Title

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Authors

de Vere, Amber Jocelyn
Lilley, Malin K.
Highfill, Lauren

Peer reviewed

Do Pinnipeds have Personality? Broad Dimensions and Contextual Consistency of Behavior in Harbor Seals (*Phoca vitulina*) and California Sea Lions (*Zalophus californianus*).

Amber J. de Vere[1], Malin K. Lilley[1] and Lauren Highfill[2]

[1]The University of Southern Mississippi, U.S.A.
[2]Eckerd College, U.S.A.

Personality has now been studied in species as diverse as chimpanzees and cuttlefish, but marine mammals remain vastly underrepresented in this area. A broad range of traits have been assessed only once in each of bottlenose dolphins and California sea lions, while consistent individual differences in a few specific behaviors have been identified in grey seals. Furthermore, the context component of definitions of personality is not often assessed, despite evidence that animals may show individual patterns of behavioral consistency across contexts. The current study therefore aimed to use behavioral coding to assess underlying personality factors and consistency across contexts in two marine mammal species: California sea lions and harbor seals. In both species, two personality factors were extracted using exploratory factor analysis. Both were broadly similar across species; the first, Boldness, resembled human Extraversion, and to some extent Openness, with sea lions exhibiting a greater social component. The second factor was labeled Routine Activity, and may contain some Conscientiousness-like traits. Species-specific patterns were also identified for interactive behaviors across two contexts. However, there was substantial individual variation in the frequency of these behaviors, as well as some animals who did not conform to group-level trends. This study therefore provides novel evidence for broad personality factors and both group- and individual-level patterns of contextual consistency in two pinniped species.

In non-human animal research, terms such as temperament, behavioral syndromes, and personality have been used synonymously (Gosling & John, 1999; Sih, Bell, Johnson, & Ziemba, 2004). Most share the general requirements of individual differences in behavior that are consistent over time and contexts. When studying non-human personality, behavioral coding is one of the primary methods used, in which the frequency of behaviors selected from species-specific ethograms are recorded across multiple observations (Watters & Powell, 2012). Various statistical methods are used to cluster behaviors into factors, which are interpreted based on the functions of the behaviors they contain. One subset of this method is naturalistic coding, where animals are observed behaving as they choose to without any human intervention (Freeman & Gosling, 2010). The predominantly bottom-up nature of behavioral coding makes it more likely that traits relevant to the focal species are included, therefore lending itself well to unstudied species for which relevant traits are likely not yet known.

Research into non-human animal personality historically concentrated on a small number of behavioral axes, predominantly shy-bold, exploration-avoidance, aggression, activity, and sociability (Réale, Reader, Sol, Mcdougall, & Dingemanse, 2007). However, studies investigating the underlying dimensional structure of a broad range of traits have increased, often using the widely accepted human model of personality, the Five Factor Model (Goldberg, 1990), as a theoretical framework. In this model, an individual high on Openness to Experience is intelligent, perceptive, and curious, while a highly Conscientious one is organized, reliable, and predictable. High Extraversion can be described by traits such as social, playful, and energetic, and Agreeableness refers to friendliness, tolerance, and generosity. Finally, a highly Neurotic individual is fearful,

nervous, and submissive (Goldberg, 1990). The use of this model facilitates comparisons across species, thus providing insight into the evolution of personality. Indeed, such personality structures are now available for a great variety of species, from chimpanzees (King & Figueredo, 1997) to cuttlefish (Carere et al., 2015). While animal studies have replicated all five of the human personality factors, Extraversion, Neuroticism and Agreeableness have emerged most often (Gosling & John, 1999). Openness to Experience has shown slightly lower generality, but this may be at least partially attributable to methodological issues. Conscientiousness emerged as a distinct factor only in chimpanzees and humans (Gosling & John, 1999), although a factor containing traits associated with Conscientiousness has since been found in several other species, including bottlenose dolphins (Highfill & Kuczaj, 2007). Activity did not consistently emerge as a separate factor, while one distinct factor unique to animals, Dominance, emerged in seven species and correlated significantly with dominance rankings (Gosling & John, 1999).

Animal research has also increasingly considered the context component of personality. While there is some disagreement regarding the best way to define context, here it is defined as all external stimuli that can affect an individual (Stamps & Groothuis, 2010). Where context is considered in personality studies, contextual generality is typically measured. Generality refers to patterns of consistency in behavior across contexts for a group of individuals (Stamps & Groothuis, 2009), practically leading to the expectation that an individual who is bolder than another in one context will also be the bolder of the two in a different context. However, evidence is beginning to emerge that identifies the importance of also considering other types of contextual consistency, such as contextual plasticity, which describes patterns of behavior across contexts at the individual level (Stamps & Groothuis, 2009). For example, one individual may be bolder than another in response to a novel person, but not to a novel conspecific. Such individual patterns of contextual plasticity have been identified in bottlenose dolphins, in which only some individuals were consistent in several personality traits across all of three contexts, while other dolphins were consistent across some but not all (Kuczaj, Highfill, & Byerly, 2012). However, broad personality assessments do not often directly assess behavioral consistency across contexts, at either the group or individual level.

