Personality Structure in Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

Comparative studies can help identify selective pressures that contributed to species differences in the number and composition of personality domains. Despite being adapted to an aquatic lifestyle and last sharing a common ancestor with primates some 95 million years ago, bottlenose dolphins (*Tursiops truncatus*) resemble nonhuman primate species in several behavioral and cognitive traits. For example, like chimpanzees (*Pan troglodytes*), dolphins live in fission-fusion societies, use tools, and have relatively large brains. To determine the extent to which these and other factors contribute to the evolution of personality structure, we examined personality structure in 134 bottlenose dolphins. Personality was measured in 49 dolphins using a 42-item questionnaire, and in 85 dolphins using a version of the questionnaire that included 7 additional items. We found four domains. Three—openness, sociability, and disagreeableness—resembled personality domains found in nonhuman primates and other species. The fourth, directedness, was a blend of high conscientiousness and low neuroticism, and was unique to dolphins. Unlike other species, dolphins did not appear to have a strong dominance domain. The overlap in personality structure between dolphins and other species suggests that selective pressures, such as those related to group structure, terrestrial lifestyles, morphology, and social learning or tool use are not necessary for particular domains to evolve within a species.

Introduction

An ongoing goal of personality research is to understand the evolutionary origins of personality structure, that is, the number and composition of personality domains, in humans and other animals (Gosling & Graybeal, 2007; Weiss, 2018). Work in humans has shown that personality structure arises from genetic correlations between personality traits (McCrae et al., 2001; Rowe, 1982; Yamagata et al., 2006), and that individual differences in personality traits are associated with fitness-related outcomes, including reproduction (Alvergne et al., 2010; Gurven et al., 2014; Jokela et al., 2011), health, and longevity (Strickhouser et al., 2017). However, although these findings indicate that natural selection may play a role in the evolution of personality structure, it is unclear what selective pressure or pressures led to species similarities and differences in personality structure.

One set of findings that has provided insight into the evolution of personality structure concerns dominance. Broad personality factors or components related to dominance are found in many nonhuman primate species (see Freeman & Gosling, 2010 for a review). In humans, however, dominance tends to be found at lower levels of personality organization, such as the facet level (Costa & McCrae, 1995). These findings may reflect the fact that, unlike humans who have more egalitarian social structures (Boehm, 1999; von Rueden, 2020), many nonhuman primate species form linear hierarchies (Bernstein, 1981; Clutton-Brock & Huchard, 2013; Cowlishaw & Dunbar, 1991; de Ruiter & van Hooff, 1993; Fedigan, 1983; Isbell, 1991; Wittig & Boesch, 2003). In support of this explanation, a study of six macaque species (genus *Macaca*) found that the makeup of personality domains related to social competence and aggression were related to the degree to which the social style of a species was despotic (Adams et al., 2015).

To take another example, conscientiousness, which describes the extent to which individuals pay attention to detail, are diligent, and are self-disciplined, is found at the domain level in humans (Digman, 1990), but similar domains have not been found in all primate species. To date, the only nonhuman primate species that appear to possess a conscientiousness domain include chimpanzees *Pan troglodytes* (e.g., King & Figueredo, 1997) and bonobos *Pan paniscus* (Weiss et al., 2015), both of which are closely related to humans (Glazko & Nei, 2003), and two New World monkey species, namely brown capuchin monkeys *Sapajus apella* (Morton et al., 2013) and common marmosets *Callithrix jacchus* (Iwanicki & Lehmann, 2015; Koski et al., 2017)[1] that are distantly related to humans, chimpanzees, and bonobos (Glazko & Nei, 2003).

Humans, chimpanzees, bonobos, and brown capuchin monkeys typically learn to use tools by watching and practicing in the presence of other individuals using tools, and these other individuals are often the focus of the novices' (visual) attention (Coelho et al., 2015; Deák, 2014; Fragaszy et al., 2017; Nagell et al., 1993; van Schaik et al., 1999; Whiten & van de Waal, 2018). Common marmosets, however, do not use tools, but males and females of this species care for the offspring of other group members; that is, they engage in cooperative breeding (Burkart et al., 2014), which humans may also do (Hrdy, 2009). Thus, factors related to tool use (e.g., being *attentive* towards a demonstrator) and/or cooperative breeding (e.g., being *attentive* towards an infant) may be routes by which conscientiousness evolved in humans and these nonhuman primate species.

Comparative studies with other terrestrial vertebrates also contribute to our understanding of personality structure evolution. For example, horse (*Equus caballus*) personality includes a domain that appears to be a blend of extraversion and agreeableness (Lloyd et al., 2008). Similar domains have been found in Virunga mountain gorillas *Gorilla gorilla beringei* (Eckardt et al., 2015), brown capuchin monkeys (Morton et al., 2013), and

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[1] A third study of common marmosets by Inoue-Murayama et al. (2018) did not find a conscientiousness domain, although that does not appear to be the last word for that sample (Weiss et al., 2020).

macaques (Adams et al., 2015; Brent et al., 2014; Capitanio, 1999; Figueredo et al., 1995; Konečná et al., 2012; Neumann et al., 2013; Rouff et al., 2005; Stevenson-Hinde & Zunz, 1978; Uher et al., 2013; Weiss et al., 2011). Horses, like the aforementioned primate species (Shultz et al., 2011), live in stable groups (McCort, 1984) and form long-term bonds (Cameron et al., 2009). However, unlike these primate species (Hall & Brosnan, 2017; Wheeler, 2009), horses do not engage in behaviors related to tactical deception (Krueger, 2008). Thus, affiliative or other prosocial behaviors may have played a greater role than tactical deception in the evolution of personality domains that are blends of extraversion and agreeableness.

