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**Comparison of Subjective Well-Being and Personality Assessments in the Clouded
Leopard (*Neofelis nebulosa*), Snow Leopard (*Panthera uncia*), and African Lion
(*Panthera leo*)**

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The study of subjective well-being in nonhuman animals is growing in the field of psychology, but there are still only a few published studies, and the focus is on primates. To consider whether the construct of subjective well-being could be found in another mammal, this study aimed to assess subjective well-being in felids, and to examine its association with personality. Personality is one of the strongest and most consistent predictors of well-being in humans. This relationship could have important implications for other species, since personality has also been shown to affect health outcomes including stress, morbidity, and mortality. As in previous studies in nonhuman animals, we found that subjective well-being was related to Agreeableness/Openness and Neuroticism in clouded leopards, Neuroticism in snow leopards, and Impulsiveness and Neuroticism in African lions. The implications of these results for health outcomes and captive animal welfare are discussed. More research on any direct links between personality, subjective well-being, and these outcomes is important to advancing this field and adding another tool for improving captive animals' lives.

keywords: well-being, personality, felids

The study of subjective well-being in nonhuman animals has been increasing in the field of psychology. These studies, based on decades of work in humans, mostly focus on primates. Because of the relationship between well-being and health outcomes and personality shown in humans and non-human primates, subjective well-being may prove to be an important aspect of captive management for primates, as well as other species.

Subjective well-being, or happiness, is composed of four components: pleasant and unpleasant affect; life satisfaction; and satisfaction with specific domains, such as work, family, and health (DeNeve & Cooper, 1998; Steel et al., 2008). It is most often measured via self-report survey, or, in animals, caretakers fill out surveys about animals they know.

Subjective well-being is tied to human personality (e.g., DeNeve & Cooper, 1998; Costa & McCrae, 1980), and is associated with positive life events (Lyubomirsky et al., 2005) and longevity and morbidity (Diener & Chan, 2011). It is related to personality in primates (e.g., King & Landau, 2003) and Scottish wildcats (*Felis silvestris grampia*; Gartner & Weiss, 2013), and to longevity in orangutans (*Pongo abelii* and *Pongo pygmaeus*; Weiss, Adams, & King, 2011).

In addition, subjective well-being is heritable in humans (Bartels & Boomsma, 2009); chimpanzees (*Pan troglodytes*), in whom it is genetically correlated with Dominance (Weiss et al., 2002); and orangutans (Adams et al., 2012). It is also genetically correlated with personality in humans (Weiss et al., 2008). Because of these associations, understanding the relationship between subjective well-being and personality in captive populations has the potential to improve husbandry and increase health, welfare, and longevity in species that are often endangered, and are not adapted to captivity. For example, large carnivores' natural range size impacts their reactions to captivity in terms of limiting natural behaviors (Clubb & Mason, 2003).

Following a study that showed a relationship between personality and subjective well-being in Scottish wildcats (Gartner & Weiss, 2013), this research aimed to assess if any similar relationships exist in other felids. We assessed subjective well-being, and then compared it with the personality structures (reported in Gartner et al., 2014) of the clouded leopard (*Neofelis nebulosa*), which is the basal species of the genus *Panthera* (Wei et al., 2011), and the two species last to diverge in that genus: the snow leopard (*Panthera uncia*) and their phylogenetic sister species (Wei et al., 2011), the African lion (*Panthera leo*). We expected to find a relationship between subjective well-being and personality in each species, as has been found in Scottish wildcats (Gartner & Weiss, 2013), as well as in primates (Weiss et al., 2006; Weiss et al., 2009; Weiss, et al., 2011). In general, personality factors relating to negative affect, such as Neuroticism, should have a negative association with subjective well-being, while those related to positive affect, such as Agreeableness, should have a positive one.

MATERIALS AND METHODS

Species and Rater Information

All the zoos involved and the University of Edinburgh gave ethical approval for this research. Caretakers were required to have at least three months of experience with the animals in their care.

Clouded leopards and raters

Subjects included 16 clouded leopards from two zoos. The ages of the subjects ranged from 6 months to 9.58 years ($M = 4.77 \pm 3.39 SD$). There were 11 clouded leopards (5 males; 6 females) at Nashville Zoo (NZ) in Nashville, TN; and 5 clouded leopards (2 males; 3 females) at Port Lympne Wild Animal Park (PL) in Lympne, Kent, United Kingdom. Seven caretakers rated the clouded leopards (NZ: $n = 4$, PL: $n = 3$).