Marine Mammal Personality

Despite the well-documented complex social lives and extensive behavioral repertoires of many marine mammals (e.g., Marino, 2002), there has been remarkably little personality research in these animals. The bottlenose dolphin is one of only two marine mammal species to have been assessed on a wide range of traits (Highfill & Kuczaj, 2007). In this species, trait ratings provided evidence for analogs of the five human factors, with remarkable stability between ratings made before and after subjects were displaced by Hurricane Katrina. Members of this species have also been reliably rated on a subset of traits across several contexts: interactions with humans, the environment, and conspecifics (Kuczaj et al., 2012), suggesting individual patterns of contextual consistency.

To date, there is extremely minimal literature describing personality in any pinniped taxa. Only this year was the first trait rating assessment of any pinniped species, the California sea lion, published (Ciardelli, Weiss, Powell & Reiss, 2017). Zookeeper ratings of 16 sea lions revealed three factors: Extraversion/Impulsivity, Dominance/Confidence, and Reactivity/Unreliability. The first of these predominantly contained traits paralleling the human Extraversion and Openness dimensions, while the third resembled Agreeableness and Neuroticism. Finally, Dominance/Confidence showed greatest resemblance to several factors related to dominance in other non-human species, but with a distinct non-aggressive focus.

Beyond this single trait rating paper, there is fairly substantial evidence of stable individual differences on a few specific behavioral axes in wild gray seals. The time spent alert by dominant, resident male seals was highly individually consistent across two consecutive breeding seasons (Twiss & Franklin, 2010). Two subsequent studies then used a remote-control vehicle (RCV) for experimental testing in the field. Pup-checking behaviors by females and aggressive behaviors by males in response to RCV approach were highly repeatable over a short retest interval (Twiss, Culloch & Pomeroy, 2011), and females tested again in the following year showed reasonable consistency, but with large individual differences in the extent of this repeatability (Twiss, Cairns, Culloch, Richards, & Pomeroy, 2012). The authors suggest that this variability could be a result of their small sample size, but there may also be lifetime trends of change in personality traits in these animals, as there are in humans (Roberts, Walton, & Viechtbauer, 2006) that are currently unknown. Within one breeding season, individual pup-checking rates were not consistent between undisturbed and RCV disturbed contexts. The authors attribute these differences in reactivity to the RCV as being indicative of differing positions on a proactive-reactive behavioral axis (Twiss et al., 2012), but these results could also indicate the presence of individually specific patterns of consistency across contexts, as in bottlenose dolphins (Kuczaj et al., 2012). Finally, newly weaned wild seal pups showed individual differences in aggressive, affiliative and checking behaviors across two contexts: exposure to familiar or unfamiliar conspecifics (Robinson et al., 2015).

These studies provide substantial evidence for stable and consistent individual differences in several behaviors in gray seals, and a single trait rating evaluation of California sea lions. However, further broad assessments of a wide range of traits are needed. In particular, a comprehensive behavioral coding evaluation of personality traits in any pinniped species is lacking. Although such an assessment would maximize ecological validity if conducted with a wild population, in practice, it is challenging and time-consuming to reliably identify a sufficient number of animals on enough occasions to collect a substantial amount of behavioral data. Furthermore, assessments of captive populations are not only less challenging, but also may allow individualized welfare provisions to be made. Finally, the behaviors measured in each of the discussed gray seal studies occur on land; it would, therefore, be advantageous to assess a broader behavioral repertoire, including behaviors occurring when pinnipeds are submerged.

Further study of other marine mammals can therefore yield a new source of personality data, with implications for welfare, management, and cross-species comparisons. This study used behavioral coding to provide the first comprehensive assessment of personality using this method in two marine mammal species: California sea lions and harbor seals. At least one reliable personality factor was expected to emerge in each species. There was predicted to be considerable overlap between the factor(s) elucidated across species, although species-specific differences were expected to relate to life-history features. Factors were also expected to show some parallels to human personality factors, given the previously elucidated generality of Extraversion, Agreeableness, and Neuroticism (Gosling & John, 1999). Patterns of both contextual generality and individual plasticity were also examined across two contexts: interactions towards other animals and interactions towards the environment. California sea lions were expected to interact more with other animals compared to harbor seals, due to the former's more social life history (Bigg, 1981). However, individual differences in both species were predicted to occur in the extent to which interactive behaviors were directed towards animals versus the environment.

