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Personality Structure in the Domestic Cat (*Felis silvestris catus*), Scottish Wildcat (*Felis silvestris grampia*), Clouded Leopard (*Neofelis nebulosa*), Snow Leopard (*Panthera uncia*), and African Lion (*Panthera leo*)

Citation for published version:

Gartner, MC, Powell, DM & Weiss, A 2014, 'Personality Structure in the Domestic Cat (*Felis silvestris catus*), Scottish Wildcat (*Felis silvestris grampia*), Clouded Leopard (*Neofelis nebulosa*), Snow Leopard (*Panthera uncia*), and African Lion (*Panthera leo*): A Comparative Study' *Journal of Comparative Psychology*, vol 128, no. 4, pp. 414-426. DOI: 10.1037/a0037104

Digital Object Identifier (DOI):

[10.1037/a0037104](https://doi.org/10.1037/a0037104)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Journal of Comparative Psychology

Publisher Rights Statement:

© Gartner, M. C., Powell, D. M., & Weiss, A. (2014). Personality Structure in the Domestic Cat (*Felis silvestris catus*), Scottish Wildcat (*Felis silvestris grampia*), Clouded Leopard (*Neofelis nebulosa*), Snow Leopard (*Panthera uncia*), and African Lion (*Panthera leo*): A Comparative Study. *Journal of Comparative Psychology*. 10.1037/a0037104

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Running head: PERSONALITY IN FIVE FELIDS

Personality Structure in the Domestic Cat (*Felis silvestris catus*), Scottish Wildcat (*Felis silvestris grampia*), Clouded Leopard (*Neofelis nebulosa*), Snow Leopard (*Panthera uncia*), and African Lion (*Panthera leo*): A Comparative Study

Marieke Cassia Gartner, David M. Powell, Alexander Weiss

Marieke Cassia Gartner, School of Philosophy, Psychology and Language Sciences, Department of Psychology, The University of Edinburgh, Edinburgh, United Kingdom; David M. Powell, Wildlife Conservation Society, Bronx Zoo, Department of Mammalogy, Bronx, NY, United States; Alexander Weiss, School of Philosophy, Psychology and Language Sciences, Department of Psychology, The University of Edinburgh, Edinburgh, United Kingdom and Scottish Primate Research Group, United Kingdom.

Thanks go to all of the zoos and all of the caretakers who participated in this work.

Correspondence should be directed to Marieke Cassia Gartner, School of Philosophy, Psychology and Language Sciences, Department of Psychology, The University of Edinburgh, Edinburgh, United Kingdom, marieke.gartner@gmail.com.

Abstract

While the study of non-human personality has increased in the last decade, there are still few studies on felid species, and the majority focus on domestic cats. We assessed the structure of personality and its reliability in five felids—domestic cats, clouded leopards, snow leopards, African lions, and previous data on Scottish wildcats—and compared the results. In addition to the benefits of understanding more about this taxon, comparative studies of personality structure have the potential to provide information on evolutionary relationships among closely related species. Each of the species studied was found to have three factors of personality. Scottish wildcats' factors were labeled Dominance, Agreeableness, and Self Control; domestic cats' factors were Dominance, Impulsiveness, and Neuroticism; clouded leopards' factors were Dominance/Impulsiveness, Agreeableness/Openness, and Neuroticism; snow leopards' factors were Dominance, Impulsiveness/Openness, and Neuroticism; and African lions' factors were Dominance, Impulsiveness, and Neuroticism. The Neuroticism and Impulsiveness factors were similar, as were two of the Dominance factors. A taxon-level personality structure also showed three similar factors. Age and sex effects are also discussed.

keywords: personality, animals, phylogeny, felids

Personality Structure in the Domestic Cat (*Felis silvestris catus*), Scottish Wildcat (*Felis silvestris grampia*), Clouded Leopard (*Neofelis nebulosa*), Snow Leopard (*Panthera uncia*), and African Lion (*Panthera leo*): A Comparative Study

Although studies on non-human personality have increased dramatically over the last decade, there is still much work to be done, with research often focused on just a few taxa. With 150 articles on primates (Freeman & Gosling, 2010) and 51 on canids (Jones & Gosling, 2005), there are just 20 on felids (Gartner & Weiss, 2013a), and these mostly focus on domestic cats (*Felis silvestris catus*). However, because of the many applications and implications of personality for health, longevity, and well-being (Powell & Gartner, 2012; Gartner & Weiss, 2013b; Wielebnowski, 1999; Wielebnowski et al., 2002), there is a need for more work to be done on more species in general, and wild cats specifically, especially for those kept in captivity, who may be challenged due to their size and natural range in the wild (Clubb & Mason, 2003). That is, larger animals are at a disadvantage in captive settings due to the inherently smaller amount of space they have for their size. Similarly, the larger their natural range, the more captivity inhibits them from performing such natural behaviors as ranging around large territories. Personality is an important part of assessing an animal's welfare, as it has been shown to have an effect on a variety of health outcomes, as it does in humans, including immune function (e.g., Capitanio et al., 2008), morbidity (e.g., Natoli et al., 2005), chronic stress (e.g., Wielebnowski et al., 2002), mortality (e.g., Weiss, Gartner, Gold & Stoinski, 2013), and well-being (e.g., King & Landau, 2003), as well as on zoo management, including welfare (e.g., Wielebnowski, 1999), captive breeding (e.g., Wielebnowski, 1999), and enclosure grouping (e.g., Stoinski, Lukas, Kuhar, & Maple, 2004), and conservation (e.g., Bremner-Harrison, Prodohl, & Elwood 2004). Therefore, including personality in an overall assessment of captive care or conservation may add a dimension that affects treatments and outcomes more efficiently, more completely, or in a more complex way.

Comparative studies not only increase knowledge of each species, but also elucidate relationships among closely related species that may suggest evolutionary pathways (Gosling & Graybeal, 2007). Personality has been shown to have genetic underpinnings in both humans (e.g., Bouchard & Loehlin, 2001) and apes (e.g., Weiss, King, & Figueredo, 2000), and has been shown to have adaptive value (e.g., Sih & Watters, 2005; Réale et al., 2010; King, Weiss, & Farmer, 2005). For instance, using this approach, Weiss, King, and Perkins (2006) supported the suggestion that the evolutionary origins of Conscientiousness are relatively recent (Gosling & John, 1999) by showing that orangutans (*Pongo abelii* and *Pongo pygmaeus*), which are the most distantly related great ape to humans, do not have a Conscientiousness factor; humans and chimpanzees (*Pan troglodytes*) do.

To carry out such a comparison, a similar scale needs to be used across species (King & Weiss, 2011; Weiss & Adams, 2008, 2013). Personality studies in felids have been varied, and while there are some similarities, the small amount of wild cat data (six studies in all: Coleman & Mellgren, submitted; Gartner & Powell, 2012; Gartner & Weiss, 2013b; Phillips & Peck, 2007; Wielebnowski, 1999; Wielebnowski et al., 2002) and the differences among the methodology used with domestic cats (Gartner & Weiss, 2013a) make comparison difficult.

