, appears to be the earliest empirical proof of the use of
396 a questionnaire for the welfare assessment on the order. Therefore, facilities housing cetaceans
397 could use welfare questionnaires to gradually monitor welfare, so as to intervene if needed
398 (Whitham and Wielebnowski, 2009). Additionally, it has been shown that personality is related
399 to welfare in cetaceans, primates and felids. Thus, according to our results, those Introverted and
400 less Dominant killer whales should be monitored more cautiously.

401

402 **5. Conclusions**

403 Our research represents the first empirical evidence of the utility of a welfare questionnaire for
404 cetaceans, with (a) acceptable standards of reliability obtained among a high number of raters
405 with high level of contact with the animals, and (b) validity evidenced with the correlations
406 found with personality and subjective well-being questionnaires. It is crucial for cetacean
407 welfare to increase the research efforts in this area. Therefore, future direction of this topic,
408 must identify effective and useful assessment tools and applied them in an effort to improve
409 cetacean welfare. Moreover, this study suggest that associations between personality and
410 welfare previously found in primates, are also found in a cetacean species, probably due to
411 evolutionary convergences.

412 **Acknowledgements**

413 This research has been funded by Loro Parque Foundation's grant (SS-116-2016-1). The author
414 ML is a Serra Húnter Fellow. The authors wish to thank Loro Parque and SeaWorld for their
415 facilities in order to complete this project and all the raters for helping in the questionnaires'
416 assessment. The authors also thank the trainers, curators, and veterinarians involved in the care
417 of the killer whales. We also thank Tiziana Annone for the English revision of this article.

418 **Authorship statement**

419 This study was designed and conceptualized by YU and SO. YU, JA and TR coordinated the
420 collection of the ratings at Loro Parque and SeaWorld. YU analyzed and interpreted the data.

421 The paper itself was written by YU. The paper was reviewed before submission by YU, SO,
422 TR, ML and JA. All authors read and approved the final manuscript.

423 We conducted this research in accordance with all national and institutional guidelines for the
424 care and management of cetaceans established by Loro Parque and SeaWorld.

425 **References**

426 Adams, M.J., King, J.E., Weiss, A., 2012. The majority of genetic variation in orangutan
427 personality and subjective well-being is nonadditive. *Behav. Genet.* 42, 675–686.
428 <https://doi.org/10.1007/s10519-012-9537-y>

429 Baird, R.W., 2000. The killer whale: foraging specializations and group hunting, in: Mann, J.,
430 Connor, R.C., Tyack, P., Whitehead, H. (Eds.), *Cetacean Societies*. University of Chicago
431 Press, Chicago, pp. 127–153.

432 Bearzi, M., Stanford, C.B., 2007. Dolphins and African apes: comparisons of sympatric socio-
433 ecology. *Contrib. to Zool.* 76, 235–254. <https://doi.org/10.1163/18759866-07604003>

434 Blokhuis, H.J., 2008. International cooperation in animal welfare: the Welfare Quality® project.
435 *Acta Vet. Scand.* 50, S10. <https://doi.org/10.1186/1751-0147-50-S1-S10>

436 Brando, S., Broom, D.M., Acasuso-Rivero, C., Clark, F., 2018. Optimal marine mammal
437 welfare under human care: Current efforts and future directions. *Behav. Processes* 156,
438 16–36. <https://doi.org/https://doi.org/10.1016/j.beproc.2017.09.011>

439 Campbell, D.T., Fiske, D.W., 1959. Convergent and discriminant validation by the multitrait-
440 multimethod matrix. *Psychol. Bull.* 56, 81–105. <https://doi.org/10.1037/h0046016>

441 Capitanio, J.P., 2011. Nonhuman primate personality and immunity: Mechanisms of health and
442 disease., in: Weiss, A., King, J.E., Murray, L. (Eds.), *Personality and Temperament in*
443 *Nonhuman Primates*. Springer, New York, pp. 233–255.

444 Carere, C., Maestriperi, D., 2013. *Animal personalities: behavior, physiology, and evolution*.
445 University of Chicago Press, Chicago.

446 Clegg, I.L.K., Borger-Turner, J.L., Eskelinen, H.C., 2015. C-Well: The development of a
447 welfare assessment index for captive bottlenose dolphins (*Tursiops truncatus*). *Anim.*
448 *Welf.* 24, 267–282. <https://doi.org/10.7120/09627286.24.3.267>

449 Clegg, I.L.K., Butterworth, A., 2017. Assessing the Welfare of Cetacea, in: Butterworth, A.
450 (Ed.), *Marine Mammal Welfare: Human Induced Change in the Marine Environment and*
451 *Its Impacts on Marine Mammal Welfare*. Springer, Cham, Switzerland, pp. 183–211.
452 https://doi.org/10.1007/978-3-319-46994-2_12

453 Clegg, I.L.K., Delfour, F., 2018. Can We Assess Marine Mammal Welfare in Captivity and in
454 the Wild? Considering the Example of Bottlenose Dolphins. *Aquat. Mamm.* 44, 181–200.
455 <https://doi.org/10.1578/AM.44.2.2018.181>

456 Clegg, I.L.K., Rödel, H.G., Mercera, B., van der Heul, S., Schrijvers, T., de Laender, P.,
457 Gojceta, R., Zimmitti, M., Verhoeven, E., Burger, J., Bunschoek, P.E., Delfour, F., 2019.
458 Dolphins' Willingness to Participate (WtP) in Positive Reinforcement Training as a
459 Potential Welfare Indicator, Where WtP Predicts Early Changes in Health Status. *Front.*
460 *Psychol.* 10. <https://doi.org/10.3389/fpsyg.2019.02112>