Although comparative studies offer a promising method to help understand how personality structure evolved, they have been largely limited to terrestrial vertebrates. As a consequence, it is too soon to exclude the possibility that factors related to living on land, such as habitat types, locomotion, physical anatomy, diet, and how individuals communicate, are responsible for similarities in personality structure. The importance of studying personality in non-terrestrial species is highlighted by recent studies of marine mammals. Ciardelli et al. (2017) found, for example, an extraversion/impulsivity and dominance/confidence domain in California sea lions (*Zalophus californianus*), which resembled domains found in terrestrial species. Ciardelli et al. also found a reactivity/undependability domain, which resembled the human-directed agreeableness domain that Gosling (1998) found in spotted hyenas (*Crocuta crocuta*). In another study, Úbeda et al. (2019) found three domains—extraversion, dominance, and “conscien-agreeableness”—in orcas (*Orcinus orca*), which resembled the domains found in California sea lions,[2] and a fourth domain, careful, that was not found in California sea lions or in

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[2] Conscien-agreeableness, like human-directed agreeableness, appeared to be reflected versions of reactivity/undependability.

terrestrial mammals. Together, these studies of marine mammals suggest that personality domains like dominance, extraversion, and reactivity/undependability evolved in response to selective pressures other than those related to living exclusively on land, and that the evolution of the domain careful may have been attributable to selective pressures unique to orcas or, perhaps, cetaceans in general.

To extend work on non-terrestrial animals, we obtained data using a personality rating scale designed for another cetacean species, the bottlenose dolphin (*Tursiops truncatus*). Although prior studies of bottlenose dolphins have not examined personality structure, they have demonstrated that observer ratings are stable across time, show satisfactory levels of interobserver agreement (Highfill & Kuczaj, 2007), and are correlated with data from behavioral codings (Moreno et al., 2017) and social network centrality (Díaz López, 2020).

The second aim of our study was to better understand what evolutionary factors contributed to species variation in personality structure. To do this, we compared the structure of bottlenose dolphins to those reported in primates and other species. Unlike primates, for example, dolphins spend most of their lives underwater (Hastie et al., 2003), lack hands for object manipulation, have a diet that consists mainly of fish (Walker et al., 1999), and use echolocation to forage, explore, and navigate their environment (Au, 1993). However, despite these and other differences, and last sharing a common ancestor with primates some 95 million years ago (Kumar & Hedges, 1998), dolphins share several behavioral and cognitive traits with primates, including great apes. Dolphins, for example, form complex social bonds (Lusseau et al., 2006; Moreno & Acevedo-Gutiérrez, 2016), use tools and display cultural traditions (Krützen et al., 2005), engage in prosocial behavior (Nakahara et al., 2017), possess cognitive abilities related to imitation, cooperation, and vocal recognition (Bruck, 2013; Jaakkola et al., 2018; Jaakkola et al., 2010), have non-conceptive sex (Furuichi et al., 2013), and engage in sexual coercion and Machiavellian behavior

(Kuczaj et al., 2001; Wallen et al., 2016). Thus, overlapping dolphin and primate personality structures would suggest that characteristics of primates that are not shared with dolphins (e.g. morphology, diet, terrestrial lifestyles, and sensory perception) are not necessary for such personality domains to evolve, and that the characteristics that primates share with dolphins played a greater role.

Method

Ethics

This and similar studies were declared to be exempt from review by the Research Ethics Committee of the University of Edinburgh. The dolphin facilities were accredited by relevant authorities (IMATA, EAAM, and WAZA) and complied with the ethical guidelines of those authorities as well as local legislation.

Subjects

The subjects were 134 bottlenose dolphins of which 56 were male and 78 were female. Age data were not available for two females. Of the 132 other dolphins, age ranged from 2 to 52 years and the mean age was 16.8 years (*SD* = 10.6). In males, age ranged from 2 to 40 years and the mean age was 14.2 years (*SD* = 11.0). In females, age ranged from 4 to 52 years and the mean age was 18.8 years (*SD* = 9.9).

Dolphins were housed with at least 1 conspecific in 15 facilities located in 8 countries: 7 from Dolphin Discovery in Mexico (Six Flags, Costa Maya, Los Cabos, Isla Mujeres, Cozumel, Vallarata, and Puerto Aventuras) housed 20 males and 37 females, 2 facilities in France (Parc Astérix and Planète Sauvage) housed 8 males and 7 females, the Dolphin Research Center in the United States housed 7 males and 9 females, Dolphin Academy in Curaçao housed 2 males and 5 females, Dolfinarium in the Netherlands housed 6 males and 5 females, Kolmården in Sweden housed 2 males and 6 females, Dolphin Encounters in the Bahamas housed 6 males and 7 females, and Dolphin Discovery in the

Cayman Islands housed 4 males and 3 females. Visitors could touch and/or swim with dolphins at all facilities except for Parc Astérix and Planète Sauvage.

Questionnaire

Dolphins were rated on the Dolphin Personality Questionnaire (see supplementary materials). Printed instructions asked raters to indicate on a 5-point scale the extent to which each item was characteristic of the dolphin (1 = *very uncharacteristic* to 5 = *very characteristic*). The instructions also asked raters to not discuss their ratings among themselves or with others.

The questionnaire included 49 items adopted from primate personality questionnaires (King & Figueredo, 1997; Stevenson-Hinde & Zunz, 1978; Weiss et al., 2009) judged to be relevant to dolphin personality based on a consensus from staff at the Dolphin Research Center who had many years of experience working with dolphins. Each item consisted of a trait label followed by one or more sentences describing the item in the context of dolphin behavior. For example, the descriptor for “Exhibitionistic, flamboyant” was “Behaves as if deliberately trying to attract attention.” A dolphin that scored high on this item might, for example, try to attract attention from visitors or staff as they walk past their aquarium by blowing bubbles or making noises from their blow hole until the human looks at them.