This study aimed to address this absence, by assessing and comparing the personality structure of five species of felid: Scottish wildcats (*Felis silvestris grampia*; data from Gartner & Weiss, 2013b) and their closely related counterparts domestic cats, the clouded leopard (*Neofelis nebulosa*), which is the basal species of Panthera (Wei, Wu, Zhu, & Jiang, 2011), snow leopards (*Panthera uncia*), and African lions (*Panthera leo*). In addition, one personality structure was obtained for all five species by combining data from the species in the study, to assess the possibility of a stable personality structure across the taxon. If one exists, it would represent evidence that personality has not evolved considerably in modern cats. This work was based on original work that showed that an adaptation of a human personality scale (the Five-Factor Model) could be used to assess chimpanzee personality (King & Figueredo, 1997). In humans,

five factors best describe personality: Openness to Experience, Conscientiousness, Extraversion, Agreeableness, and Neuroticism (McCrae & Costa, 1987). In chimpanzees, similar factors to these are also found, with the addition of a Dominance factor (King & Figueredo, 1997).

Following this work, this scale was replicated with chimpanzees (King et al., 2005; Weiss, King, & Hopkins, 2007; Weiss et al., 2009), and used to assess personality in orangutans (Weiss et al., 2006), Rhesus macaques (*Macaca mulatta*; Weiss, Adams, Widdig, & Gerald, 2011), and brown capuchins (Morton et al., 2013), in addition to Scottish wildcats (Gartner & Weiss, 2013b).

The five species were chosen based on availability of captive-held individuals, in addition to the relationships among the species. Starting with the basal species—the clouded leopard—of *Panthera*, we then chose the most distantly related species in that genus, the phylogenetic sister species African lions and snow leopards (Wei et al., 2011). To compare different lineages, the Scottish wildcat and domestic cat were chosen from the genus *Felis*.

Because domestic cats evolved from the African wildcat (*Felis silvestris lybica*; Driscoll et al., 2007), we expect that there should be a close relationship between the personality structures of the Scottish wildcat and the domestic cat, since the Scottish wildcat is a subspecies, as is the African wildcat, of the European wildcat (*Felis silvestris*; Beaumont et al., 2001). However, domestication and/or the isolation of the Scottish wildcat on the British Isles may have played a role in the evolution of their personality, which may lead to differences. In addition, behavioral differences between the two species, with the Scottish cat being purely solitary (Macdonald & Barrett, 1993) and the domestic cat semi-solitary (Liberg, Sandell, Pontier, & Natoli, 2000), may also lead to differences. While snow leopards and African lions diverged at the same time (Wei et al., 2011), and therefore may have similar personality structures, their social structures as well as their ecologies are so different—one solitary and living in the mountains of Asia, the other social and living in the deserts and open woodlands of Africa (Nowell & Jackson, 1996)—that it is possible that this may have played a role in the development of personality. Finally, the personality structure of the clouded leopard should be informative about the other species, as

clouded leopards were the first to speciate (Wei et al., 2011), and therefore differences from their personality structure may suggest indications of the evolution of felid personality.

Method

Species and Rater Information

All the zoos involved and the University of Edinburgh gave ethical approval for this research.

Scottish wildcats and raters. As discussed in Gartner and Weiss (2013a), subjects included 25 Scottish wildcats from three zoos. The age of the subjects ranged from 1 to 15 years ($M = 3.67 \pm 3.14$ *SD*). There were eight wildcats (3 males; 5 females) at Port Lympne Wild Animal Park (PL), in Lympne, Kent, UK; nine wildcats (2 males; 5 females, 2 unknown) at the Highland Wildlife Park (HWP), Kincaig, Kingussie, UK; and eight wildcats (4 males; 4 females) at the British Wildlife Centre (BWC), in Lingfield, Surrey, UK. Eight caretakers rated the wildcats (PL: $n = 3$; HWP: $n = 3$; BWC: $n = 2$).

Domestic cats and raters. Subjects included 100 domestic cats from two shelters. The age of the subjects ranged from 1 month to 19 years ($M = 4.85 \pm 4.64$ *SD*). There were 85 cats (39 males, 44 females, 2 unknown) at Cats Protection (CP) in Kirkintilloch, Scotland, UK; and 15 cats (6 males; 9 females) at KittyKind (KK) in New York, New York, US. Twenty-one caretakers rated the domestic cats (CP: $n = 6$; KK: $n = 15$).

Clouded leopards and raters. Subjects included 16 clouded leopards from two zoos. The age 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 in Nashville, TN, US (NZ); and 5 clouded leopards (2 males; 3 females) at PL. 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 age 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, US; 4 snow leopards

(3 males; 1 female) at ABQ BioPark (ABQ), in Albuquerque, New Mexico, US; 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 2 zoos. The age 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, US; and 8 lions (2 males; 6 females) at West Midland Safari Park (WMSP) in Bewdley, Worcestershire, UK. Seven caretakers rated the African lions (LCS: $n = 3$; WMSP: $n = 4$).

Procedure

The 45-item personality survey was based on previous felid personality surveys (Feaver, Mendl, & Bateson, 1986; Gartner & Powell, 2012; Wielebnowski, 1999) and the Hominoid Personality Questionnaire (King & Figueredo, 1997) as described in Gartner and Weiss (2013a). To compare personality structures across all felids, individual species were not assigned specific traits. The survey included a specific description to be used for each trait. These traits were rated on a seven-point Likert scale, where “1”, “not at all,” meant the trait did not describe the animal at all, and “7”, “very much so,” meant the trait described the animal to a great degree.

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, as in previous studies (e.g., Weiss et al., 2011; Morton et al., 2013; Lee & Moss, 2012). $ICC(3,1)$ s were compared across species.

We then ran parallel analyses for both scales for each species, as well as examining the scree plots, to determine the number of components to extract (Horn, 1965; O'Connor, 2000).

We followed these analyses with principal components analyses (PCA) for both scales for each species. We also ran regularized exploratory factor analyses (REFA; Jung & Lee, 2011; Jung & Takane, 2008), which are designed for small sample sizes, for all species. Factor extraction for the regularized exploratory factor analysis was conducted with MATLAB 7.12.0.635 (R2011a), using a program provided by Sunho Jung. Factor loadings in these analyses were derived via unweighted least squares and we assumed that unique variances did not differ across items. The components or factors were rotated using the varimax procedure in R version 2.15.1 (R Core Team, 2012) for the REFA and IBM SPSS for the PCA. We use the term factor throughout the paper in a general sense to avoid switching between the terms component and factor.

For the overall taxon personality scale, we standardised the data before running the principal components analysis, in order to avoid confounding the covariation of traits across individuals with covariation across species, following a procedure used in cross-cultural studies of human personality (McCrae, Terracciano, & 78 Members of the Personality Profiles Cultures Project, 2005).