461 Connor, R.C., Mann, J., Tyack, P.L., Whitehead, H., 1998. Social evolution in toothed whales.
462 *Trends Ecol. Evol.* 13, 228–232. [https://doi.org/10.1016/S0169-5347\(98\)01326-3](https://doi.org/10.1016/S0169-5347(98)01326-3)

463 de Bruyn, P.J.N., Tosh, C.A., Terauds, A., 2013. Killer whale ecotypes: is there a global model?
464 *Biol. Rev. Camb. Philos. Soc.* 88, 62–80. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-185X.2012.00239.x)
465 [185X.2012.00239.x](https://doi.org/10.1111/j.1469-185X.2012.00239.x)

466 de Waal, F.B.M., 2007. *Chimpanzee politics: Power and sex among apes*. Johns Hopkins
467 University Press, Baltimore.

468 Deary, I.J., Weiss, A., Batty, G.D., 2010. Intelligence and personality as predictors of illness
469 and death: How researchers in differential psychology and chronic disease epidemiology
470 are collaborating to understand and address health inequalities. *Psychol. Sci. Public*

471 Interes. Suppl. 11, 53–79. <https://doi.org/10.1177/1529100610387081>

472 DeNeve, K.M., Cooper, H., 1998. The happy personality: A meta-analysis of 137 personality
473 traits and subjective well-being. *Psychol. Bull.* 124, 197–229.
474 <https://doi.org/10.1037/0033-2909.124.2.197>

475 Ferketich, S.L., Figueredo, A.J., Knapp, T.R., 1991. Focus on psychometrics. The multitrait–
476 multimethod approach to construct validity. *Res. Nurs. Health* 14, 315–320.
477 <https://doi.org/10.1002/nur.4770140410>

478 Figueredo, A.J., Ferketich, S.L., Knapp, T.R., 1991. Focus on psychometrics. More on mtmm:
479 The role of confirmatory factor analysis. *Res. Nurs. Health* 14, 387–391.
480 <https://doi.org/10.1002/nur.4770140510>

481 Freeman, H.D., Gosling, S.D., 2010. Personality in nonhuman primates: A review and
482 evaluation of past research. *Am. J. Primatol.* 72, 653–671.
483 <https://doi.org/10.1002/ajp.20833>

484 Freeman, H.D., Gosling, S.D., Schapiro, S.J., 2011. Comparison of methods for assessing
485 personality in nonhuman primates., in: Weiss, A., King, J., Murray, L. (Eds.), *Personality
486 and Temperament in Nonhuman Primates. Developments in Primatology: Progress and
487 Prospects.* Springer, New York, pp. 17–40.

488 Gartner, M.C., Powell, D.M., Weiss, A., 2016. Comparison of Subjective Well-Being and
489 Personality Assessments in the Clouded Leopard (*Neofelis nebulosa*), Snow Leopard
490 (*Panthera uncia*), and African Lion (*Panthera leo*). *J. Appl. Anim. Welf. Sci.* 19, 294–302.
491 <https://doi.org/10.1080/10888705.2016.1141057>

492 Gartner, M.C., Weiss, A., 2013a. Personality in felids: A review. *Appl. Anim. Behav. Sci.* 144,
493 1–13. <https://doi.org/10.1016/j.applanim.2012.11.010>

494 Gartner, M.C., Weiss, A., 2013b. Scottish wildcat (*felis silvestris grampia*) personality and
495 subjective well-being: Implications for captive management. *Appl. Anim. Behav. Sci.* 147,

496 261–267. <https://doi.org/10.1016/j.applanim.2012.11.002>

497 Gorsuch, R.L., 1983. Factor analysis. Erlbaum Associates, New Jersey.

498 Gosling, S.D., 2001. From mice to men: What can we learn about personality from animal
499 research? *Psychol. Bull.* 127, 45–86. [https://doi.org/10.1037/0033-](https://doi.org/10.1037/0033-2909.127.1.45)
500 [2909.127.1.45](https://doi.org/10.1037/0033-2909.127.1.45)

501 Hennessy, M.B., Kaiser, S., Sachser, N., 2009. Social buffering of the stress response:
502 Diversity, mechanisms, and functions. *Front. Neuroendocrinol.* 30, 470–482.
503 <https://doi.org/10.1016/j.yfrne.2009.06.001>

504 Hill, S.P., Broom, D.M., 2009. Measuring zoo animal welfare: theory and practice. *Zoo Biol.*
505 28, 531–544. <https://doi.org/10.1002/zoo.20276>

506 Horn, J.L., 1965. A rationale and test for the number of factors in factor analysis. *Psychometrika*
507 30, 179–185. <https://doi.org/10.1007/BF02289447>

508 Inoue-Murayama, M., Yokoyama, C., Yamanashi, Y., Weiss, A., 2018. Common marmoset
509 (*Callithrix jacchus*) personality, subjective well-being, hair cortisol level and AVPR1a,
510 OPRM1, and DAT genotypes. *Sci. Rep.* 8, 1–15. [https://doi.org/10.1038/s41598-018-](https://doi.org/10.1038/s41598-018-28112-7)
511 [28112-7](https://doi.org/10.1038/s41598-018-28112-7)

512 Joblon, M.J., Pokras, M., Morse, B., Harry, C., Rose, K.S., Sharp, S.M., Niemeyer, M.E.,
513 Patchett, K., Sharp, W., Moore, M.J., 2014. Body condition scoring system for delphinids
514 based on short-beaked common dolphins (*Delphinus delphis*). *J. Mar. Anim. Their Ecol.* 7,
515 5–13.