Snow leopards and raters

Subjects included 17 snow leopards from three zoos. The ages of the subjects ranged from 1 to 15 years old ($M = 6.56 \pm 4.68 SD$). There were 11 snow leopards (6 males; 5 females) at the Bronx Zoo (BZ) in Bronx, New York; 4 snow leopards (3 males; 1 female) at ABQ BioPark (ABQ) in Albuquerque, New Mexico; and 2 snow leopards (1 male; 1 female) at Norden's Ark (NA) in Bohuslän, Sweden. Nine caretakers rated the snow leopards (BZ: $n = 6$, ABQ: $n = 2$, NA: $n = 1$).

African lions and raters

Subjects included 21 African lions from two zoos. The ages of the subjects ranged from 3 to 15 years old ($M = 11.52 \pm 3.39 SD$). There were 13 lions (3 males; 10 females) at Lion Country Safari (LCS) in Loxahatchee, Palm Beach County, Florida; and 8 lions (2 males; 6 females) at West Midland Safari Park (WMSP) in Bewdley, Worcestershire, United Kingdom. Seven caretakers rated the African lions (LCS: $n = 3$; WMSP: $n = 4$).

Procedure

The four-item subjective well-being survey was modeled on the one developed for chimpanzees by King and Landau (2003), and altered to include a fifth item that addressed solitary versus multi-animal enclosures. As a result, there were two social interaction items: one that accounted for animals being housed alone by assessing interactions with human caretakers, and one that assessed interactions with conspecifics. Another item assessed the balance of positive and negative affect. An additional item measured personal control, asking whether the cat was effective in achieving his or her goals. Finally, the last item asked how happy the rater would be being the specific cat being rated (Table 1). These items were rated on a seven-point Likert scale, where 1 was "least" and 7 was "most."

Table 1

Analyses

Analyses were carried out using IBM SPSS 19 for Macintosh, unless otherwise noted. Inter-rater reliabilities were calculated using the intraclass correlation coefficients $ICC(3,1)$ (the reliability of individual ratings) and $ICC(3,k)$ (the reliability of the mean ratings of k raters) (Shrout & Fleiss, 1979). Items that were not reliable, defined as having an $ICC(3,1)$ and/or an $ICC(3,k)$ less than or equal to zero were omitted from further analyses. Each $ICC(3,1)$ was compared across species.

We ran parallel analyses, as well as examined scree plots, to determine the number of components to extract (Horn, 1965; O'Connor, 2000). We followed these analyses with principal components analyses. As in previous studies (e.g., Gartner & Weiss, 2013), we defined factor loadings $\geq |0.4|$ as salient for the principal components analyses. Items with multiple salient loadings were assigned to the factor with the highest loading. Based on these loadings, we created unit-weighted factor scores (Gorsuch, 1983), which we then transformed into z -scores.

We correlated subjective well-being with personality factors reported previously (Gartner et al., 2014). All analyses were calculated for each species, and then for all the species combined, along with Scottish wildcat well-being data (from Gartner & Weiss, 2013) to assess whether subjective well-being could be assessed on the taxon level.

RESULTS

Inter-Rater Reliability

Clouded leopards

The reliabilities of individual ratings of subjective well-being, $ICC(3,1)$, were .40 (ability to achieve goals), .61 (pleasure from social interactions with other clouded leopards), .62 (moods), .66 (be the clouded leopard), and .86 (pleasure from social interactions with

people). The reliabilities of mean ratings, $ICC(3,k)$, were .70 (ability to achieve goals), .85 (pleasure from social interactions with other clouded leopards), .85 (moods), .87 (be the clouded leopard), and .96 (pleasure from social interactions with people).

Snow leopards

The reliabilities of individual ratings of subjective well-being, $ICC(3,1)$, were .16 (pleasure from social interactions with people), .18 (ability to achieve goals), .21 (be the snow leopard), .51 (pleasure from social interactions with other snow leopards), and .51 (moods). The reliabilities of mean ratings, $ICC(3,k)$, were .53 (pleasure from social interactions with people), .57 (ability to achieve goals), .61 (be the snow leopard), .86 (pleasure from social interactions with other snow leopards), and .86 (moods).