As in previous studies (e.g., Gartner & Weiss, 2013b), we defined factor loadings $\geq |0.4|$ as salient for the PCA, and $\geq |0.3|$ for the REFA, which yields more conservative loadings (Jung & Lee, 2011; e.g., Gartner & Weiss, 2013b, Konečná, Weiss, Lhota, & Wallner, 2012). 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.

Finally, factors across species were compared using orthogonal targeted Procrustes rotation (Schönemann, 1966). This entails rotating one set of factor loadings with another to maximise fit and to minimise the sums of squares of deviations from a target matrix, while maintaining orthogonality (McCrae et al., 1996). Factor congruences were calculated to identify matching factors. In this work, Procrustes rotations were carried out using syntax developed by Fischer and Fontaine (2011).

Results

Inter-rater reliability

Scottish wildcats. As reported in Gartner and Weiss (2013b), the reliabilities of individual ratings, $ICC(3,1)$, ranged from .04 (quitting) to .75 (aggressive to conspecifics), with a mean reliability of .41. The reliabilities of mean ratings, $ICC(3,k)$, ranged from .10 (quitting) to .89 (aggressive to conspecifics), with a mean reliability of .59 (for individual reliabilities for all species, see Table S1).

Domestic cats. The reliabilities of the individual ratings, $ICC(3,1)$, ranged from .07 (fearful of conspecifics) to .73 (aggressive to people), with a mean reliability of .35. The reliabilities of the mean ratings, $ICC(3,k)$, ranged from .18 (fearful of conspecifics) to .90 (aggressive to people), with a mean reliability of .58. The $ICCs$ for the items quitting, aimless, smart, vigilant and deliberate were negative, and so were excluded from further analysis.

Clouded leopards. The reliabilities of individual ratings, $ICC(3,1)$, ranged from .01 (reckless) to .80 (aggressive to people), with a mean reliability of .37. The reliabilities of mean ratings, $ICC(3,k)$, ranged from .04 (reckless) to .93 (aggressive to people), with a mean reliability of .61. The $ICCs$ for the items decisive, deliberate, fearful of conspecifics, persevering, quitting, and stingy were negative, and so were excluded from further analysis.

Snow leopards. The reliabilities of individual ratings, $ICC(3,1)$, ranged from .02 (self-assured) to .64 (playful), with a mean reliability of .26. The reliabilities of mean ratings, $ICC(3,k)$, ranged from .08 (self-assured) to .89 (playful). The $ICCs$ for the items persevering, smart, dominant, independent, quitting, aimless, tense, and decisive were negative, and so were excluded from further analysis.

African lions. The reliabilities of individual ratings, $ICC(3,1)$, ranged from .04 (distractible) to .81 (submissive), with a mean reliability of .34. The reliabilities of mean ratings, $ICC(3,k)$, ranged from .11 (distractible) to .94 (submissive), with a mean reliability of .58. The

ICCs for the items predictable, impulsive, and vigilant were negative, and so were excluded from further analysis.

ICC(3,1) comparison across species. Domestic cat ICC(3,1)s correlated with clouded leopard ($r = .55, p < .01$), Scottish wildcat ($r = .41, p < .01$), and snow leopard ($r = .55, p < .01$) reliabilities. Scottish wildcat ICC(3,1)s correlated with clouded leopard ($r = .39, p < .01$) ICC(3,1)s; and clouded leopard ICC(3,1)s correlated with snow leopard ($r = .41, p < .01$) ICC(3,1)s. African lion reliabilities did not correlate significantly with any other species: clouded leopard ($r = -.01, p = .93$), domestic cat ($r = .21, p = .18$), Scottish wildcat ($r = .23, p = .14$), snow leopard ($r = -.09, p = .55$); Scottish wildcat reliabilities did not correlate significantly with snow leopard reliabilities ($r = .24, p = .11$).

Taxon. For the personality items, the reliabilities of individual ratings, ICC(3,1), ranged from .03 (quitting) to .56 (playful), with a mean reliability of .32. The reliabilities of mean ratings, ICC(3, k), ranged from .11 (quitting) to .83 (playful), with a mean reliability of .60.

Principal Components Analysis

Scottish wildcats. This structure was taken from a previous study (Gartner & Weiss, 2013b), in which three factors were found: Dominance, Agreeableness, and Self Control.

Domestic cats. PCA, parallel analysis, and examination of the scree plot indicated that three factors accounting for 53.19% of the variance were described by the ratings. We compared the results of the PCA and the REFA: $\phi = .99$ for the first domain, $\phi = .99$ for the second, and $\phi = .94$ for the third, indicating equality. (For REFA loadings, see Table S2).

Based on the pattern of factor loadings and previous research on trait groupings, we labeled these factors Dominance, Impulsiveness, and Neuroticism (see Table 1). The reliabilities of individual ratings, ICC(3,1), were .31 for Dominance, .42 for Impulsiveness, and .55 for Neuroticism. The reliabilities of mean ratings, ICC(3, k), were .58 for Dominance, .69 for Impulsiveness, and .79 for Neuroticism.

Clouded leopards. Parallel analysis indicated that two factors were described by the ratings, accounting for 59.65% of the variance, while examination of the scree plot indicated that there were three factors, accounting for 69.93% of the variance. A REFA indicated three factors as well (Table S3). We compared the results of the three-factor solution PCA with the REFA by calculating Tucker's congruence coefficients (Wrigley & Neuhaus, 1955): $\phi=.98$ for the first domain, $\phi=.98$ for the second, and $\phi=.98$ for the third. Values of .70 and above are considered to have mild agreement, .80 and above high agreement, and .90 and above equality (Sakamoto et al., 1998).

Because of these results, and based on the pattern of factor loadings and previous research on trait groupings, we labeled the factors Neuroticism, Agreeableness/Openness, and Dominance/Impulsiveness (see Table 2). The reliabilities of individual ratings, $ICC(3,1)$, were .80 for Neuroticism, .90 for Agreeableness/Openness, and .47 for Dominance/Impulsiveness. The reliabilities of mean ratings, $ICC(3,k)$, were .93 for Neuroticism, .97 for Agreeableness/Openness, and .76 for Dominance/Impulsiveness.

Snow leopards. PCA, parallel analysis, and examination of the scree plot indicated that three factors accounting for 71.06% of the variance were described by the ratings. We compared the results of the PCA and the REFA: $\phi=.97$ for the first domain, $\phi=.97$ for the second, and $\phi=.97$ for the third, indicating equality. (For REFA loadings, see Table S4).

Based on the pattern of factor loadings and previous research on trait groupings, we labeled the three factors Neuroticism, Impulsiveness/Openness, and Dominance (see Table 3). The reliabilities of individual ratings, $ICC(3,1)$, were .36 for Neuroticism, .44 for Dominance, and .71 for Impulsiveness/Openness. The reliabilities of mean ratings, $ICC(3,k)$, were .70 for Neuroticism, .91 for Impulsiveness/Openness, and .76 for Dominance.