Method

Subjects

Subjects were eleven California sea lions (*Zalophus californianus*) and seven harbor seals (*Phoca vitulina*) at Six Flags Discovery Kingdom, Vallejo, CA (Table 1). Two of the sea lions gave birth during the data collection period, so data was collected for their pups from birth onwards. Two of the harbor seals were born a few weeks before data collection began, and were weaned during the study period. Analyses were conducted and reported with and without these young animals, to check for potential confounds related to early developmental changes. Animals were housed across three locations: Seal Cove (SC), Sea Lion Stadium (SLS), and the Marine Research Centre (MRC). Seal Cove is a public exhibit, while animals housed at the stadium were involved in daily shows, and/or behavioral training. Two sea lions, numbers 8 and 17, were housed at MRC for the purposes of rehabilitating a rescued animal, number 11, and one of the sea lion mothers and her pup (numbers 15 and 13 respectively) were relocated here during the study to encourage nursing to occur (Table 1).

Table 1
Subject Animal Demographic Information and Location

Animal	Age (years)	Sex	Species	Location
1	13	M	Seal	SLS
2	11	F	Seal	SC
3	10	F	Seal	SC
4	2	F	Seal	SC
5	1	F	Seal	SC
6	0.2	F	Seal	SC/SLS
7	0.2	M	Seal	SC/SLS
8	20	M	Sea lion	MRC
9	20	M	Sea lion	SLS
10	13	M	Sea lion	SLS
11	2	M	Sea lion	MRC
12	0.1	M	Sea lion	SC/MRC
13	0.1	M	Sea lion	SC
14	20	F	Sea lion	SC
15	9	F	Sea lion	SC/MRC
16	4	F	Sea lion	SLS
17	2	F	Sea lion	MRC
18	1	F	Sea lion	SLS

Note: SLS = Sea Lion Stadium, MRC = Marine Research Centre, SC = Seal Cove.

Data Collection

Video recordings were made on two to six days per week over the summer of 2016. Focal follows (Altmann, 1974) were made of each animal for 7.5 min slots, twice a day. Session one focal follow slots were carried out between 7:30 a.m. and 12:30 p.m., and session two slots between 11:00 a.m. and 4:00 p.m. There was always a minimum of 30 min between the two sessions. Within one session, the order in which each location was visited was randomized. Then, within each location, the order in which animals were filmed was randomized. Forty morning and 40 afternoon sessions were collected in total, amounting to 80 focal follows and 10 h of focal follow data for each animal. Less data was collected for the sea lion pups born during the study period (7.5 hours of data for animal 12, 6.75 hours for animal 13). Visitor presence or absence was recorded for each slot, as visitors have previously been found to alter harbor seal behavior (Stevens, Thyssen, Laevens, & Vervaeke, 2013).

Data Analysis

An ethogram was generated from previous studies of pinniped behavior (Hawker, 2006; Hunter, Bay, Martin, & Hatfield, 2002; Olsen, 2013; Renouf, 1993; Smith & Litchfield, 2010; Stevens et al., 2013; Wittmaack, Lahvis, Keith, & Self-Sullivan, 2015). Several novel and/or unexpected behaviors were observed during data collection, so were added to the ethogram (i.e., jaw open/close, hit, chew, push, pool rest, haul to pool, pool to land, pool scan, pushup, whine, open mouth, object obstruction; see Table S1 in the supplementary materials). The frequency of these behaviors during each slot was coded, and then grouped into categories (as defined in ethogram; see Table S1) to deal with low frequencies of some individual behaviors. Some categories were formed based on those established in previous research, such as play and aggression (Hawker, 2006; Hunter et al., 2002; Renouf, 1993), while others were based on clear physical characteristics, such as resting and movement in/out of water. Any behaviors that did not have a clear basis for grouping in this way were retained as separate categories, such as open mouth and jaw open/close. One set of four focal follows per animal (7 h of video recordings) were coded by a second observer, and a second set was re-coded by the primary observer, in order to assess inter- and intra-coder reliability, respectively. Exploratory factor analyses were conducted for each species, using direct oblimin rotation. Analyses were run both including and excluding the two young pups of each species, to provide a check for age effects on any elucidated dimensional structure.

For context analyses, four interactive behavioral categories were identified: social play, aggression, mating, and tactile. The frequency of these behaviors in each focal follow was coded according to whether they were directed towards seals, sea lions, humans, or the environment. Mating behaviors occurred too infrequently for inclusion in analyses, as did behaviors directed towards humans. Behaviors directed towards animals of the other species were extremely infrequent, so the seal and sea lion recipient categories were collapsed into an overall animal category. Any focal follow that occurred while a mother was nursing this season's pup were excluded from these analyses, due to the drastically increased interaction between mother and pup, compared to typical interactions between animals. This resulted in the exclusion of all contextual data for the two sea lion pups, who had not weaned by the end of the data collection period.