516 Jung, S., Lee, S., 2011. Exploratory factor analysis for small samples. *Behav. Res. Methods* 43,
517 701–709. <https://doi.org/10.3758/s13428-011-0077-9>

518 Jung, S., Takane, Y., 2008. Regularized common factor analysis, in: Shigemasu, K., Okada, A.,
519 Imaizumi, T., Hoshino, T. (Eds.), *New Trends in Psychometrics*. Universal Academy
520 Press, Tokyo, Japan, pp. 141–149.

521 Justice, W.S.M., O'Brien, M.F., Szyszka, O., Shotton, J., Gilmour, J.E.M., Riordan, P.,
522 Wolfensohn, S., 2017. Adaptation of the animal welfare assessment grid (AWAG) for
523 monitoring animal welfare in zoological collections. *Vet. Rec.* 181, 143–143.
524 <https://doi.org/10.1136/vr.104309>

525 Kagan, R., Carter, S., Allard, S., 2015. A Universal Animal Welfare Framework for Zoos. *J.*
526 *Appl. Anim. Welf. Sci.* 18, S1–S10. <https://doi.org/10.1080/10888705.2015.1075830>

527 Kikusui, T., Winslow, J.T., Mori, Y., 2006. Social buffering: relief from stress and anxiety.
528 *Philos. Trans. R. Soc. B Biol. Sci.* 361, 2215–2228. <https://doi.org/10.1098/rstb.2006.1941>

529 King, J.E., Figueredo, A.J., 1997. The Five-Factor Model plus Dominance in Chimpanzee
530 Personality. *J. Res. Pers.* 31, 257–271. <https://doi.org/10.1006/jrpe.1997.2179>

531 King, J.E., Landau, V.I., 2003. Can chimpanzee (*Pan troglodytes*) happiness be estimated by
532 human raters? *J. Res. Pers.* 37, 1–15. [https://doi.org/10.1016/S0092-6566\(02\)00527-5](https://doi.org/10.1016/S0092-6566(02)00527-5)

533 Kumar, S., Hedges, S.B., 1998. A molecular timescale for vertebrate evolution. *Nature* 392,
534 917–920. <https://doi.org/10.1038/31927>

535 Likert, R., 1932. A technique for the measurement of attitudes. *Arch. Psychol.* 22, 140–155.

536 Lott, R., Williamson, C., 2017. Cetaceans in Captivity, in: Butterworth, A. (Ed.), *Marine*
537 *Mammal Welfare. Animal Welfare.* Springer, New York, pp. 161–181.
538 https://doi.org/10.1007/978-3-319-46994-2_11

539 Marino, L., 2017. Cetacean cognition, in: Kalof, L. (Ed.), *The Oxford Handbook of Animal*
540 *Studies.* Oxford University Press, New York, pp. 227–239.

541 Marino, L., 2011. Cetaceans and Primates Convergence in Intelligence and Self-Awareness. *J.*
542 *Cosmol.* 14, 1063–1079. <https://doi.org/https://doi.org/10.1159/000063731>

543 Marino, L., 2002. Convergence of complex cognitive abilities in cetaceans and primates. *Brain.*
544 *Behav. Evol.* 59, 21–32. <https://doi.org/10.1159/000063731>

545 Meagher, R.K., 2009. Observer ratings: Validity and value as a tool for animal welfare research.
546 *Appl. Anim. Behav. Sci.* 119, 1–14. <https://doi.org/10.1016/j.applanim.2009.02.026>

547 Melfi, V.A., 2009. There are big gaps in our knowledge, and thus approach, to zoo animal
548 welfare: a case for evidence-based zoo animal management. *Zoo Biol.* 28, 574–588.
549 <https://doi.org/10.1002/zoo.20288>

550 Mellor, D.J., Hunt, S., Gusset, M. (Eds.), 2015. *Caring for wildlife: the world zoo and aquarium*
551 *animal welfare strategy*. WAZA Executive Office, Gland, Switzerland.

552 Morris, P., Doe, C., Godsell, E., 2008. Secondary emotions in non-primate species? Behavioural
553 reports and subjective claims by animal owners. *Cogn. Emot.* 22, 3–20.
554 <https://doi.org/10.1080/02699930701273716>

555 O’connor, B.P., 2000. SPSS and SAS programs for determining the number of components
556 using parallel analysis and Velicer’s MAP test. *Behav. Res. Methods, Instruments,*
557 *Comput.* 32, 396–402. <https://doi.org/10.3758/BF03200807>

558 O’Connor, L.E., Berry, J.W., Landau, V., King, J., Pederson, A., Weiss, A., Silver, D., 2001.
559 Chimpanzee psychopathology and subjective well-being and social adjustment, in:
560 Landau, V. (Ed.), *ChimpanZoo 2000. ChimpanZoo: Research, Education and Enrichment*
561 *Program, Tucson, AZ*, pp. 24–32.