There were four types of items. One type consisted of a single adjective, for example “Aggressive”. Another type consisted of a pair of adjectives, for example “Active, energetic”. A third type consisted of two versions of single trait adjectives with one version referring to the trait in the context of interactions with dolphins, for example, “Sociable (with dolphins)”, and one version referring to the trait in the context of interactions with people, for example, “Sociable (with people)”. The fourth type consisted of two versions of adjective pairs, with one version referring to the trait in the context of interactions with dolphins and another referring to the trait in the context of interactions with people.

Raters and Ratings

There were 82 raters. Raters were staff members who agreed to participate in the study, knew the dolphins that they rated for at least one year, and had observed these dolphins in various contexts (e.g., feeding, training, and visitor swimming programs). Raters from facilities in Mexico completed questionnaires that were translated into Spanish by a native English speaker who was fluent in Spanish and then back-translated by a native Spanish speaker who was fluent in English. All other raters completed the English-language version of the questionnaire. Each rater rated between 1 and 16 dolphins (mean = 6.7, *SD* = 5.8).

One hundred and three dolphins were rated on all 49 items. In addition, due to a clerical error, 31 dolphins—16 at the Dolphin Research Center, 8 at Kolmården, and 7 at the Dolphin Academy—were rated on only 42 of the items. In 2012 (6 years after being assessed on the 42 items) the dolphins at the Dolphin Research Center were rated on the 7 additional items. However, because we did not want to introduce method variance into our data, we omitted ratings of these dolphins on those seven items. Each of the 134 dolphins was rated by between 1 and 13 raters (mean = 4.1, *SD* = 3.5).

Analyses

We used R version 3.6.3 (R Core Team, 2020) to conduct our analyses. Unless otherwise specified, all functions were from version 1.9.12 of the psych package (Revelle, 2019).

Missing Data

We received 548 completed questionnaires. For the 230 ratings of the 31 dolphins rated on the 42-item questionnaire, there were a total of 9660 possible ratings and no missing data. For the 318 ratings of the 103 dolphins who were rated on the 49-item questionnaire, there were a total of 15,582 possible ratings of items. Of these possible ratings, 560 responses were left blank: 1 item was left blank on 39 questionnaires, 2 were left blank on 14 questionnaires, 3 were left blank on 3 questionnaires, 5 were left blank on 8 questionnaires, 7 were left blank on 35 questionnaires, 8 were left blank on 11 questionnaires, 10 were left blank on 2 questionnaires, 11 were left blank on 1 questionnaire, 15 were left blank on 3 questionnaires, and 35 were left blank on 1 questionnaire.

We omitted seven questionnaires in which raters left more than one sixth (nine or more) of the questions blank (cf. Costa & McCrae, 1992; Morton et al., 2013). This cut-point corresponded to the number of missing items that exceeded the 95th percentile. After excluding these ratings, we were left with 230 ratings of the 31 dolphins rated on the 42-item questionnaire and 311 ratings of the 103 dolphins rated on the 49-item questionnaire. We replaced the remaining missing ratings in these data with the mean rating for that item across all non-missing data. Similar methods for handling missing data have yielded correlation matrices similar to those obtained using alternative methods (see, e.g., Costa et al., 1985).

Interrater Reliabilities of Items

For dolphins that had been rated by at least two raters, we used a custom function to calculate two intraclass correlation coefficients (Shrout & Fleiss, 1979) for each of the 49 items. The first intraclass correlation coefficient, $ICC(3,1)$, indicates the reliability of single ratings. The second, $ICC(3,k)$, indicates the reliability of the mean scores across k raters.

Exploratory Factor Analysis

Our factor analyses were based on the mean scores for each trait across raters per dolphin. We followed procedures used in other studies of nonhuman primates (e.g., Weiss et al., 2015), which have been described in Weiss (2017). However, we were forced to deviate from this approach in two ways. First, based on earlier analyses, we included an additional test to determine the number of factors. Second, the results of our initial factor analysis led us to conduct two pre-registered factor analyses.

Our initial factor analysis was based on a correlation matrix obtained from data on all 134 dolphins on all 49 questionnaire items. Because 31 dolphins were not rated on the 7 additional items, we used the corFiml function to obtain the full information maximum likelihood correlation matrix.

Simulation studies indicate that the sample size required for exploratory factor analysis depends on the communalities, that is, the proportion of the variance in each item that is explained by the factors, the number of items, and the number of factors (de Winter et al., 2009; MacCallum et al., 1999; Mundfrom et al., 2005). Similar studies of nonhuman primates have typically found a wide range of item communalities and anywhere from three to six factors. For example, a study of bonobos that were rated on 54 items found item communalities that ranged from .14 to .82 and six factors (Weiss et al., 2015). Based on the aforementioned simulation studies, we determined that, depending on the number of factors, we would need 60 to 100 subjects. The present sample size should thus be adequate.

To determine how many factors to extract, we conducted parallel analyses (Horn, 1965) using the fa.parallel function. Because a recent simulation study showed that parallel analysis is more likely to recover the correct number of *factors* when it tests for the number of eigenvalues from *principle components* that exceed the 95th percentile of 1000 sets of eigenvalues from simulated data (Auerswald & Moshagen, 2019), we examined the results for components. We then used the VSS function to determine the number of factors that led to the lowest Bayesian Information Criterion (BIC; Schwarz, 1978). We judged the degree of evidence against there being no difference between the lowest BIC and the next lowest BIC using criteria described in the second table on page 777 of Kass and Raftery (1995). Specifically, differences in BIC that were equal to or exceeded 2 were evidence against the null hypothesis that the solution with fewer factors did not differ in fit from a solution with more factors. Finally, we checked the scree plots.