African lions

The reliabilities of individual ratings of subjective well-being, $ICC(3,1)$, were .30 (be the lion), .36 (pleasure from social interactions), .37 (ability to achieve goals), and .37 (moods). The reliabilities of mean ratings, $ICC(3,k)$, were .52 (be the lion), .59 (pleasure from social interactions), .60 (ability to achieve goals), and .60 (moods).

Taxon

The reliabilities of individual ratings of subjective well-being, $ICC(3,1)$, were .29 (ability to achieve goals), .40 (be the cat), .46 (pleasure from social interactions with conspecifics), .49 (moods), and .70 (pleasure from social interactions with people). The reliabilities of mean ratings, $ICC(3,k)$, were .57 (ability to achieve goals), .68 (be the cat), .74 (pleasure from social interactions with conspecifics), .76 (moods), and .88 (pleasure from social interactions with people).

Principal Components Analysis

Clouded leopards

Principal components and parallel analysis and examination of the scree plot indicated that one factor accounting for 83.81% of the variance was described by the ratings for all items (see Table 2 for all species' PCA results). The reliability of individual ratings, $ICC(3,1)$, was .82, and the reliability of mean ratings, $ICC(3,k)$, was .94.

Table 2

Snow leopards

Principal components and parallel analysis and examination of the scree plot indicated that one factor accounting for 83.64% of the variance was described by the ratings for all items. The reliability of individual ratings, $ICC(3,1)$, was .40, and the reliability of mean ratings, $ICC(3,k)$, was .80.

African lions

Principal components and parallel analysis and examination of the scree plot indicated that one factor accounting for 81.53% of the variance was described by the ratings for all items. The reliability of individual ratings, $ICC(3,1)$, was .51 and the reliability of mean ratings, $ICC(3,k)$, was .72.

Taxon

Principal components and parallel analysis and examination of the scree plot indicated that one factor accounting for 72.69% of the variance was described by the ratings for all items. The reliability of individual ratings, $ICC(3,1)$, was .67, and the reliability of mean ratings, $ICC(3,k)$, was .87.

Correlations between Personality Factors and Subjective Well-Being

In clouded leopards, subjective well-being was negatively correlated with the factor Neuroticism and positively correlated with the factor Agreeableness/Openness (see Table 3

for all species' correlations). In snow leopards, subjective well-being was negatively correlated with Neuroticism. Subjective well-being was negatively correlated with African lion Neuroticism and Impulsiveness.

Table 3 here

Subjective well-being did not correlate with any of the taxon personality factors. To better understand this result, we conducted additional analyses. We calculated the correlations between the individual traits and subjective well-being in each species, and then calculated the correlations between the individual traits and overall felid measure of subjective well-being (Table 4). Six traits were correlated with subjective well-being across three species: affectionate, calm, fearful of people, suspicious, tense, and trusting. Only insecure was the same across all four species. Each species except Scottish wildcats had traits that correlated with subjective well-being only within the species. For clouded leopards, these were cool, cooperative, friendly to conspecifics, and smart. For snow leopards, these were individualistic and predictable. For African lions, they were constrained, dominant, fearful of conspecifics, persevering, stable, submissive, and timid.

Table 4 here

DISCUSSION

Subjective well-being ratings were reliable across raters for all species. The reliabilities of the dimensions were similar to those found in humans (McCrae & Costa, 1987; Pavot & Diener, 1993), chimpanzees (Weiss et al., 2009), orangutans (Weiss et al., 2006), rhesus macaques (*Macaca mulatta*; Weiss et al., 2011), and brown capuchin monkeys (*Cebus apella*; Morton

et al., 2013), all of which were measured using a similar instrument. As expected, each felid species had one or more personality factors associated with subjective well-being. In all species, the factor Neuroticism was negatively related to subjective well-being.