562 Pearson, H.C., 2011. Sociability of female bottlenose dolphins (*Tursiops* spp.) and chimpanzees
563 (*Pan troglodytes*): Understanding evolutionary pathways toward social convergence. *Evol.*
564 *Anthropol. Issues, News, Rev.* 20, 85–95. <https://doi.org/10.1002/evan.20296>

565 Prado-Martinez, J., Sudmant, P.H., Kidd, J.M., Li, H., Kelley, J.L., Lorente-Galdos, B.,
566 Veeramah, K.R., Woerner, A.E., O’Connor, T.D., Santpere, G., Cagan, A., Theunert, C.,
567 Casals, F., Laayouni, H., Munch, K., Hobolth, A., Halager, A.E., Malig, M., Hernandez-
568 Rodriguez, J., Hernando-Herraez, I., Prüfer, K., Pybus, M., Johnstone, L., Lachmann, M.,
569 Alkan, C., Twigg, D., Petit, N., Baker, C., Hormozdiari, F., Fernandez-Callejo, M., Dabad,

570 M., Wilson, M.L., Stevison, L., Camprubí, C., Carvalho, T., Ruiz-Herrera, A., Vives, L.,
571 Mele, M., Abello, T., Kondova, I., Bontrop, R.E., Pusey, A., Lankester, F., Kiyang, J.A.,
572 Bergl, R.A., Lonsdorf, E., Myers, S., Ventura, M., Gagneux, P., Comas, D., Siegismund,
573 H., Blanc, J., Agueda-Calpena, L., Gut, M., Fulton, L., Tishkoff, S.A., Mullikin, J.C.,
574 Wilson, R.K., Gut, I.G., Gonder, M.K., Ryder, O.A., Hahn, B.H., Navarro, A., Akey, J.M.,
575 Bertranpetit, J., Reich, D., Mailund, T., Schierup, M.H., Hvilsom, C., Andrés, A.M., Wall,
576 J.D., Bustamante, C.D., Hammer, M.F., Eichler, E.E., Marques-Bonet, T., 2013. Great ape
577 genetic diversity and population history. *Nature* 499, 471–475.
578 <https://doi.org/10.1038/nature12228>

579 Reiss, D., Marino, L., 2001. Mirror self-recognition in the bottlenose dolphin: A case of
580 cognitive convergence. *Proc. Natl. Acad. Sci.* 98, 5937–5942.
581 <https://doi.org/https://doi.org/10.1073/pnas.101086398>

582 Rendell, L., Whitehead, H., 2001. Culture in whales and dolphins. *Behav. Brain Sci.* 24, 309–
583 324. <https://doi.org/https://doi.org/10.1017/S0140525X0100396X>

584 Robinson, L.M., Altschul, D.M., Wallace, E.K., Úbeda, Y., Llorente, M., Machanda, Z.,
585 Slocombe, K.E., Leach, M.C., Waran, N.K., Weiss, A., 2017. Chimpanzees with positive
586 welfare are happier, extraverted, and emotionally stable. *Appl. Anim. Behav. Sci.* 191.
587 <https://doi.org/10.1016/j.applanim.2017.02.008>

588 Robinson, L.M., Waran, N.K., Leach, M.C., Morton, F.B., Paukner, A., Lonsdorf, E., Handel,
589 I., Wilson, V.A.D., Brosnan, S.F., Weiss, A., 2016. Happiness is positive welfare in brown
590 capuchins (*Sapajus apella*). *Appl. Anim. Behav. Sci.* 181, 145–151.
591 <https://doi.org/10.1016/j.applanim.2016.05.029>

592 Rollin, B.E., 2006. *Science and Ethics*. Cambridge University Press, Cambridge.
593 <https://doi.org/10.1017/CBO9780511617218>

594 Rousing, T., Wemelsfelder, F., 2006. Qualitative assessment of social behaviour of dairy cows
595 housed in loose housing systems. *Appl. Anim. Behav. Sci.* 101, 40–53.

596 <https://doi.org/10.1016/j.applanim.2005.12.009>

597 Sandvik, E., Diener, E., Seidlitz, L., 1993. Subjective Well-Being: The Convergence and
598 Stability of Self-Report and Non-Self-Report Measures. *J. Pers.* 61, 317–342.
599 <https://doi.org/10.1111/j.1467-6494.1993.tb00283.x>

600 Schaefer, S.A., Steklis, H.D., 2014. Personality and subjective well-being in captive male
601 western lowland gorillas living in bachelor groups. *Am. J. Primatol.* 76, 879–889.
602 <https://doi.org/10.1002/ajp.22275>

603 Shrout, P.E., Fleiss, J.L., 1979. Intraclass correlations: Uses in assessing rater reliability.
604 *Psychol. Bull.* 86, 420–428. <https://doi.org/10.1037/0033-2909.86.2.420>

605 Simpson, E.A., Robinson, L.M., Paukner, A., 2019. Infant rhesus macaque (*Macaca mulatta*)
606 personality and subjective well-being. *PLoS One* 14, e0226747.
607 <https://doi.org/10.1371/journal.pone.0226747>

608 Steel, P., Schmidt, J., Shultz, J., 2008. Refining the relationship between personality and
609 subjective well-being. *Psychol. Bull.* 134, 138–161.
610 <https://doi.org/https://doi.org/10.1037/0033-2909>

611 Stevenson-Hinde, J., Zunz, M., 1978. Subjective assessment of individual rhesus monkeys.
612 *Primates* 19, 473–482. <https://doi.org/10.1007/BF02373309>