After determining the likely number of factors, we used maximum likelihood factor analysis to extract factors and subjected these factors to an orthogonal (varimax) and oblique (promax) rotation. If the oblique rotation yielded factors that differed in their meaning from the varimax-rotated factors, or factors that were highly correlated, we interpreted these factors. Otherwise, we interpreted the varimax-rotated factors.

As in previous studies (e.g., Weiss et al., 2015), for interpreting factors, we defined salient loadings as those equal to or greater than |.4|. When labeling factors, to the extent that it was possible, we used labels from the human and animal personality literature. As such, if a factor resembled a five-factor model domain or facet (Costa & McCrae, 1995), or a domain found in multiple species, such as dominance (Freeman & Gosling, 2010), we assigned this factor the same label. In cases where factors appeared to be a blend of two or more domains, we based our label on comparable human personality styles (Costa & McCrae, 1998) or types (Vollrath & Torgersen, 2002). In all cases, these labels should be considered tentative until future studies establish the nomological network of the factors (Cronbach & Meehl, 1955).

We preregistered two of our factor analyses (10.17605/OSF.IO/3CWJE) with the Open Science Foundation website (https://osf.io/3cwje). We conducted these analyses to address the importance of considering an item’s context when analyzing dolphin personality ratings (Kuczaj et al., 2012). As such, for the first pre-registered analysis we excluded items that referred to “people” and in the second we excluded items that referred to “dolphins”. Each pre-registered analysis was therefore based on 42 items. Based on the results of simulation studies described earlier, we determined that, depending on the number of factors, we would need from 60 to 130 subjects. We used the same approach as in our initial analyses to determine the number of factors and to extract, rotate, interpret, and label the factors.

Interrater and Internal Consistency Reliabilities of Factors

To determine the interrater reliabilities of individual ratings and mean ratings for our factors, we computed unit-weighted factor scores (Gorsuch, 1983) by assigning each item to a factor. Items were assigned to a factor if they had the highest salient loading on a factor. We then assigned a weight of +1, -1, or 0 to each loading depending on whether the loading was salient and positive, salient and negative, or not salient, respectively. We used the alpha function to obtain internal consistency reliabilities (Cronbach's alphas) for each factor based on the items that made up the factor score.

Results

Interrater Reliabilities of Items

All of the interrater reliabilities were greater than zero (see Table 1). Therefore, consistent with previous studies (e.g., Weiss et al., 2015), we did not exclude any items from further analyses.

Table 1

Interrater Reliabilities of the 49 Items

Item	*ICC*(3,1)	*ICC*(3,*k*)
Dominant [a]	.59	.87
Active, energetic [a]	.56	.85
Submissive [a]	.53	.83
Intelligent [a]	.52	.83
Distractible [b]	.50	.76
Playful [a]	.49	.81
Temperamental [a]	.49	.81
Friendly (to people) [a]	.48	.81
Clumsy [a]	.48	.75
Jealous [a]	.47	.80
Cunning [a]	.45	.79
Fearful, nervous [a]	.45	.78
Lazy [a]	.45	.78
Suspicious [a]	.45	.79
Bold, brave [a]	.44	.78
Erratic [a]	.44	.78
Exhibitionistic, flamboyant [a]	.43	.78
Stubborn [a]	.43	.77

Calm, equable (with people) [a]	.42	.76
Enthusiastic, spirited [a]	.42	.77
Creative, inventive [a]	.41	.76
Sociable (with people) [a]	.41	.76
Curious, inquisitive [a]	.40	.75
Friendly (to dolphins) [a]	.40	.75
Shy, timid [a]	.40	.76
Flexible, adaptable [a]	.39	.74
Impulsive [a]	.39	.74
Easygoing [a]	.38	.74
Helpful (to people) [a]	.37	.73
Predictable, consistent [a]	.37	.73
Punctual, prompt [a]	.37	.73
Affectionate, warm (with people) [a]	.35	.71
Calm, equable (with dolphins) [a]	.35	.71
Independent [a]	.34	.70
Helpful (to dolphins) [a]	.33	.69
Scatterbrained [a]	.33	.69
Aggressive [a]	.32	.68
Cautious [a]	.32	.68
Irritable [a]	.32	.68
Excitable [a]	.29	.65
Affectionate, warm (with dolphins) [a]	.28	.64
Sociable (with dolphins) [a]	.28	.64
Vocal [a]	.25	.60
Persistent [a]	.21	.54
Decisive [b]	.19	.44
Thoughtful (of dolphins) [b]	.18	.42
Thoughtful (of people) [b]	.13	.32
Perceptive (of people) [b]	.08	.22
Perceptive (of dolphins) [b]	.06	.17
M	.37	.70
SD	.12	.15

Note. [a] One of the 42 items that all dolphins were rated on; interrater reliabilities of these items were based on 522 observations by 78 raters of 115 subjects ($k = 4.54$). [b] Interrater reliabilities of the seven items were based on the subset of dolphins rated on these items; interrater reliabilities of these items were based on 300 observations by 51 raters of 92 subjects ($k = 3.26$).

Initial Exploratory Factor Analysis

The scree plot (see Figure S1) indicated that there were five, six, or seven factors. Parallel analysis indicated that six components had eigenvalues greater than those obtained from random data (see Figure S2). The lowest BIC (-2548.053) was associated with a four-factor solution. The next lowest (-2545.132) was associated with a five-factor solution. Given these results, we extracted four, five, and six factors, which we rotated using the promax procedure. The fifth factor in the five-factor solution only loaded on the items “Affectionate, warm (with dolphins)” and “Affectionate, warm (with people)”. The sixth factor in the six-factor solution only had unique loadings on the items “Thoughtful (of dolphins)” and “Thoughtful (of people)”; the fifth factor in this solution only had unique loadings on “Affectionate, warm (with dolphins)” and “Affectionate, warm (with people)”. Based on these results, we judged that the five- and six-factor solutions should not be retained.