African lions. PCA, parallel analysis, and examination of the scree plot indicated that three factors accounting for 65.10% of the variance were described by the ratings. The Tucker's

congruence coefficients between the PCA and the REFA were $\phi=.99$ for the first domain, $\phi=.94$ for the second, and $\phi=.99$ for the third. (For REFA loadings, see Table S5).

Based on the pattern of factor loadings and previous research on trait groupings, we labeled the three factors Neuroticism, Dominance, and Impulsiveness (see Table 4). The reliabilities of individual ratings, $ICC(3,1)$, were .74 for Dominance, .55 for Impulsiveness, and .76 for Neuroticism. The reliabilities of mean ratings, $ICC(3,k)$, were .91 for Dominance, .81 for Impulsiveness, and .92 for Neuroticism.

Taxon. Parallel analysis indicated five factors (with a .0008 difference between the actual eigenvalue and that derived by parallel analysis for the fifth factor), while examination of the scree plot indicated four. We therefore examined three factor structures, one with five factors, one with four, and one with three, since the individual species each had three factors.

In each grouping, there were three clear factors, which we labeled Neuroticism, Impulsiveness, and Dominance. In the five-factor solution, the fourth factor had elements of Conscientiousness and, on the opposite end, Neuroticism. The fifth factor had four positive loadings: solitary, independent, individualistic, and vigilant, and two negative ones: affectionate and friendly to conspecifics. Most of the traits in the fourth factor of the five-factor solution loaded onto Dominance in the four-factor solution, with the exception of smart, which loaded onto Neuroticism. In the four-factor solution, the fourth factor had the same loadings as the fifth factor in the five-factor solution. Four of the six traits in this fourth factor were reassigned in the three-factor solution, and made sense as part of these factors. Affectionate and friendly to conspecifics loaded on the negative end of Neuroticism, or Emotional Stability; solitary loaded on Neuroticism; and vigilant loaded on Dominance. Independent and individualistic were the only traits that dropped out from the salient loadings with this solution. Therefore, we used the three-factor solution for further analysis (see Table 5).

The reliabilities of individual ratings, $ICC(3,1)$, were .37 for Impulsiveness, .53 for Dominance, and .58 for Neuroticism, with a mean reliability of .49. The reliabilities of mean

ratings, $ICC(3,k)$, were .69 for Impulsiveness, .81 for Dominance, and .84 for Neuroticism, with a mean reliability of .78.

Personality factor comparisons

To compare the five sets of factors, i.e. structures, orthogonal targeted Procrustes rotations were used (McCrae, Zonderman, Costa, Bond, & Paunonen, 1996). Congruence coefficients were calculated to compare the results (Table 6). Neuroticism species congruences ranged from .70 to .89; Impulsiveness congruences ranged from .70 to .81. There was only one relationship among the Dominance factors that was found across species. Clouded leopard Dominance was related to Scottish wildcat Dominance ($\phi=.74$). For a trait-to-trait comparison of personality domains across species included in this research, in addition to other research on big cats, non-human primates, and humans, see Table 7.

Age and Sex Effects

As Scottish wildcats age, they are rated as more Agreeable ($r = .56, p = .006$), while clouded leopards are rated as less Agreeable/Open ($r = -.66, p = .006$). Domestic cats are rated as less Impulsive as they age ($r = -.54, p < .001$), as are snow leopards ($r = -.61, p = .009$).

Female African lions ($M = .26, SD = .91$) are rated as more Impulsive than males ($M = -.83, SD = .88$): $t(19) = 2.35, p = .03, d = 1.22$), but only when using the results from the regularised exploratory analysis. There were no age effects in African lions. No other age or sex effects were found.

Discussion

Personality 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 (Weiss et al., 2011), and brown capuchin monkeys (Morton et al., 2013), all of which were measured using a similar instrument. In addition, reliabilities were similar to studies using different

measures in a variety of species (Gosling, 2001; Jones & Gosling, 2005; Uher, Asendorpf, & Call, 2008; Gartner & Weiss, 2013b).

Although we expected some similarities in personality structures, especially between Scottish wildcats and domestic cats and snow leopards and lions due to their close genetic relationships, the similarity across all species was unexpected. A comparison of the reliabilities across species showed that most of the species' $ICC(3,1)$ s correlated significantly, with the exception of African lions, and Scottish wildcats as compared with snow leopards. These results show that there is something different in the ratings for African lions, especially—perhaps to do with the fact that they are the only purely social species among the felids, with adults living in both female-only and male-only groups (small, male-only groups exist in cheetahs [*Acinonyx jubatus*]; female groups in domestic cats; Macdonald, Yamaguchi, & Kerby, 2000). The highest reliabilities in lions, but not in any other species, were for the adjectives dominant and submissive.

Other than lions, most cat species are either solitary or semi-solitary, and therefore their behavior is often similar, in terms of hunting, territory establishment (including marking), and mating, for example. This indicates that overall felid personality structures may have evolved early on in cat species, but that some part of lion personality structure may have evolved more recently, and that that evolution may be due to behavioral traits (such as social behavior) that are found only in that species. This is an indication of the adaptive nature of personality, which is also seen in the health outcomes cited in the introduction. This adaptive nature lends itself well to the study of both proximate and ultimate causes of evolution, as well as understanding related behaviors that may have co-evolved with personality (Carere & Locurto, 2011).

Scottish wildcat personality structure

Scottish wildcats were one of two species with an Agreeableness dimension. It was, however, moderately related to the other species' Impulsiveness factors (traits related to Impulsiveness are found on the negative end of the Conscientiousness factor). The traits on the

negative end of Scottish wildcat Agreeableness were all related to Neuroticism; however, this factor did not show congruence with any of the other species' Neuroticism factors. The traits that are similar across Scottish wildcat Agreeableness and the Impulsiveness factors in other species are related to Extraversion and Openness, while the traits that loaded the highest on Scottish wildcat Agreeableness (cooperative, friendly, and trusting) are absent from Impulsiveness in the other species, but instead show up in the negative loadings of Neuroticism, as Emotional Stability. Some traits related to Openness, such as curious or playful, are often anecdotally associated with cats. It is not surprising then, that these traits load on factors across cat species. There are several possibilities that might explain the difference in how they manifest themselves in factors.