613 Tomasello, M., Call, J., 1997. *Primate cognition*. Oxford University Press, New York.

614 Úbeda, Y., Fatjó, J., Rostán, C., Crailsheim, D., Gomara, A., Almunia, J., Llorente, M., 2020. A
615 preliminary investigation on the evaluation of psychopathologies in a group of ex-pet and
616 ex-performer chimpanzees (*Pan troglodytes*): A rating approach based on the Diagnostic
617 and Statistical Manual of Mental Disorders (DSM). *J. Vet. Behav.*
618 <https://doi.org/10.1016/j.jveb.2020.08.006>

619 Úbeda, Y., Ortín, S., Leger, J.S., Llorente, M., Almunia, J., 2018. Personality in captive Killer
620 Whales (*Orcinus orca*): A rating approach based on the five-factor model. *J. Comp.*

621 Psychol. 133, 252–261. <https://doi.org/10.1037/com0000146>

622 Vazire, S., Gosling, S.D., Schapiro, S.J., 2007. Measuring Personality in Animals, in: Robins,
623 R.W., Fraley, R.C., Krueger, R. (Eds.), Handbook of Research Methods in Personality
624 Psychology. The Guilford Press, New York, pp. 190–206.

625 Weinstein, T.A., Capitanio, J.P., Gosling, S.D., 2008. Personality in animals, in: John, O.P.,
626 Robins, R.W., Pervin, L.A. (Eds.), Handbook of Personality: Theory and Research. The
627 Guilford Press, New York, pp. 328–348.

628 Weiss, A., Adams, M.J., King, J.E., 2011a. Happy orang-utans live longer lives. Biol. Lett. 7,
629 872–874. <https://doi.org/10.1098/rsbl.2011.0543>

630 Weiss, A., Adams, M.J., Widdig, A., Gerald, M.S., 2011b. Rhesus Macaques (*Macaca mulatta*)
631 as Living Fossils of Hominoid Personality and Subjective Well-Being. J. Comp. Psychol.
632 125, 72–83. <https://doi.org/10.1037/a0021187>

633 Weiss, A., Inoue-Murayama, M., Hong, K.W., Inoue, E., Udono, T., Ochiai, T., Matsuzawa, T.,
634 Hirata, S., King, J.E., 2009. Assessing chimpanzee personality and subjective well-being
635 in japan. Am. J. Primatol. 71, 283–292. <https://doi.org/10.1002/ajp.20649>

636 Weiss, A., King, J.E., Enns, R.M., 2002. Subjective well-being is heritable and genetically
637 correlated with Dominance in chimpanzees (*Pan troglodytes*). J. Pers. Soc. Psychol. 83,
638 1141–1149. <https://doi.org/10.1037/0022-3514.83.5.1141>

639 Weiss, A., King, J.E., Murray, L. (Eds.), 2011c. Personality and Temperament in Nonhuman
640 Primates. Springer-Verlag, New York.

641 Weiss, A., King, J.E., Perkins, L., 2006. Personality and subjective well-being in orangutans
642 (*Pongo pygmaeus* and *Pongo abelii*). J. Pers. Soc. Psychol. 90, 501–511.
643 <https://doi.org/10.1037/0022-3514.90.3.501>

644 Weiss, A., Yokoyama, C., Hayasi, T., Inoue-Murayama, M., 2020. Personality, subjective well-
645 being, and the serotonin 1a receptor gene in common marmosets (*Callithrix jacchus*).

646 bioRxiv 2020.04.30.069773. <https://doi.org/https://doi.org/10.1101/2020.04.30.069773>

647 Wemelsfelder, F., 2007. How animals communicate quality of life: The qualitative assessment
648 of behaviour. *Anim. Welf.* 16, 25–31.

649 Whiten, A., 2000. Chimpanzee cognition and the question of mental re-representation, in:
650 Sperber, D. (Ed.), *Meta-Representations*. Oxford University Press, New York, pp. 139–
651 167.

652 Whitham, J.C., Wielebnowski, N., 2013. New directions for zoo animal welfare science. *Appl.*
653 *Anim. Behav. Sci.* 147, 247–260. <https://doi.org/10.1016/j.applanim.2013.02.004>

654 Whitham, J.C., Wielebnowski, N., 2009. Animal-based welfare monitoring: using keeper
655 ratings as an assessment tool. *Zoo Biol.* 28, 545–560. <https://doi.org/10.1002/zoo.20281>

656 Wojciechowska, J.I., Hewson, C.J., Stryhn, H., Guy, N.C., Patronek, G.J., Timmons, V., 2005.
657 Development of a discriminative questionnaire to assess nonphysical aspects of quality of
658 life of dogs. *Am. J. Vet. Res.* 66, 1453–1460. <https://doi.org/10.2460/ajvr.2005.66.1453>

659 Wolfensohn, S., Sharpe, S., Hall, I., Lawrence, S., Kitchen, S., Dennis, M., 2015. Refinement of
660 welfare through development of a quantitative system for assessment of lifetime
661 experience. *Anim. Welf.* 24, 139–149. <https://doi.org/10.7120/09627286.24.2.139>