The four-factor solution explained 48% of the variance, did not include factors that only loaded on the two variants of a single trait, and all four of its factors were interpretable. The factor correlations from this solution ranged from very small to medium in size, and the promax-rotated factors did not differ from their varimax-rotated counterparts (congruence coefficients were equal to .99, .96, .98, and .97). We therefore interpreted the varimax-rotated factors. However, the resulting varimax- and promax-rotated solutions (see Table S1) were problematic in that none of the factors had salient loadings on eight (~16%) and nine (~18%) items, respectively. Moreover, the items that referred to “people” and to “dolphins” measured the same constructs, that is, in nearly all cases, the same factor loaded on both versions of the item. This finding suggests that, by including both versions of the items, we did the equivalent of including the same item twice. Because this might distort the factor structure, we conducted preregistered analyses that only included one version of each of these items.

Preregistered Exploratory Factor Analyses of Dolphin-Directed Traits

The scree plot indicated that there were four or five factors (see Figure S3). Parallel analysis indicated that five components had eigenvalues greater than those derived from random data (see Figure S4). The lowest BIC (-1895.001) was associated with a four-factor solution and the next lowest was associated with a five-factor solution (-1875.723). Given these results, we retained four factors (see Tables 2 and S2) which explained 49% of the variance. Two factor correlations were medium in size with one being close to large. The factor congruences were .98, .98, .94, and .97, with the lowest of these indicating that one of the oblique factors may differ from its orthogonal counterpart. We thus interpreted the promax-rotated factors. The first factor (Directedness) was characterized by loadings that described behavioral consistency and focus, boldness, and low emotional arousal. The second factor (Openness) was characterized by loadings that described a tendency to be active and to investigate the environment. The third factor (Sociability) was characterized by loadings on traits related to extraversion and to agreeableness. The fourth factor (Disagreeableness) was characterized by loadings on items describing a tendency to be aggressive, jealous, despotic, and obstinate.

Table 2

Standardized Loadings (Pattern Matrix) and Factor Correlations for Analysis in Which People-Directed Items were Excluded

Item	Factor				
	Dir ^{R}	Opn	Soc	Dis	h^2
Scatterbrained	**-.96**	-.10	.33	.14	.746
Shy, timid	**-.90**	-.08	.15	-.11	.737
Distractible	**-.83**	-.04	.10	.18	.652
Clumsy	**-.70**	-.10	.17	.02	.416
Submissive	**-.69**	.17	.25	**-.42**	.527
Fearful, nervous	**-.67**	.00	-.17	-.10	.583
Bold, brave	**.58**	.27	.18	.33	.699
Erratic	**-.54**	.15	-.16	.28	.551
Decisive	**.53**	.16	.11	.19	.433
Punctual, prompt	**.43**	.28	.27	-.12	.478
Cautious	-.32	-.30	-.04	-.15	.269
Perceptive	.24	-.02	.08	-.07	.092
Thoughtful	.16	-.15	.12	-.13	.117
Playful	-.07	**.91**	.17	-.24	.767
Active, energetic	.03	**.85**	-.11	-.15	.649
Enthusiastic, spirited	.12	**.82**	.23	-.05	.778
Creative, inventive	.06	**.80**	.14	-.04	.675
Curious, inquisitive	-.04	**.74**	.25	.06	.644

Lazy	-.35	**-.74**	.37	.32	.566
Exhibitionistic, flamboyant	-.13	**.60**	.13	.19	.488
Excitable	-.36	**.60**	-.23	-.06	.537
Intelligent	.38	**.60**	-.10	.06	.533
Vocal	-.01	**.49**	.00	.01	.240
Impulsive	-.35	**.41**	-.10	.29	.504
Persistent	.26	**.40**	.21	.17	.408
Friendly	-.34	.19	**.84**	-.16	.647
Helpful	-.13	.09	**.76**	-.05	.517
Sociable	-.09	.27	**.59**	.11	.393
Predictable, consistent	.18	-.11	**.49**	.02	.356
Easygoing	.36	-.17	**.45**	.01	.498
Suspicious	**-.40**	-.06	**-.45**	-.03	.543
Flexible, adaptable	.27	**.41**	**.44**	-.08	.585
Calm, equable	.31	-.16	**.43**	-.03	.438
Affectionate, warm	-.06	.02	.38	.11	.117
Cunning	.12	.00	-.30	.21	.147
Stubborn	-.27	**-.46**	.22	**.81**	.598
Jealous	-.05	.18	.11	**.69**	.581
Dominant	**.52**	-.14	-.07	**.65**	.592
Aggressive	-.03	.18	.07	**.56**	.414
Independent	.23	-.09	-.05	**.56**	.324
Irritable	-.10	-.03	-.15	**.49**	.322
Temperamental	-.26	.22	-.33	.36	.548
Proportion of variance	.16	.16	.09	.08	

	Factor Correlations			
	Dir	Opn	Soc	Dis
Dir	1.00			
Opn	.08	1.00		
Soc	.49	.04	1.00	
Dis	-.05	.38	-.25	1.00

Note. N = 134. Factors were rotated using the promax procedure. Dir = Directedness, Opn = Openness, Soc = Sociability, Dis = Disagreeableness. Salient loadings are in bold. h^2 = communalities. ^{R} Factor loadings multiplied by -1.

Although we decided to retain four factors, we also extracted five factors, which we subjected to a promax rotation. The first four factors resembled those from the four-factor solution shown in Table 2. The fifth factor loaded on the items “Cautious” and “Perceptive”. One interpretation of this factor is that it was a facet of neuroticism.