Anecdotally, Scottish wildcats are thought to be untameable. Similarly, their very close relative, the European wildcat (*Felis silvestris*), has been shown to exhibit fewer affiliative behaviors than other small felids (Cameron-Beaumont, Lowe, & Bradshaw, 2002). African wildcats, however, are thought to be more agreeable (Cameron-Beaumont et al., 2002); this is the basis of one theory as to why domestic cats evolved from that subspecies of wildcat, since tameability and attention-soliciting are considered to be pre-adaptations for domestication (Price, 2002). Similarly, instead of adaptations, these characteristics may have been incidental responses to the environment (Hare, Wobber, & Wrangham, 2012), which had one subspecies favoring affiliative individuals, while the other either did not, or favoured more aggressive individuals. Another possibility as to why Scottish wildcats have an Agreeableness factor is that they are not as untameable as believed, and are perhaps more like the African wildcat than previously thought. Assessing the personality of other species of wildcat, then, especially the African wildcat, would be instructive.

As Scottish wildcats age, they are rated as more Agreeable—this is in line with results from other species, such as humans (McCrae et al., 1999) and chimpanzees (King et al., 2008).

Domestic cat personality structure

Domestic cat personality ratings define three factors. Dominance had the highest loadings on the traits aggressive to conspecifics, bullying, and dominant; Impulsiveness had the highest loadings on excitable, active, and playful, traits normally associated with neuroticism and extraversion, but traits that reflect Impulsiveness were more numerous, including eccentric, impulsive, distractible, and reckless. We named this factor Impulsiveness based on findings in chimpanzees, which showed two facets to Conscientiousness: predictability, which included adjectives predictable, (not) impulsive, (not) reckless, (not) erratic, and (not) disorganised, and tameness, which included adjectives (not) defiant, (not) irritable, (not) aggressive, and (not) jealous (King et al., 2008). Neuroticism had the highest loadings on anxious, insecure, and tense, suspicious, and fearful of people.

Interestingly, the only age difference found in this study was among domestic cats. As cats age, they become less Impulsive. In domestic cats this dimension is comprised of such traits as active and playful. It makes sense, then, that this factor decreases with age, as play also decreases in older animals (West, 1974) as does activity in general, as in most species. These traits, which are associated with some aspects of Extraversion (social vitality), also decrease in humans as they age during certain time periods (Roberts, Walton, & Viechtbauer, 2006). Similarly, other traits in this factor included elements on the Conscientious scale, and in humans, Conscientiousness increases with age (Roberts, Walton, & Bogg, 2005; Roberts et al., 2006), as it does in chimpanzees (King et al., 2008).

Clouded leopard personality structure

There were three factors defined by the clouded leopard personality ratings, as interpreted via examination of a scree plot and regularized exploratory factor analysis. However, parallel analysis indicated two, so this research would benefit from replication and perhaps a larger sample size, although studies have shown that small sample sizes can reveal stable personality structures (de Winter, Dodou, & Wieringa, 2009; Konečná et al., 2012).

Neuroticism had the highest loadings on the traits insecure, fearful of people, and suspicious. The second, Agreeableness/Openness, had the highest loadings on distractible, playful, and curious, but had more loadings on traits related to Agreeableness. Finally, Dominance/Impulsiveness had the highest loadings on erratic, reckless, and impulsive, but had more loadings on traits related to Dominance.

The two-factor structure was comprised of Neuroticism/Impulsiveness and Agreeable. The first had the highest loadings on the traits suspicious, eccentric, and vigilant, and the second on active, friendly to people, and affectionate. All traits related to Dominance/Impulsiveness in the three-factor structure loaded on Neuroticism/Impulsiveness except jealous, predictable, and constrained, which loaded on Agreeableness.

Age is positively related to Agreeableness/Openness, which may reflect traits related to Agreeableness more, as this factor tends to increase with age in other species as well (humans: McCrae et al., 1999; chimpanzees: King et al., 2008).

Snow leopard personality structure

Snow leopard personality ratings define three factors. Neuroticism had the highest loadings on the traits suspicious, fearful of people, and aggressive to people; Impulsiveness/Openness had the highest loadings on active, curious, and inquisitive; and Dominance had the highest loadings on stingy, aggressive to conspecifics, and jealous. There were many more unreliable traits rated in snow leopards than in the other cats.

Impulsiveness/Openness is negatively related to age. This has some similarity to other species: Openness decreases as humans (McCrae et al., 1999) and chimpanzees age (King et al., 2008).

African lion personality structure

African lion personality ratings define three factors. Dominance had the highest loadings on the traits jealous, stingy, and aggressive to conspecifics; Impulsiveness had the highest

loadings on the traits active, erratic, and eccentric; and Neuroticism had the highest loadings on fearful of people, insecure, and tense.

Male African lions in this sample were rated as more Dominant than females. Because of the lions' unique social structure in the felid taxon, a harem-style composition, this result makes sense. Similar results are also seen in chimpanzees (Weiss, et al., 2007; King et al., 2008). While humans do not have a Dominance factor, males rate higher on a facet of Extraversion called assertiveness (Costa, Terracciano, & McCrae, 2001).

Female African lions were rated as more Impulsive than males. This result may be related to African lion biology. Aspects of Extraversion in this factor (active and playful) may play a role in this result. As mainly females interact with their cubs, this may increase their ratings on this factor. Female lions are also directly affected by group living—the larger the pride, the more successful females are in reproducing, and they live longer lives (Mosser & Packer, 2009). In addition, since females do essentially all of the hunting in a pride, it makes sense that they would be rated as more active. These elements of Extraversion, therefore, may play a role in group cohesion.

Relationships among personality factors

Domestic cat, lion, and snow leopard Neuroticism and Scottish wildcat Dominance are inter-related to varying degrees. Scottish wildcats do not have a Neuroticism domain, and traits related to Neuroticism loaded on both Dominance and (negative) Agreeableness. While there is a moderate relationship between clouded leopard Neuroticism and Scottish wildcat Agreeableness, there is no relationship between the latter and domestic cat Neuroticism. Domestic cat Neuroticism is highly related to clouded leopard Neuroticism, however.

Scottish wildcat Agreeableness, along with domestic cat Impulsiveness, lion Impulsiveness, clouded leopard Agreeableness/Openness and snow leopard Impulsiveness/Openness are all inter-related, mostly moderately, with the snow leopard and lion factors being highly related. The Impulsiveness factors were not related across species.

Clouded leopard Dominance/Impulsiveness was similar to Scottish wildcat Dominance. This was the only relationship among the Dominance factors that were found in each species, which may indicate differences in how individuals interact across the species studied. The traits aggressive to conspecifics, bullying, and jealous loaded on all species' Dominance factors, while dominant loaded on all but snow leopards, and stingy loaded all but clouded leopards. Other than these traits, there was variation among other traits that loaded both positively and negatively on the various species' Dominance factors, which may explain these results. Research on behavioral indicators of Dominance may be of use in understanding these results.