There has been only one other study using this scale for well-being in cat species (Scottish wildcat: Gartner & Weiss, 2013), so a comparison to previous results is not applicable here. However, there are some similarities in the relationship between personality and well-being found in cat species and the relationship found in primates. The link between well-being and Neuroticism in clouded leopards, snow leopards, and African lions is not surprising, as it replicates results in humans—Neuroticism is the strongest predictor of well-being in humans (Steel et al., 2008)—and other primates (chimpanzees: Weiss et al., 2009; orangutans: Weiss et al., 2006; rhesus macaque Anxiety: Weiss et al., 2011; squirrel monkeys [*Saimiri boliviensis*]: Wilson, personal communication). Neuroticism is known to have a negative impact on health outcomes, from immunology to morbidity to mortality (Capitani, 2011; Deary et al., 2010), as well as mood disorders and anxiety (e.g., Clark et al., 1994), so it makes sense that that the result generalizes across multiple species.

Clouded leopard Agreeableness/Openness is positively related to well-being. This is again unsurprising, as related factors in other species have a similar relationship to well-being (humans: Steel et al., 2008, DeNeve & Cooper, 1998; chimpanzees: Weiss et al., 2009; orangutans: Weiss et al., 2006; gorilla Extraversion/Agreeableness: Schaefer & Steklis, 2014; rhesus macaque Friendliness: Weiss et al., 2011). Because Agreeableness was not related to well-being in Scottish wildcats, it is possible that the facets related to Openness were the ones driving the relationship in clouded leopards.

Although snow leopard Impulsiveness/Openness did not correlate with subjective well-being overall, two of the items that make up subjective well-being did. Both moods and pleasure derived from social interactions with people correlated with this personality factor.

This may be an artifact of the small sample size. Alternatively, it could be that the relationship between the item moods and well-being was reflecting the Openness aspect of the factor, as has been found in other species, while the item social interactions may reflect the importance of the keeper-animal relationship (Wielebnowski, 1999; Carlstead et al., 1999).

In African lions, well-being is negatively related to Impulsiveness. This may be due to its elements of low Conscientiousness, since Conscientiousness is known to impart protective aspects for human health (Deary et al., 2010) and is positively related to well-being in humans. Similarly, Scottish wildcat Self-Control, positively related to well-being, has elements of Conscientiousness and also low Neuroticism (Gartner & Weiss, 2013).

None of the overall taxon factors were related to overall subjective well-being. The differences in the relationship between traits and well-being in each species may offer clues as to why this may be. For example, clouded leopard traits that correlated with subjective well-being (cool, cooperative, friendly to conspecifics, and smart) indicate that positive interactions are important for their well-being, including those within their social structure and possibly with their human caretakers (friendly to conspecifics, cooperative). Snow leopards only had two traits that correlated with well-being—individualistic and predictable. This may indicate that environment is important for this species' well-being. African lion traits that correlated with subjective well-being seem to indicate that elements of their social structure are important for well-being, especially in terms of the dominance structure found in this species. Despite overall personality similarities in these species, these results hint at species differences in well-being.

These results have the potential to be useful to captive management, including increasing health and welfare. Well-being may be a good marker for health outcomes, as personality may be influencing health via subjective well-being. For example, captive

orangutans rated higher in subjective well-being experienced increased longevity compared to those rated lower (Weiss, Adams, & King, 2011). In addition, extraverted gorillas (*Gorilla gorilla gorilla*) have increased longevity (Weiss et al., 2013). This may be related to the fact that most of the variance in subjective well-being is due to personality, because of the association of Neuroticism with negative affect and Extraversion with positive affect (Costa & McCrae, 1980). Therefore, understanding personality and its relationship to well-being may allow for more targeted care for those individuals more at risk (those rated higher on personality factors negatively associated with subjective well-being), allowing for increased welfare and therefore the increase of natural behaviors. For example, since personality may influence how an animal responds to new environments, it is likely that subjective well-being may as well. This relationship, therefore, could be used to predict an animal's behavior in response to the design of exhibits, introduction to a social group, environmental enrichment, or even to zoo visitors (Powell & Gartner, 2011).

There is much room for future study on personality and its relationship to well-being, from replication in the current species to assessment in other felids, and other non-human animals. This would allow for further understanding of the evolution of personality and well-being in felids, as well as other species. There are few studies of animals that link subjective well-being to health outcomes including welfare directly—however, there is work in the farm animal welfare field that is related, although different methods are used (Wemelsfelder et al., 2001). For example, pigs housed on extensive farms were rated as more happy and lively than those housed in intensive conditions (Temple et al., 2011). This, then, is clearly an important area for future work. In addition, there has been no comparison with physiological or physical indicators in well-being studies using this measure; including this type of data might be useful in further elucidating well-being and its relationship to personality.