662

663

664 Table 1

665 *Inter-rater reliabilities of welfare' items*

Item	ICC(3,1)	ICC(3,k)
1. Good physical condition	.37	.97
2. Good feeding habit	.10	.85
3. Good health	.45	.98
4. Present injuries	.43	.97
5. Environment inspection	.37	.97
6. Abnormal behavior	.31	.96
7. Stereotypical behavior	.19	.92
8. Self-injury behavior	.49	.98
9. Species-typical behavior	.20	.92
10. Threatening/dominant displays	.59	.99
11. Receive aggressive behaviors	.40	.97
12. Perform aggressive behaviors	.42	.97
13. Enjoys environmental enrichment	.53	.98
14. Likes changing enclosure	.46	.98
15. Likes changing group	.57	.98
16. Attachment to objects	.47	.98
17. Enclosure exploration	.21	.93
18. Breaching behavior	.52	.98
19. Motionless behavior	.54	.98
20. Problem solving	.08	.82
21. Frustration and stress	.60	.99
22. Self-directed behavior	.08	.80
23. Novelty acceptance	.79	.99
24. Social integration	.35	.96
25. Active affiliative context	.07	.79
26. Passive affiliative context	.51	.98
27. Avoids contact with conspecifics	.61	.99
28. Isolation	.55	.98
29. Playful engagement	.50	.98
30. Demanded to play	.49	.98
31. Normal sexual response	.31	.96
32. Vocalization	.24	.94
33. Seeks trainer attention	.45	.98
34. Dependency on humans	.38	.97
35. Adapts to routine	.56	.98
36. Collaboration in management	.51	.98
37. Interacts Humans > Conspecifics	.58	.99
38. Happy individual	.62	.99
39. Good Welfare	.22	.93

666 *Note.* First column indicates numbers and abbreviations of welfare items. Welfare items can be
667 consulted on supplementary materials.

668

669 Table 2

670 *Inter-rater reliabilities of subjective well-being items*

Item	ICC(3,1)	ICC(3,k)
1. Happy	.37	.97
2. Social interactions	.55	.98
3. Achieve goals	.35	.96
4. Be killer whale	.46	.98

671 Note: Item numbers and abbreviations refer sequentially to the four items described in

672 *Subjective Well-being Questionnaire* Section.

	Principal Component Analysis						Regularized Exploratory Factor					
	F1	F2	F3	F4	F5	F6	F1	F2	F3	F4	F5	F6
5. Environment inspection	.83	.08	.02	.07	-.08	.00	.81	.02	.14	.00	-.10	.00
13. Enjoy environmental enrichment	.72	.01	.10	.03	.12	.20	.67	-.02	.20	-.01	.09	.19
17. Enclosure exploration	.63	.34	-.04	-.03	-.17	.09	.61	.32	.07	-.07	-.11	.05
19. Motionless behavior	-.62	-.04	.56	.09	-.08	.10	-.67	.00	.39	.28	-.16	.14
16. Attachment to objects	-.62	-.02	.48	.05	-.06	-.03	-.64	-.01	.32	.21	-.13	.00
23. Novelty acceptance	.60	.04	-.26	.19	-.04	-.06	.61	.01	-.19	.05	-.02	-.04
35. Adapts to routine	.57	-.03	.16	.04	-.08	-.08	.46	-.03	.16	.02	-.08	-.02
14. Likes changing enclosure	.56	.40	.00	.25	.04	.13	.60	.32	.06	.19	.05	.05
15. Likes changing group	.47	.32	-.18	.13	.12	.30	.51	.28	-.09	.05	.15	.18
28. Isolation	-.09	-.80	-.01	.23	.06	.14	-.12	-.76	-.15	.14	-.03	.31
29. Playful engagement	.19	.74	-.10	-.07	-.32	-.11	.24	.72	-.03	-.06	-.22	-.24
27. Avoids contact with conspecifics	.18	-.64	-.15	.23	.11	-.02	.15	-.60	-.20	.12	.05	.11
25. Active affiliative context	.12	.62	.05	-.08	-.23	.38	.16	.65	.10	-.05	-.12	.24
30. Demanded to play	.32	.61	.10	-.03	.05	-.27	.32	.46	.19	.01	.05	-.36
24. Social integration	.32	.52	.11	.23	.09	-.11	.35	.38	.11	.19	.07	-.17
26. Passive affiliative context	-.14	.44	-.09	.10	.19	-.31	-.04	.27	-.05	.09	.15	-.33
6. Abnormal behavior	-.28	-.17	.67	-.08	-.23	.13	-.38	-.12	.54	.05	-.31	.19
7. Stereotypical behavior	-.05	-.20	.62	-.15	-.13	-.03	-.18	-.16	.50	-.03	-.19	.05
22. Self-directed behavior	.14	.27	.59	-.25	.22	.01	.02	.19	.61	-.07	.15	-.04
8. Self-injury behavior	.07	.20	.58	-.10	.17	.08	-.01	.12	.53	.02	.07	.03
9. Species-typical behavior	.47	-.04	-.54	.21	.16	.16	.42	-.04	-.46	.02	.22	.14
4. Present injuries	.27	.09	.38	-.16	.05	-.04	.14	.06	.36	-.06	.01	-.03
1. Good physical condition	.15	-.04	-.27	.74	.08	-.13	.28	-.12	-.39	.59	.03	-.10
39. Good Welfare	.24	-.04	-.37	.64	-.11	.21	.37	-.02	-.41	.44	-.09	.23
3. Good health	-.04	-.21	-.12	.62	.05	-.34	.05	-.28	-.27	.47	-.02	-.22
38. Happy individual	.19	.22	-.24	.52	-.12	.42	.31	.25	-.32	.35	-.06	.35
2. Good feeding habit	-.25	-.19	.28	.50	.41	.05	-.21	-.27	.11	.48	.27	.09
31. Normal sexual response	.36	-.17	-.21	.49	-.11	.43	.43	-.10	-.30	.31	-.09	.47
21. Frustration and stress	.16	-.01	-.21	-.02	.71	.18	.17	-.06	-.07	.01	.69	.13
12. Performs aggressive behaviors	.07	.01	-.39	-.11	.59	.18	.10	.00	-.22	-.09	.60	.10
11. Receives aggressive behaviors	.14	.34	-.11	-.04	-.59	.06	.17	.38	-.10	-.11	-.46	.01
10. Threatening/dominant displays	-.02	-.37	.21	-.03	.56	-.05	-.09	-.40	.21	.06	.43	.01
36. Collaboration in Management	.16	-.15	-.02	.37	-.52	.16	.19	-.06	-.17	.21	-.45	.22
18. Breaching behavior	.05	.04	.00	.14	.45	-.02	.08	-.07	.02	.12	.32	-.05
32. Vocalize	.24	.33	-.22	.14	-.39	.38	.31	.40	-.21	.03	-.27	.28
34. Dependency on Humans	.07	-.19	-.06	.05	.06	.67	.08	-.08	-.07	-.01	.07	.57
20. Problem solving	.08	.04	-.06	.07	-.11	-.47	.06	.01	-.07	.04	-.08	-.31
37. Interacts Humans > Conspecifics	.30	-.37	.11	.19	-.12	.45	.25	-.25	.02	.10	-.12	.49
33. Seeks trainer attention	-.35	.03	.23	-.20	-.07	.37	-.35	.10	.19	-.10	-.05	.27