These results suggest that the felid personality factors Neuroticism and Impulsiveness have not evolved much since modern cats split off from *Carnivora*, although until genetic analyses are done this is uncertain. There is no obvious connection between either of these factors and adaptability, or to the felid predator way of life. It is possible that the results are related to the status of all the species in the study as captive animals, as contemporary evolution (Hendry & Kinnison, 1999) may play a role in the strengthening or weakening of traits (McDougall, Réale, Sol, & Reader, 2006). A study of personality in wild-living felids, then, might be helpful in understanding the results. Studies have been done on groups of free-living domestic cats (e.g., Natoli et al., 2005), however they are limited to behavioral and not trait-based analyses. A possibility would be to look at animals housed in sanctuaries, such as lions in Africa; however, this would still present problems for the current methodology as the knowledge of the caretakers is probably much different than the knowledge of zookeepers, who spend more time in close proximity with the animals in their care. In addition, this approach was used in chimpanzees, but no difference in factor structure attributable to environment was found (King et al., 2005).

Taxon personality structure

The combined personality ratings of the five species also define three factors. Neuroticism had the highest loadings on the traits fearful of people, suspicious, and insecure;

Dominance had the highest loadings on the traits dominant, deliberate, and aggressive to conspecifics; and Impulsiveness had the highest loadings on impulsive, excitable, and erratic. This type of information could be useful for practical situations, for instance in zoos, where time is at a premium. Because there does seem to be a consistent personality structure across the taxon, one survey could be used, facilitating the process of personality assessment, saving time and energy, and increasing sample sizes (Watters & Powell, 2012).

Personality factors in terms of other animals

Using a different survey, Wielebnowski (1999) also found three factors of personality in cheetahs: Tense-Fearful (with high positive loadings on tense, fear of conspecifics, fear of people, and insecure, and high negative loadings on self-assured, curious, and calm); Vocal-Excitable (comprised of vocal, excitable, playful, active, smart, and aggressive to people), and Aggressive (aggressive to people and to conspecifics).

With another survey, based partly on Wielebnowski's (1999), Phillips and Peck (2007) labeled a three-factor solution for tiger (*Panthera tigris*) personality, which included Extraversion, Agreeableness, and Youthfulness. Extraversion was comprised of skittish, oblivious, vigilant, and active; Agreeableness included careless, aggressive, focus, intelligent, and obedient; and Youthfulness included playful, excitable, impulsive, and curious.

Although the labels are different, there are clear similarities across species, even using different versions of trait-based surveys. The Tense-Fearful factor in cheetahs may relate to the Neuroticism factor in the five species we studied. Vocal-Excitable in cheetahs and Extraversion in tigers might be similar to the Impulsiveness factor in the present study, and Aggressive in cheetahs might be similar to Dominance. It would be worth using the same method on all species in order to conduct a direct comparison, or comparing the labels used in each study for similarities, especially in cheetahs, as they are separate from the *Panthera* line, which included all of the big cat species in this study.

Evolution of personality

Has personality in cats evolved since the taxon broke off from *Carnivora*? Without genetic data, it is hard to say, however, it looks like little has changed, from the clouded leopard, the basal species of *Panthera* that split from a common ancestor 8.7-10.8 million years ago (Johnson et al., 2006; Wei et al., 2001, who suggest that the species be included in this genus) to the last to split, the domestic cat lineage, which split 6.2-6.7 million years ago (Johnson et al., 2006). It is possible that the scales used here may be missing items relevant to wild animals, although this is unlikely to have a large effect, given evolutionary history affects captive animals as well as wild (and that in previous studies, there was little difference in personality structures of animals living in different settings: King et al., 2005).

Future Research

One limitation of this study was that although the survey used was identical across species, the PCA calculations were not, because different species had different (in both number and name) unreliable items removed, a finding that mostly likely also reflects species differences. Therefore, it is possible that structural differences among the species might be artifacts. This is seen in personality research conducted with humans, where a broad range of surveys have been used, but there is a good degree of overlap, and a similar set of personality factors found (e.g., the Five Factor Model, the Big Five, etc.; Digman, 1990). It makes sense, then, that this would also be the case for other species. However, future work on developing the questionnaire used here would be valuable to eventually include a set of traits that generally work in all felid species. Along this line, future studies should also include more species of felids, to assess whether these differences and similarities are consistent across the taxon. This would allow for further understanding of the evolution of personality in felids. In addition, more studies are also needed on direct or indirect links between personality and welfare, and health and conservation outcomes in a variety of felid species.

Conclusion

Across the five felid species we assessed, personality structure was strikingly similar, and also seemed to be related to other studies' findings, such as in cheetahs (Wielebnowski, 1999) and tigers (Phillips & Peck, 1997). An overall taxon personality structure reflected this similarity, with factors labeled Dominance, Neuroticism, and Impulsiveness. These results suggest that personality structure may have evolved in smaller units than factors, perhaps at the trait level. In addition, the similarity may allow for a more generalized approach to captive care of felids based on personality—that is, felids of these species rated higher on Neuroticism, for example, may be able to have similar treatments to address any welfare issues, including health outcomes, associated with that personality factor. However, it would be important to assess more felid species' personality structures, and also direct links to welfare and health outcomes, as well as to conservation outcomes.

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Table 1
Domestic cat factor structures of mean trait ratings

Item	Principal components analysis: Varimax rotation		
	Neuroticism	Impulsiveness	Dominance
Anxious	.89	-.09	.06
Insecure	.87	-.21	-.11
Tense	.87	-.20	-.09
Stable	-.86	-.16	-.08
Affectionate	-.86	.06	-.00
Friendly to people	-.85	.00	-.29
Trusting	-.84	.02	-.11
Cool	-.83	-.08	.11
Calm	-.82	-.22	-.12
Suspicious	.85	.01	.13
Fearful of people	.82	-.24	.04
Timid	.80	-.24	-.18
Self-assured	-.74	.27	.06
Aggressive to people	.73	.08	.45
Cooperative	-.72	-.28	-.24
Curious	-.53	.51	.27
Constrained	.53	-.47	-.10
Excitable	.01	.81	.19
Active	-.34	.72	.07
Playful	-.42	.66	.18
Eccentric	.13	.62	.21
Impulsive	.52	.56	.08
Distractible	-.12	.52	.25
Reckless	.40	.51	.45
Independent	.08	-.45	.22
Aggressive to conspecifics	.37	.06	.68
Bullying	-.01	.07	.63
Submissive	-.06	-.02	-.62
Dominant	-.08	-.03	.54
Erratic	.42	.44	.50
Jealous	.08	.41	.49
Stingy	.19	.06	.43
Individualistic	.20	.31	.42
Persevering	-.03	.29	.42
Predictable	-.25	-.42	.40
Decisive	-.13	.02	.39
Vocal	-.16	.35	.26
Solitary	.08	-.29	.12
Fearful of conspecifics	.31	-.16	.08
Friendly to conspecifics	-.36	.22	-.30

Note: Salient loadings are in boldface.