Further, recent studies in rats, dogs, rhesus macaques, and starlings have begun to show that, like humans, those animals' affective states may be judged from cognitive bias tests (tests that measure the influence of affect on cognitive processes, especially judgement; Mendl et al., 2009). It would be interesting, therefore, to look at the possibility of a relationship between the results of cognitive bias tasks and subjective well-being and personality. Finally, anticipatory behavior has been shown to be linked to both the dopaminergic and opioid systems of the brain (Spruijt et al., 2001), so it would be interesting to see if there are any links between subjective well-being and this type of behavior, especially in terms of its applications to captive management (Watters, 2014).

CONCLUSION

Subjective well-being can be measured reliably in felid species, and it is related to personality in similar ways as in primate species, including humans. Because of this relationship, it is likely that subjective well-being is also related to health and life outcomes in felids, which may have implications for captive management.

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REFERENCES

- Adams, M.J., King, J.E., & Weiss, A. (2012). The majority of genetic variation in orangutan personality and subjective well-being is nonadditive. *Behavior Genetics, 42*, 675-686.
- Bartels, M., & Boomsma, D.I. (2009). Born to be happy? The etiology of subjective well-being. *Behavior Genetics, 39*, 605-615.
- Capitanio, J.P. (2011). Nonhuman primate personality and immunity: Mechanisms of health and disease. In A. Weiss, J.E. King, & L. Murray (Eds.), *Personality and Temperament in Nonhuman Primates* (pp. 233-255). New York: Springer.
- Carlstead, K., Mellen, J., & Kleiman, D.G. (1999). Black rhinoceros (*Diceros bicornis*) in US zoos: I. Individual behavior profiles and their relationship to breeding success. *Zoo Biology, 18*, 17-34.
- Clark, L.A., Watson, D., & Mineka, S. (1994). Temperament, personality, and the mood and anxiety disorders. *Journal of Abnormal Psychology, 103*, 103-116.
- Clubb, R., & Mason, G. (2003). Captivity effects on wide-ranging carnivores. *Nature, 425*, 473-474. doi: 10.1038/425473a
- Costa, P.T. Jr., & McCrae, R.R. (1980). Influence of Extraversion and Neuroticism on subjective well-being: Happy and unhappy people. *Journal of Personality and Social Psychology, 38*, 668-678.
- Deary, I.J., Weiss, A., & Batty, G.D. (2010). Intelligence and personality as predictors of illness and death: How researchers in differential psychology and chronic disease epidemiology are collaborating to understand and address health inequalities. *Psychological Science in the Public Interest, 11*, 53-79.
- DeNeve, K.M., & Cooper, H. (1998). The happy personality: A meta-analysis of 137 personality traits and subjective well-being. *Psychological Bulletin, 124*, 197-229.

- Diener, E., & Chan, M.Y. (2011). Happy people live longer: Subjective well-being contributes to health and longevity. *Applied Psychology: Health and Well-Being*, 3, 1-43. doi: 10.1111/j.1758-0854.2010.01045.x
- Diener, E., Suh, E.M., Lucas, R.E., & Smith, H.L. (1999). Subjective well-being: Three decades of progress. *Psychological Bulletin*, 125, 276-302.
- Gartner, M.C., & Weiss, A. (2013). Scottish wildcat (*Felis silvestris grampia*) personality and subjective well-being: Implications for captive management. *Journal of Applied Animal Behaviour Science*, 147, 261-267.
- Gartner, M.C., Powell, D.M., & Weiss, A. (2014). Personality structure in five felids (*Felis silvestris catus*, *Felis silvestris grampia*, *Neofelis nebulosa*, *Panthera uncia*, and *Panthera leo*): A comparative study. *Journal of Comparative Psychology*, 128, 414-426.
- Gorsuch, R.L. (1983). *Factor Analysis* (2nd ed.). Hillsdale, NJ: Lawrence Erlbaum.
- Horn, J.L. (1965). A rationale and test for the number of factors in factor-analysis. *Psychometrika*, 30, 179-185.
- King, J.E., & Landau, V.I. (2003). Can chimpanzee (*Pan troglodytes*) happiness be estimated by human raters? *Journal of Research in Personality*, 37, 1-15. doi: 10.1016/S0092-6566(02)00527-5
- Lyubomirsky, S., King, L., & Diener, E. (2005). The benefits of frequent positive affect: Does happiness lead to success? *Psychological Bulletin*, 131, 803-855. doi: 10.1037/0033-2909.131.6.803
- McCrae, R.R., & Costa, P.T. Jr. (1987). Validation of the five-factor model of personality across instruments and observers. *Journal of Personality and Social Psychology*, 52, 81-90.