Preregistered Exploratory Factor Analyses of Human-Directed Traits

The scree plot indicated that there were four or five factors (see Figure S5). Parallel analysis indicated that four components had eigenvalues greater than those derived from random data (see Figure S6). The lowest BIC (-1984.411) was associated with a four-factor solution. The next lowest BIC (-1967.476) was associated with a five-factor solution. Given these results, we extracted four factors (see Tables 3 and S3) which explained 51% of the variance. Except for one medium-sized correlation, the factor correlations were small. There were no major differences between the varimax and promax-rotated solutions: one congruence coefficient was equal to .96, two were equal to .98, and one was equal to .99. We thus interpreted the varimax-rotated structure. Aside from the fact that the item "Dominant" had its largest loading (.58) on directedness rather than disagreeableness (.50), these factors were nearly identical to those from the previous preregistered analysis.

To test whether the two structures were rotational variants, we used a custom R function to conduct a targeted orthogonal Procrustes rotation (McCrae et al., 1996). For this analysis, the loading matrix was the varimax-rotated structure that included the human-directed items and the target matrix was the varimax-rotated structure that included the dolphin-directed items. The factor congruences were .964, .978, .932, and .946 for directedness, openness, sociability, and disagreeableness, respectively, the congruence for the overall structure was .959, and only five items had congruences below .95 (see Table S4).

Table 3

Standardized Loadings (Pattern Matrix) and Factor Correlations for Analysis in Which Dolphin-Directed Items were Excluded

Item	Factor				
	Opn	Dir ^{R}	Soc	Dis	h^2
Playful	**.87**	-.01	.11	-.13	.779
Enthusiastic, spirited	**.82**	.19	.22	.02	.766
Creative, inventive	**.81**	.15	.08	.02	.679
Curious, inquisitive	**.79**	.07	.12	.09	.647
Active, energetic	**.78**	.06	-.12	-.03	.624
Exhibitionistic, flamboyant	**.65**	-.04	.03	.27	.496

Intelligent	**.61**	**.42**	-.07	.07	.558
Lazy	**-.61**	-.27	.19	.21	.523
Excitable	**.52**	-.33	-.34	.12	.511
Vocal	**.48**	.03	-.06	.07	.237
Persistent	**.48**	.33	.26	.14	.422
Impulsive	**.45**	-.24	-.34	.37	.507
Cautious	-.36	-.33	-.13	-.09	.264
Scatterbrained	-.07	**-.81**	-.09	.21	.721
Shy, timid	-.15	**-.81**	-.18	.01	.712
Distractible	.00	**-.68**	-.19	.31	.602
Submissive	.06	**-.67**	.06	-.30	.545
Bold, brave	**.40**	**.66**	.22	.19	.674
Fearful, nervous	-.08	**-.65**	-.36	.05	.571
Clumsy	-.11	**-.62**	-.12	.11	.426
Dominant	.05	**.58**	-.02	**.50**	.596
Decisive	.22	**.54**	.29	.13	.446
Punctual, prompt	.30	**.42**	**.41**	-.18	.472
Friendly	.22	-.14	**.79**	.06	.699
Helpful	.15	-.02	**.79**	.03	.648
Calm, equable	-.07	.22	**.79**	.02	.677
Easygoing	-.09	.35	**.63**	-.10	.539
Suspicious	-.14	**-.42**	**-.60**	.10	.569
Predictable, consistent	-.04	.21	**.57**	-.07	.372
Temperamental	.25	-.18	**-.56**	**.43**	.587
Sociable	**.52**	-.07	**.55**	.11	.595
Flexible, adaptable	**.46**	.31	**.51**	-.14	.588
Erratic	.18	**-.42**	**-.48**	.35	.563
Thoughtful	-.09	.14	.36	-.02	.159
Cunning	.04	.12	-.32	.21	.162
Perceptive	.08	.10	.22	-.10	.074
Stubborn	-.23	-.13	-.02	**.72**	.593
Jealous	.37	.07	.00	**.67**	.597
Aggressive	.31	.06	.03	**.60**	.462
Irritable	.06	-.05	-.22	**.53**	.338
Independent	.04	.29	-.06	**.51**	.347
Affectionate, warm	.06	.11	.04	-.28	.098
Proportion of variance	.16	.14	.13	.08	

Note. *N* = 134. Factors were rotated using the varimax procedure. Dir = Directedness, Opn = Openness, Soc = Sociability, Dis = Disagreeableness. Salient loadings are in bold. h^2 = communalities. ^{R} Factor loadings multiplied by -1.

Factor Reliabilities

The interrater reliabilities and internal consistency alphas are presented in Table 4. The reliabilities of unit-weighted factor scores that were based on the results of our preregistered analyses ranged from acceptable to excellent.

Table 4

Interrater and Internal Consistent Reliability Estimates for Unit-Weighted Factor Scores Based on Salient Loadings from Varimax-Rotated Factors

Factor	*ICC*(3,1)	*ICC*(3,*k*)	Standardized alpha
Dolphin-oriented			
Openness	.60	.87	.90
Directedness [a]	.59	.87	.86
Sociability	.57	.86	.84
Disagreeableness	.64	.89	.77
Human-oriented			
Openness	.60	.87	.90
Directedness [a]	.63	.88	.87
Sociability	.65	.89	.68
Disagreeableness	.60	.87	.76

Note. Interrater reliability estimates were based on 522 observations of 115 subjects by 78 raters (k = 4.54). [a] Directedness scores were only based on the items with salient items that all dolphins were rated on. We therefore did not include the items decisive, clumsy, and distractible in these scores.