Table 2
Clouded leopard factor structures of mean trait ratings

Item	Principal components analysis: Varimax rotation		
	Neuroticism	Agreeableness/ Openness	Dominance/ Impulsiveness
Self assured	-.95	-.14	-.00
Insecure	.91	-.17	.06
Fearful of people	.89	-.38	-.06
Cool	-.88	.28	-.28
Suspicious	.86	-.15	.34
Calm	-.85	.13	-.34
Eccentric	.79	.24	.31
Solitary	.78	-.24	.01
Trusting	-.72	.54	-.18
Tense	.69	-.34	.47
Smart	-.69	.08	.26
Stable	-.61	-.25	-.61
Independent	-.61	-.60	-.06
Vigilant	.59	.33	.51
Friendly to conspecifics	-.57	.48	.00
Distractible	-.06	.93	-.13
Playful	-.03	.91	.15
Curious	.00	.89	-.03
Affectionate	-.45	.80	-.02
Friendly to people	-.52	.79	.08
Cooperative	-.27	.77	.13
Active	-.30	.77	.50
Excitable	.44	.67	.50
Aggressive to people	.46	-.62	.46
Vocal	-.45	.55	.46
Timid	.23	.51	.05
Erratic	.17	.05	.91
Reckless	-.07	-.05	.79
Impulsive	.30	.37	.79
Aggressive to conspecifics	.34	-.31	.73
Dominant	.02	.04	.67
Predictable	.32	-.37	-.66
Individualistic	.14	.07	.59
Submissive	-.35	.04	-.54
Anxious	.52	-.06	.54
Constrained	.10	-.41	-.53
Bullying	.32	-.08	.46
Jealous	-.02	.40	.42
Aimless	.35	.14	.21

Note: Salient loadings are in boldface.

Table 3
Snow leopard factor structures of mean trait ratings

Item	Principal components analysis: Varimax rotation		
	Neuroticism	Impulsiveness/ Openness	Dominance
Trusting	-0.91	.08	-.01
Friendly to people	-0.86	.18	-.14
Suspicious	.85	-.10	.43
Fearful of people	.83	.02	.38
Affectionate	-0.80	.18	.26
Aggressive to people	.79	-.16	-.16
Cool	-0.72	-0.53	.06
Stable	-0.66	-.29	-.05
Calm	-0.65	-0.53	.32
Individualistic	.63	-.27	.09
Timid	.62	.09	.58
Anxious	.60	.50	-.01
Insecure	.59	.19	.52
Distractible	.54	.31	.42
Active	-.02	.87	.15
Curious	-.14	.85	.20
Playful	.18	.79	.42
Excitable	.10	.76	-.17
Reckless	-.17	.70	-.46
Impulsive	.44	.69	.18
Eccentric	.08	.61	.00
Bullying	.01	.02	-.87
Stingy	.06	.45	-.82
Aggressive to conspecifics	-.05	-.24	-.82
Predictable	.22	-.34	.77
Friendly to conspecifics	-.19	.38	.75
Submissive	.17	.08	.70
Solitary	-.11	-.49	-.70
Vocal	-.04	.10	.69
Jealous	-.01	.51	-.67
Erratic	.38	.42	-.62
Cooperative	.07	-.07	.60
Constrained	-.12	-.31	.44
Vigilant	-.04	.44	-.24
Fearful of conspecifics	.34	.09	-.09
Deliberate	.29	-.18	.12
Self-assured	-.30	-.43	.19

Note: Salient loadings are in boldface.

Table 4
African lion factor structures of mean trait ratings

Item	Principal components analysis: Varimax rotation		
	Neuroticism	Impulsiveness	Dominance
Fear of people	.88	.01	-.14
Insecure	.84	.42	-.20
Tense	.84	.47	-.16
Timid	.84	.20	-.24
Fearful of conspecifics	.82	.37	-.31
Deliberate	-.80	-.27	.27
Constrained	.79	.35	-.31
Trusting	-.79	.13	-.21
Self assured	-.78	-.49	.31
Suspicious	.74	.04	-.28
Anxious	.72	.65	-.16
Submissive	.71	.47	-.39
Persevering	-.69	.06	.35
Stable	-.67	-.52	-.07
Solitary	.61	-.01	-.50
Calm	-.60	-.53	-.37
Affectionate	-.59	.22	-.22
Decisive	-.56	-.28	.54
Quitting	.55	.02	-.66
Friendly to conspecifics	-.55	.07	-.22
Smart	-.52	-.51	-.27
Curious	-.51	.46	.07
Dominant	-.51	-.48	.63
Cool	-.48	-.44	.02
Aggressive to conspecifics	-.43	.05	.74
Active	-.03	.77	.00
Erratic	.26	.75	.14
Eccentric	-.19	.75	-.16
Distractible	.29	.71	-.25
Aimless	.11	.70	-.20
Excitable	.39	.69	-.31
Reckless	-.28	.65	.35
Playful	-.23	.59	-.37
Independent	-.28	-.57	-.28
Vocal	-.29	-.44	.41
Jealous	-.19	.00	.82
Stingy	-.20	-.16	.77
Aggressive to people	.11	.16	.74
Bullying	-.36	-.28	.74
Friendly to people	-.34	-.02	-.56
Individualistic	-.05	.07	-.42
Cooperative	-.09	-.12	.05

Note: Salient loadings are in boldface.

Table 5
Overall felid factor structure of mean trait ratings

Item	Neuroticism	Dominance	Impulsiveness
Trusting	-.85	.05	-.07
Fearful of people	.80	-.22	.01
Friendly to people	-.76	-.26	.16
Suspicious	.75	-.13	.28
Affectionate	-.73	-.32	.18
Insecure	.67	-.56	.26
Friendly to conspecifics	-.67	-.29	.05
Tense	.66	-.44	.34
Aggressive to people	.60	.52	.17
Cool	-.60	.25	-.42
Cooperative	-.59	-.06	.04
Playful	-.58	-.18	.57
Solitary	.56	-.08	-.10
Calm	-.55	.24	-.48
Anxious	.54	-.48	.32
Timid	.54	-.57	.14
Active	-.51	.08	.60
Self-assured	-.49	.62	-.35
Stable	-.48	.13	-.50
Fearful to conspecifics	.41	-.38	.12
Dominant	.05	.78	.06
Deliberate	.08	.68	-.27
Aggressive to conspecifics	.35	.66	.23
Stingy	.07	.64	.26
Decisive	-.14	.64	-.27
Persevering	-.17	.61	.13
Constrained	.24	-.60	-.14
Submissive	.07	-.58	.15
Bullying	.06	.55	.12
Jealous	-.02	.47	.47
Vigilant	.11	.43	.24
Impulsive	.16	.16	.79
Excitable	-.22	-.01	.74
Erratic	.28	.01	.72
Eccentric	.18	.12	.70
Reckless	.03	.13	.67
Distractible	-.16	-.06	.59
Aimless	.09	-.09	.58
Predictable	.5	.17	-.56
Individualistic	.20	.33	.38
Curious	-.38	.34	.33
Vocal	-.38	.18	.27
Quitting	.17	-.38	.09
Smart	-.23	.34	-.24
Independent	.13	.33	-.30