- Mendl, M., Burman, O.H.P., Parker, R.M.A., & Paul, E.S. (2009). Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science*, *118*, 161-181.
- Morton, F.B., Lee, P.C., Buchanan-Smith, H.M., Brosnan, S.F., Thierry, B., Paukner, A., de Waal, F.B.M., Widness, J., Essler, J.L., & Weiss, A. (2013). Personality structure in brown capuchin monkeys (*Sapajus apella*): Comparison with chimpanzees (*Pan troglodytes*), orangutans (*Pongo ssp.*), and Rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology*, *127*, 282-298. doi: 10.1037/a0031723
- O'Connor, B.P. (2000). SPSS and SAS programs for determining the number of components using parallel analysis and Velicer's MAP test. *Behavior Research Methods Instruments & Computers*, *32*, 396-402.
- Pavot, W., & Diener, E. (1993). The affective and cognitive context of self-reported measures of subjective well-being. *Social Indicators Research*, *28*, 1–20.
- Powell, D.M., & Gartner, M.C. (2011). Applications of personality to the management and conservation of nonhuman animals. In M. Inoue-Murayama, S. Kawamura, & A. Weiss (Eds.), *From genes to animal behavior: Social structures, personalities, communication by color* (pp. 185-199). Tokyo: Springer.
- Schaefer, S.A., & Steklis, H.D. (2014). Personality and subjective well-being in captive male western lowland gorillas living in bachelor groups. *American Journal of Primatology*, *76*, 879-889.
- Shrout, P.E., & Fleiss, J.L. (1979). Intraclass correlations—uses in assessing rater reliability. *Psychological Bulletin*, *86*, 420-428.
- Spruijt, B.M., van den Bos, R., & Pijlman, F.T.A. (2001). A concept of welfare based on reward evaluating mechanisms in the brain: anticipatory behaviour as an indicator for the state of reward systems. *Applied Animal Behaviour Science*, *72*, 145-171.

- Steel, P., Schmidt, J., & Shultz, J. (2008). Refining the relationship between personality and subjective well-being. *Psychological Bulletin*, *134*, 138-161.
- Temple, D., Manteca, X., Velarde, A., & Dalmau, A. (2011). Assessment of animal welfare through behavioural parameters in Iberian pigs in intensive and extensive conditions. *Applied Animal Behaviour Science*, *131*, 29-39.
- Watters, J.V. (2014). Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. *Zoo Biology*, *33*, 251-256.
- Wei, L., Wu, X.B., Zhu, L.X., & Jiang, Z.G. (2011). Mitogenomic analysis of the genus *Panthera*: *Science China Life Sciences*, *54*, 917-930. doi: 10.1007/S11427-011-4219-1
- Weiss, A., Adams, M.J., & King, J.E. (2011). Happy orang-utans live longer lives. *Biology Letters*, *7*, 872-874. doi: 10.1098/Rsbl.2011.0543
- Weiss, A., Adams, M.J., Widdig, A., & Gerald, M.S. (2011). Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology*, *125*, 72-83. doi: 10.1037/A0021187
- Weiss, A., Bates, T.C., & Luciano, M. (2008). Happiness is a personal(ity) thing: The genetics of personality and well-being in a representative sample. *Psychological Science*, *19*, 205-210.
- Weiss, A., Gartner, M., Gold, K.C., & Stoinski, T.S. (2012). Extraversion predicts longer survival in gorillas: an 18-year longitudinal study. *Proceedings of the Royal Society B*, *280*, 1-5.
- Weiss, A., Inoue-Murayama, M., Hong, K.W., Inoue, E., Udono, T., Ochiai, T., ... King, J.E. (2009). Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology*, *71*, 283-292. doi: 10.1002/Ajp.20649