Discussion

We found interrater reliabilities of single ratings for items that were comparable to those found in previous studies of marine mammal personality (Ciardelli et al., 2017; Úbeda et al., 2019). These reliability estimates were also comparable to the repeatabilities of behavioral tests, such as the novel object test, and were, in fact, higher than the repeatabilities found in studies of many vertebrates (Bell et al., 2009). We also found that, in the context of this sample and the types of humans that the dolphins would have interacted with, that, when there were two versions of an item, one referring to “people” and one referring to “dolphins”, both versions loaded on the same factor. In other words, dolphins rated as, for example, “Friendly to dolphins”, tended to also be rated as “Friendly to people”. In two preregistered exploratory factor analyses, one that excluded items directed to people and another that excluded items directed to dolphins, we found evidence for four similar domains, namely openness, directedness, sociability, and disagreeableness. The interrater reliabilities and internal consistency reliabilities of these domains were high.

There were similarities and differences between the personality structure that we found and the personality structures of orcas (Úbeda et al., 2019) and California sea lions (Ciardelli et al., 2017). In terms of similarities, as in the present study, neither the study of orcas nor that of California sea lions found evidence for a neuroticism domain. Similarly, orca extraversion and California sea lion extraversion/impulsivity loaded on many of the same traits that openness loaded on in dolphins. In terms of differences, orca dominance and California sea lion dominance/confidence loaded on many of the same traits that dolphin disagreeableness and directedness loaded on, indicating that the traits related to dominance in dolphins were more weakly intercorrelated than they were in orcas or California sea lions. Orcas and California sea lions also differed from dolphins in terms of the location of items related to conscientiousness. In dolphins, these items loaded onto directedness, which was named after a personality style characterized by high conscientiousness and low neuroticism (Costa & McCrae, 1998). In orcas, these items loaded onto “conscien-agreeableness”, which resembled a style of character related to being an effective altruist (Costa & McCrae, 1998) and careful, which resembled a style of anger control related to being easy-going (Costa & McCrae, 1998). In California sea lions, these items loaded onto reactivity/undependability, which resembled orca “conscien-agreeableness”. Finally, unlike dolphins, neither orcas nor California sea lions appeared to have a sociability domain characterized by traits related to extraversion and agreeableness. Collectively, because our study and the studies by Úbeda et al. (2019) and Ciardelli et al. (2017) used different, albeit partially overlapping, questionnaires, attempts to interpret the evolutionary bases of these differences need to be made with caution until large, multi-site studies of these species are conducted using the same personality questionnaire.

Our finding of a dolphin openness domain supports a pattern seen in primates whereby such dimensions are found in intelligent, group-living species, such as chimpanzees (Dutton, 2008; Freeman et al., 2013; King & Figueredo, 1997) and bonobos (Weiss et al., 2015). Consistent with this explanation is the absence of an openness domain in orangutans *Pongo* spp. (Weiss et al., 2006), which are intelligent species that do not live in stable social groups with continuous and daily physical interactions (Galdikas, 1985a, 1985b, 1985c). Further support comes from a study of horses, which are relatively intelligent (Matsuzawa, 2017), live in stable social groups (McCort, 1984), and have an openness domain (Lloyd et al., 2008). Further studies on taxa varying in intelligence and sociality will help determine the extent to which one or both of these factors contributed to the evolution of openness.

We did not find strong evidence for a dominance domain. Instead, in our preregistered analyses, we found that two cardinal markers of dominance (“Dominant” and “Submissive”) were located between directedness and disagreeableness. These findings are unusual since strong dominance domains surface repeatedly in studies of nonhuman primates (Freeman & Gosling, 2010) and other species (Ciardelli et al., 2017; Gartner, 2014; Gartner & Weiss, 2013; Gosling & John, 1999; Jones & Gosling, 2005; Úbeda et al., 2019). Moreover, with the exception of an early study of personality in dogs that identified a factor labeled “emotion VI” (Cattell & Korth, 1973, pp. 22-23, 26-27), a directedness domain has not been identified in nonhuman primates (Freeman & Gosling, 2010), felids (Gartner et al., 2014; Gartner & Weiss, 2013), marine mammals (Ciardelli et al., 2017; Úbeda et al., 2019), or other species (Gosling, 2001; Gosling & John, 1999). It has also not been found in more recent studies of dogs (Jones & Gosling 2005).

The closest match for this configuration of traits occurs in rhesus macaques. However, in that species, only the item “Dominant” was split between two domains, namely dominance (loading =.57) and confidence (loading = .55) (Weiss et al., 2011). Confidence in rhesus macaques was also more strongly defined by items relating to neuroticism than was directedness in dolphins, the latter being more strongly defined by loadings on items relating to low conscientiousness.

One possible explanation for these findings is that our questionnaire did not sample enough traits related to dominance. However, this explanation can probably be excluded given that, in studies of nonhuman primates, large differences have been identified between the dominance domains of rhesus macaques (Weiss et al., 2011) and, for example, chimpanzees (Weiss et al., 2009), both of which were rated on the same questionnaire. A second possibility stems from the finding that, unlike rhesus macaques (Thierry, 2000), bottlenose dolphins are not especially despotic (Yamamoto et al., 2015). In a similar vein, a third possibility is that, like humans, where traits like “Dominant” and “Submissive” are located between extraversion and agreeableness (McCrae & Costa, 1989; Traupman et al., 2009), dolphin societies are not strongly characterized by a hierarchy. This latter explanation is consistent with the finding that, although captive dolphins express dominance and form social dominance hierarchies, these hierarchies are not always strongly maintained and males’ priority access to females and to food are based on size rather than on the results of contests (Shane et al., 1986). Orcas, however, appear to have a dominance personality domain (Úbeda et al., 2019) despite not showing signs of forming dominance hierarchies (Ford et al., 2011). To rule out one or more of these explanations requires comparative studies of bottlenose dolphins, other cetaceans, and other clades of nonhuman primates using measures that assess a large number of comparable traits. Studies of this sort can be used, for example, to determine whether, to what extent, and in which clades social hierarchies, other forms of competition (e.g., sperm competition), or despotism contribute to the evolution of dominance domains.