675 Note. First column indicates numbers and abbreviations of welfare items. Welfare items can be
 676 consulted on supplementary materials.

677 Note. Boldface indicates salient loadings

678

679 Table 4
 680 *Correlations between P.C.A. and R.E.F.A. for the Welfare questionnaire*

	P.C.A.					
	Confidence	Sociability	Abnormal	Over. welf.	Nervous.	Self-suffic.
R.E.F.A.						
Confidence	.98	.29	-.59	.21	-.09	.08
Sociability	.23	.98	-.06	-.30	-.35	.02
Abnormal	-.29	.12	.95	-.68	.05	-.14
Over. Welf.	-.22	-.28	-.16	.91	.05	-.10
Nervous.	.04	-.10	-.20	-.07	.97	-.05
Self-suffic.	-.00	-.43	-.09	.13	-.14	.94

681 *Note:* Over. welf. = Overall welfare; Nervous. = Nervousness; Self-suffic. = Self-sufficiency

682 *Note:* Boldface indicates salient loadings

683

684
685
686
687

Table 5
Factor intercorrelation matrix for the factor obtained for the Welfare questionnaire

Factor	Confidence	Sociability	Abnormal	Over. welf.	Nervous.	Self-suffic.
Confidence	-					
Sociability	.29	-				
Abnormal.	-.39	-.14	-			
Over. Welf.	.26	-.10	-.22	-		
Nervous.	-.03	-.11	.04	-.06	-	
Self-suffic.	.33	.12	-.20	.28	-.25	-

Note: Over. welf. = Overall welfare; Nervous. = Nervousness; Self-suffic. = Self-sufficiency

688 Table 6

689 *Correlation between Personality and Welfare factors*

	Extraversion	Conscien-Agree	Dominance	Careful
Confidence	.82	-.42	.64	-.43
95%CI	[.54, .99]	[.89, -.04]	[.43, 1.30]	[-4.18, -.27]
Sociability	.22	-.06	.26	-.73
95%CI	[-.15, .50]	[-.46, .34]	[-.17, .77]	[-4.46, -1.92]
Abnormal	-.31	.07	-.60	-.25
95%CI	[-.36, .05]	[-.21, .29]	[-.69, -.20]	[-1.85, .44]
Over. welf.	.20	-.12	.17	.44
95%CI	[-.05, .14]	[-.15, .08]	[-.08, .19]	[.07, 1.03]
Nervousness	.37	-.55	-.57	-.00
95%CI	[-.01, .30]	[-.42, -.09]	[.12, .51]	[-.91, .90]
Self-suffic.	-.15	-.15	-.20	.21
95%CI	[-.21, .10]	[-.25, .12]	[-.34, .11]	[-.42, 1.29]

690 Note: Over. welf. = Overall welfare; Self-suffic. = Self-sufficiency; Conscien-Agree. =
 691 Conscien-Agreeableness

692 *Note.* Boldface correlations are significant at $p < 0.01$

693

694 Table 7

695 *Correlation between personality factors and subjective well-being factor*

	Extraversion	Conscien-Agree	Dominance	Careful
SWB	.62	-.31	.61	-.04
95%CI	[.02, .06]	[-.06, .01]	[.03, .09]	[-.17, .14]

696 Note: Conscien-Agree. = Conscien-Agreeableness

697 Note. Boldface correlations are significant at $p < 0.01$

698

699 Table 8

700 *Correlation between welfare factors and subjective well-being factor*

	Confidence	Sociability	Abnormal	Over. welf.	Nervousness	Self-suffic.
SWB	.71	-.20	-.73	.46	-.66	.29
95%CI	[.03, .07]	[-.05, .02]	[-.13, -.06]	[.03, .25]	[.06, .17]	[-.02, .12]

701 *Note:* Over. welf. = Overall welfare; Self-suffic. = Self-sufficiency

702 *Note:* Boldface correlations are significant at $p < 0.01$

703

704 **Supplementary materials (Welfare questionnaire)**

705 This questionnaire has thirty-nine questions, all relating to the welfare of the killer whales at
706 your zoo. The following scale should be used to make your ratings.