- Weiss, A., King, J.E., & Enns, R.M. (2002). Subjective well-being in heritable and genetically correlated with Dominance in chimpanzees (*Pan troglodytes*). *Journal of Personality and Social Psychology*, *83*, 1141-1149.
- Weiss, A., King, J.E., & Perkins, L. (2006). Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology*, *90*, 501-511. doi: 10.1037/0022-3514.90.3.501
- Wemelsfelder, F., Hunter, T.E.A., Mendl, M.T., & Lawrence, A.B. (2001). Assessing the 'whole animal': A free choice profiling approach. *Animal Behaviour*, *62*, 209-220. doi: 10.1006/Anbe.2001.1741.
- Wielebnowski, N.C. (1999). Behavioral differences as predictors of breeding status in captive cheetahs. *Zoo Biology*, *18*, 335-349.

Table 1
Subjective well-being survey

Item	Statement to be rated
Pleasure derived from social interactions (with people)	Estimate the extent to which social interactions with keepers or other people are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the cat. Use as many social interactions that you can recall as a basis for your judgment.
Pleasure derived from social interactions (with conspecifics)	Estimate the extent to which social interactions with other cats are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the cat. Use as many social interactions that you can recall as a basis for your judgment.
Balance of positive and negative affect	Estimate the amount of time the cat is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the cat is unhappy, bored, frightened, or otherwise in a negative mood.
Personal control	Estimate, for this cat, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired locations, devices, or materials in the enclosure. Keep in mind that each cat will presumably have its own set of goals that may be different from other cats.
Desirability of being a particular snow leopard	Imagine how happy you would be if you were this cat for a week. You would be exactly like this cat. You would behave the same way as this cat, would perceive the world the same way as this cat, and would feel things the same way as this cat.

Table 2
 Factor loadings of subjective well-being items

Item	Loadings			
	Clouded leopards	Snow leopards	African lions*	Taxon
Balance of positive and negative moods	.94	.96	.96	.95
Pleasure derived from social interactions with other felids	.83	.71	.79	.78
Pleasure derived from social interactions with people	.95	.94		.72
Ability to achieve goals	.89	.97	.91	.88
Be the cat	.97	.97	.95	.91

*The African lions were housed with conspecifics, and therefore were not rated on social interaction with people.

Table 3
 Personality factors and subjective well-being correlations (Spearman's rho)

Subject Well-Being	Clouded leopard factors			Snow leopard factors			African lion factors		
	N	A/O	D/I	N	I/O	D	N	I	D
Overall	-.79**	.55*	-.05	-.67**	.36	.20	-.66**	-.49*	.31
Balance of positive and negative moods	-.77**	.58*	-.07	-.50*	.49*	.28	-.69**	-.34	.30
Pleasure from social interaction with conspecifics	-.81**	.13	-.21	-.60*	.26	-.06	-.27	-.51*	-.00
Pleasure from social interaction with people	-.82**	.53*	-.05	-.71**	.50*	.13	-.64**	-.60**	.41
Goals	-.77**	.32	-.03	-.62**	.33	.30	-.71**	-.43	.39
Be the cat	-.80**	.57*	-.11	-.48	.45	.36	-.66**	-.49*	.31

* $p < .05$. ** $p \leq .01$.

N = Neuroticism; A = Agreeableness; O = Openness; D = Dominance; I = Impulsiveness.

Table 4

Individual personality items and subjective well-being correlations per species.

Number of species	Items	Clouded leopard	Snow leopard	African lion	Scottish wildcat
<i>All species</i>					
	Insecure	-.75**	-.53*	-.60**	-.65**
<i>3 species</i>					
	Affectionate	.68**	.74**	.45*	
	Calm	.58*		.60**	.45*
	Fearful of people	-.93**	-.55*	-.47*	
	Suspicious	-.66**	-.60**	-.60**	
	Tense	-.76**		-.74**	-.60**
	Trusting	.78**	.64**	.58**	
<i>1 species</i>					
	Cool	.77**			
	Cooperative	.58*			
	Friendly/conspecifics	.73**			
	Smart	.52*			
	Individualistic		-.72**		
	Predictable		-.53*		
	Constrained			-.50*	
	Dominant			.52*	
	Fearful/conspecifics			-.60**	
	Persistent			.78**	
	Stable			.54**	
	Submissive			-.55**	
	Timid			-.53*	

* $p < .05$. ** $p \leq .01$.