Like chimpanzees, bonobos, orangutans, and humans (see Aureli et al., 2008 for a review), dolphins' relationships are structured around fission-fusion groupings (Lusseau et al., 2006; Moreno & Acevedo-Gutiérrez, 2016; Tsai & Mann, 2013) and male dolphins (Connor et al., 1999, 2001; Connor et al., 1992), like male chimpanzees (Gilby et al., 2013), form temporary alliances. Nevertheless, unlike dolphins, chimpanzees (Dutton, 2008; Freeman et al., 2013; King & Figueredo, 1997), bonobos (Weiss et al., 2015), orangutans (Weiss et al., 2006), and humans (Digman, 1990) have independent extraversion and agreeableness factors. Dolphin sociability, instead, is similar to factors found in, for example, brown capuchin monkeys (Morton et al., 2013) and mountain gorillas (Eckardt et al., 2015), which live in stable cohesive groups (Fragaszy et al., 2004; Robbins, 1995). Group structure (e.g. fission-fusion groupings) may therefore not be a sufficient explanation for the evolution of personality factors like sociability and thus other aspects of sociality may be worth examining. More studies are needed on populations and species that differ in group size and structure, as well as the content, quality, and frequency of their social interactions (Hinde, 1976).

Dolphins appear to lack a strong neuroticism domain. Items related to neuroticism are found alongside those related to conscientiousness and so help to comprise the directedness domain. Eckardt et al. (2015) found no evidence for a neuroticism domain in their study of mountain gorillas and proposed that neuroticism may not emerge in species that live in stable and predictable environments. However, dolphins like bonobos (Weiss et al., 2015) lack neuroticism and evolved in relatively unpredictable environments. For example, unlike mountain gorillas, dolphins and bonobos do not live in stable social groups (Aureli et al., 2008; Lusseau et al., 2006; Moreno & Acevedo-Gutiérrez, 2016; Tsai & Mann, 2013) and primarily eat foods that are spatially and temporally dispersed (Gannon & Waples, 2004; Serckx et al., 2015). Even in captivity, where such conditions are arguably ‘more predictable’ than in the wild, social factors still vary for these animals (e.g., births, deaths, or changes in dominance) and diet can change seasonally depending on the availability of items from local markets (F. Blake Morton, personal observation). As such, Eckardt et al.’s proposed explanation is wanting. To further test Eckardt et al.’s hypothesis, research on wild and captive animals must define “environmental unpredictability”, particularly whether those effects are qualitative (e.g., *type* of unpredictability, such as social versus ecological) or quantitative (e.g., *degree* of unpredictability). It will also be important to test whether the degree of neuroticism varies across species as a function of the level of environmental unpredictability that existed *throughout* the evolution of that species, rather than conditions presently experienced by extant species.

Previous findings, such as those from studies of common marmosets (Iwanicki & Lehmann, 2015; Koski et al., 2017), suggest that conscientiousness evolved in species that regularly engage in behaviors that require social attentiveness. Dolphins, however, do not possess a conscientiousness domain despite engaging in socially attentive behaviors (e.g., learning by observation how to use tools; Krützen et al., 2005). Social attentiveness in general, or attentiveness related to social learning and tool use specifically, may therefore not be a necessary and sufficient condition for conscientiousness to evolve. One condition that may be necessary for conscientiousness to evolve is for species to have physical appendages that require attentional control to facilitate physical interactions with the environment, including actions related to object manipulation and providing infant care (Byrne et al., 2009). A finding consistent with this explanation is that something like conscientiousness has been found in Asian elephants *Elephas maximus* (Seltmann et al., 2018), which use their trunks to manipulate tools and other objects. A second finding comes from a study of chimpanzees, which found that conscientiousness is associated with requiring fewer tries to touch an intended target (Altschul et al., 2017). To test this ‘morphology’ hypothesis further, researchers might compare the personality structure of meerkats *Suricata suricatta*, which are cooperative breeders that provide parental care using their hands (Russell et al., 2003), to the personality structure of corvids *Corvus moneduloides*, which learn to make tools by watching others but lack hands to facilitate their learning (Taylor et al., 2012). If morphology—in addition to social attentiveness—is necessary for conscientiousness to evolve, we would expect to find such a domain in meerkats, but not in corvids.

Our findings relating to the absence of neuroticism and dominance domains, and the presence of the directedness domain, should be considered tentative. When we extracted more factors than we were probably justified to, we found evidence that neuroticism and dominance domains *might* exist, but that the questionnaire did not include enough items related to these constructs. It is therefore important to add more items related to neuroticism and dominance to this questionnaire, and then use it to study personality in bottlenose dolphins and other cetaceans. Further work is also needed using a combination of ratings, behavioral observations, and cognitive task data—all of which can provide *complementary* insights into personality structure (Koski, 2011; Weiss & Adams, 2013).

Our study suggests that dolphin personality resembles that of primates and other terrestrial species, including humans, with the exception that dolphins possess a directedness domain and do not possess a neuroticism domain. The overlap in personality structure between dolphins and other species suggests that selective pressures, such as those related to group structure, terrestrial lifestyles, morphology, and social learning or tool use, are not necessary for particular domains to evolve. Further work on cetaceans, other aquatic mammals, and other vertebrates will lead to a better understanding of the evolutionary forces that unite and divide species that inhabit the surface and depths of our planet.

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