Note: Salient loadings are in boldface

Table 6

Congruence between orthogonal Procrustes rotations among felid species personality factors

Species factors	Cat N	Cat I	Cat D	SWC D	SWC A	SWC SC	CL N	CL A/O	CL D/I	SL N	SL I/O	SL D	Lion N	Lion I	Lion D
Cat N	xx	xx	xx	.89			.86			.82			.80		
Cat I	xx	xx	xx		.76			.75			.78			.71	
Cat D	xx	xx	xx						.58			.51			.61
SWC D	.89			xx	xx	xx			.74	.70			.82		
SWC A		.76		xx	xx	xx	.71				.70			.72	
SWC SC				xx	xx	xx		.64				.39			.65
CL N	.86				.71		xx	xx	xx	.73			.71		
CL A/O		.75				.64	xx	xx	xx		.78			.67	
CL D/I			.58	.74			xx	Xx	xx			.57			.51
SL N	.82			.70						xx	xx	xx	.72		
SL I/O		.78			.70					xx	xx	xx		.81	
SL D			.51			.39			.57	xx	xx	xx			.32
Lion N	.80			.82			.71			.72			xx	xx	xx
Lion I		.71			.72			.67			.81		xx	xx	xx
Lion D			.61			.65			.51			.32	xx	xx	xx

Cat = domestic cat; SWC = Scottish wildcat; CL = clouded leopard; SL = snow leopard; Lion = African lion

N = Neuroticism; I = Impulsiveness; D = Dominance; A = Agreeableness; O=Openness; SC = Self Control

Note: .70 and above indicates moderate agreement; .80 and above indicates high agreement; .90 and above indicates equality

Table 7

Comparison of domestic cat, Scottish wildcat, snow leopard, clouded leopard, and African lion personality domains with other species

Item	Current study					Other research ¹					
	Domestic cat	Scottish wildcat	Snow leopard	Clouded leopard	African lion	Cheetah ²	Snow leopard	Tiger	Orangutan ³	Chimpanzee ³	Rhesus macaque
Active	I+	D+	I/O+	A/O+	I+	VE+	AV+	E+	E+	E+	AC+
Affectionate	N-	D-	N-	A/O+	N-				A+	E+	F+
Aggressive to conspecifics	D+	D+	D+	D/I+	D+	A+		A+	D+	C-	D-
Aggressive to people	N+	D+	N+	A/O-	D+	A+					
Aimless		SC-			I+						
Anxious	N+		N+	D/I+	N+		TA+		N+	D-	AN+
Bold											
Bullying	D+	D+	D+	D/I+	D+				D+	D+	D+
Calm	N-	SC+	N-	N-	N-	TF-	CSA+				
Clumsy			I/O+						I-	C-	AC-
Constrained	N+	D-	D-	D/I-	N+						
Cool	N-	SC+	N-	N-	N-				N-	N-	AN-
Cooperative	N-	A+	D-	A/O+			FH+				
Curious	I+	A+	I/O+	A/O+	N-	TF-	CP+	Y+	E+	O+	O+
Decisive		SC+			N-				I+	D+	F+
Defiant			D+						D+	C-	D+
Deliberate		D+			N-						
Distractible	I+		N+	A/O+	I+					C-	CO-
Dominant	D+	D+		D/I+	D+				D+	D+	D+
Eccentric	I+	D+	I/O+	N+	I+	VE+	TA+				
Erratic	D+		N+	D/I+	I+				N+	C-	AN+
Excitable	I+	D+	I/O+	A/O+	I+	VE+	TA+	Y+	N+	N+	D+
Fearful of conspecifics		A-			N+	TF+			N+	D-	CO-
Fearful of people	N+	A-	N+	N+	N+	TF+	TA+				
Friendly to		D-	D-	N-	N-				A+	E+	F+

conspicifics										
Friendly to people	N-	A+	N-	A/O+	D-		FH+			
Gentle			N-					D-	A+	D- A+
Impulsive	I+	D+	I/O+	D/I+			Y+	N+	C-	O+ E+
Independent	I-	D+		N-	I-			I+	D+	D+ N-
Individualistic	D+		N+	D/I+	D-				E-	D+ O+
Inquisitive			I/O+					E+	O+	O+ O+
Insecure	N+	A-	N+	N+	N+	TF+	TA+			
Inventive			I/O+					E+	O+	O+ O+
Irritable			N+					D+	C-	D+ A-
Jealous	D+	D+	D+	D/I+	D+			D+	C-	AN+ A-
Persevering	D+	SC+			N-			D+	D+	F+ C+
Playful	I+	A+	I/O+	A/O+	I+	VE+	CP+	Y+	E+	E+ AC+ E+
Predictable	D+	SC+	D-	D/I-				N-	C+	AC- C+
Quitting		SC-			D-				C-	AN+ C-
Reckless	I+		I/O+	D/I+	I+			D+	C-	D+ C-
Self-assured	N-	SC+	I/O-	N-	N-	TF-	CSA+			
Smart				N-	N-	VE+		A+	I+	D+ F+ O+
Solitary		SC-	D+	N	N+			E-	E-	F- E-
Stable	N-	D-	N-	N-	N-			N-	N-	CO+ N-
Stingy	D+	D+	D+		D+			D+	D+	D+ A-
Submissive	D-		D-	D/I-	N+			D-	D-	CO- A+
Suspicious	N+	A-	N+	N+	N+					
Tense	N+	SC-		N+	N+	TF+	TA+			
Timid	N+	A-	N+	A/O+	N+		TA+	N+	D-	CO- E-
Trusting	N-	A+	N-	N-	N-		FH+			
Vigilant		D+	I/O+	N+			AV+	E+		
Vocal		A+	D-	A/O+	I-	VE+				

¹ Other research as follows: cheetah (Wielebnowski, 1999), snow leopard (Gartner & Powell, 2012), tiger (Phillips & Peck, 2007), orangutan (Weiss et al., 2006), chimpanzee (Weiss et al., 2009), rhesus macaque (Weiss et al., 2011), human (Goldberg, 1990; Costa & McCrae, 1992).

¹Cheetah data from Wielebnowski (1999), factor loadings $\geq |.6|$ salient. Because this study used $\geq |.4|$ as a cutoff, we included traits that fell within this rule.

³These studies used a very similar scale as the one used in the current study; research that is not footnoted used substantially different scales.

Key. Scottish wildcats: SC=Self Control; cheetahs: A=Aggressive, VE=Vocal/Excitable, TF=Tense/Fearful; snow leopards: AV=Active/Vigilant, CP=Curious/Playful, CSA=Calm/Self Assured, FH=Friendly to Humans, TA=Timid/Anxious; tiger: Y=Youthfulness; all other species: A=Agreeableness, C=Conscientiousness, D=Dominant, E=Extraversion, I=Impulsive, N=Neuroticism, O=Openness