- 707 1. Displays either total absence or negligible amounts of the trait or state.
708 2. Displays small amounts of the trait on infrequent occasions.
709 3. Displays somewhat less than average amounts of the trait.
710 4. Displays about average amounts of the trait.
711 5. Displays somewhat greater than average amounts of the trait.
712 6. Displays considerable amounts of the trait on frequent occasions.
713 7. Displays extremely large amounts of the trait.

714 Please give a rating for each item even if your judgment seems to be based on a purely
715 subjective impression of the killer whale and you are somewhat unsure about it. Indicate your
716 rating by placing a cross in the box underneath the chosen number.

717 Finally, do not discuss your rating of any particular killer whale with anyone else, because this
718 restriction is necessary in order to obtain valid reliability coefficients for the traits.

719 -----

720 Killer whale' name:

721 Rater' name:

722 Date:

- 723 1. The killer whale has a good physical condition and a healthy appearance (color,
724 pigmentation/discoloration, fin shape, constitution/weight)

Least 1 2 3 4 5 6 7 Most

- 725 2. The killer whale has good feeding habits (food intake quantity, variety of foods, accepts all
726 meals or doses provided, accepts/rejects certain foods)

Least 1 2 3 4 5 6 7 Most

- 727 3. The killer whale is in good health (no chronic illnesses or tendency to catch illnesses)

Least 1 2 3 4 5 6 7 Most

- 728 4. The killer whale often shows visible physical injuries

Least 1 2 3 4 5 6 7 Most

- 729 5. The killer whale inspects the elements of its environment and enclosure

Least 1 2 3 4 5 6 7 Most

- 730 6. The killer whale shows abnormal and/or non-desirable behaviors

Least 1 2 3 4 5 6 7 Most

731 7. The killer whale shows stereotypies or frequent and repetitive behaviors [vomiting, pacing
732 (circling swim), biting on gates and bars, tongue playing, bobbing up and down, others...]

Least 1 2 3 4 5 6 7 Most

733 8. The killer whale shows self-injury behavior

Least 1 2 3 4 5 6 7 Most

734 9. The killer whale shows species-typical behaviors

Least 1 2 3 4 5 6 7 Most

735 10. The killer whale often performs jaw-popping and shows other threatening or dominant
736 displays towards other group members

Least 1 2 3 4 5 6 7 Most

737 11. The members of the group shows aggressive behaviors towards the killer whale

Least 1 2 3 4 5 6 7 Most

738 12. The killer whale shows aggressive behaviors towards other members of the group

Least 1 2 3 4 5 6 7 Most

739 13. The killer whale interacts and enjoys the environmental enrichment

Least 1 2 3 4 5 6 7 Most

740 14. The killer whale shows an interest in changing enclosure

Least 1 2 3 4 5 6 7 Most

741 15. The killer whale shows interest in changing the social configuration of the group

Least 1 2 3 4 5 6 7 Most

742 16. The killer whale has a special attachment to objects and struggles to separate from them

Least 1 2 3 4 5 6 7 Most

743 17. The killer whale explores and moves throughout the entire enclosure

Least 1 2 3 4 5 6 7 Most

744 18. The killer whale tends to breach

Least 1 2 3 4 5 6 7 Most

745 19. The killer whale tends to lay motionless at the bottom of the pool or floating at the surface
746 (logging behavior)

Least 1 2 3 4 5 6 7 Most

747 20. The killer whale is creative, proactive, and able to solve problems

Least 1 2 3 4 5 6 7 Most

748 21. The killer whale often gets frustrated and stressed out easily

Least 1 2 3 4 5 6 7 Most

749 22. The killer whale often performs self-directed behavior such as scratching (scratching against
750 the wall)

Least 1 2 3 4 5 6 7 Most

751 23. The killer whale accepts novelty well (new enrichments, new foods, new trainers)

Least 1 2 3 4 5 6 7 Most

752 24. The killer whale is integrated into its social group

Least 1 2 3 4 5 6 7 Most

753 25. The killer whale is actively involved in affiliative context (proactive behavior)

Least 1 2 3 4 5 6 7 Most

754 26. The killer whale is often passive in affiliative context (reactive behavior)

Least 1 2 3 4 5 6 7 Most

- 755 27. The killer whale avoids any contact with members of its group
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 756 28. The killer whale tends to be isolated from other group members
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 757 29. The killer whale engages in playful interactions
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 758 30. The killer whale is usually solicited by other group members for playing
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 759 31. The killer whale shows normal sexual responses (no aberrations or lack of response)
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 760 32. The killer whale tends to vocalize
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 761 33. The killer whale seeks the attention of his/her trainer
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 762 34. The killer whale has a high dependence on humans
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 763 35. The killer whale adapts and accepts the routine of the zoo
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 764 36. The killer whale collaborates in trainer management
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most
- 765 37. The killer whale often interacts more with humans than with other killer whales of its group
- Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most

766 38. The killer whale is overall a happy individual

Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most

767 39. The killer whale's welfare is overall good

Least ¹ ² ³ ⁴ ⁵ ⁶ ⁷ Most

768

769

770

771

772