Two mixed design ANCOVAs were performed. One compared the recipients of tactile behaviors only, while the other combined tactile, social play and aggressive behaviors into overall interactive behavior. Social play and aggressive behaviors were not examined separately because these behaviors only occurred in one context, towards other animals. In each mixed ANCOVA, behavioral frequency was entered as the dependent variable, recipient as the within-subjects dependent variable, and species as the between-subjects variable. Age and visitor presence were included as covariates, as the occurrence of behaviors such as play are known to change with age (Renouf, 1993), and visitor presence can affect overall behavior (Stevens et al., 2013). Given the large potential numbers of between-animal comparisons, individual patterns of consistency were examined descriptively to determine whether all animals conformed to species group-level patterns.

Results

Exploratory Factor Analyses

Inter-observer agreement was above the 80% criterion, at 83.4% for harbor seals and 80.2% for California sea lions. Intra-observer reliability also exceeded the criterion: 88.2% for harbor seals and 90.6% for California sea lions.

Harbor seals. The harbor seal scree plot suggested that three factors be extracted, while MAP analysis recommended two factors. After the removal of several variables, which did not load (likely due to low frequencies), a three-factor model provided a better fit to the data than four or five factors. However, Cronbach's alpha for the third factor was less than 0.4. Two factors were therefore extracted for the final model. Factor loadings were very similar when the youngest two animals were included, with only the maintenance variable decreasing its loading below 0.4 (Table 2). Cronbach's alphas and the percentage of variance explained were also very similar across both analyses (Table 2), and Bartlett's test remained significant, $p < 0.001$, although the KMO measure of sampling adequacy was better when the pups were included, 0.688 versus 0.537. Given these similarities, from this point onwards, interpretation of factors will refer to the analysis containing all harbor seals.

Table 2

Harbor Seal Factor Structure, Percentage Variance, and Cronbach Alphas, With and Without Pups

Behaviors	Factor 1 (Boldness)		Factor 2 (Routine Activity)	
	All	No pups	All	No pups
Move on land	0.856	0.854		
Alert	0.827	0.801		
Move in/out	0.756	0.821		
Tactile	0.680	0.650		
Pattern swim			0.766	0.768
Back swim			0.656	0.568
Surface swim			0.654	0.601
Resting			-0.641	-0.686
Maintenance				-0.437
% variance explained	34.5	28.9	22.4	21.9
Cronbach's alpha	0.736	0.689	0.520	0.551

Factor 1 was labeled Boldness. It contained four positively loaded variables: movement on land, movement in and out of the water, alert, and tactile behaviors. This factor explains 34.5% of total variance, with a Cronbach alpha of 0.736 (Table 2), which exceeds the recommendation of 0.7 for a novel measure (Nunnally, 1978). Resting behaviors loaded negatively on factor 2, while pattern, surface and back swimming loaded positively. This factor was labeled Routine Activity, and explains 22.4% of the total variation, but has a somewhat low alpha of 0.520.

California sea lions. The California sea lion scree plot and MAP analysis both suggested that two factors should be extracted, which proved to be the best fit to the data. Several variables had low loadings below 0.3 and were removed, many of which were due to low frequencies. As with the harbor seal analysis, factor loadings and the percentage of variance explained by each factor were very similar both with and without the youngest animals (Table 3), and sphericity was not violated in either case, $p < 0.001$. Differences between analyses were seen only in the alpha values and KMO sampling adequacy; alphas were slightly better when

these individuals were excluded (Table 3), and KMO was slightly higher, at 0.639 compared to 0.575. As the analyses were highly similar, and alpha values approached or exceeded 0.7 in both, the following interpretations will refer to the analysis containing all sea lions.

Table 3
California Sea Lion Factor Structure, Percentage Variance, and Cronbach alphas, With and Without Pups

Behaviors	Factor 1 (Boldness)		Factor 2 (Routine Activity)	
	All	No pups	All	No pups
Move in/out	0.816	0.827		
Open mouth	0.795	0.836		
Social play	0.771	0.788		
Move on land	0.664	0.709		
Random swim	0.618	0.624		
Aggression	0.554	0.598		
Tactile	0.478	0.616		
Pattern swim			0.825	0.814
Alert			0.739	0.803
Surface swim			0.732	0.710
Resting			-0.606	-0.634
Maintenance			-0.426	-0.491
Cronbach alpha	0.712	0.788	0.676	0.701
% variance explained	27.3	29.8	19.9	21.0

As in the harbor seals, factor 1 was labeled Boldness. It consists of seven variables with positive loadings: movement in and out, open mouth, social play, movement on land, random swimming, aggression, and tactile behaviors. This factor explains 27.3% of the total variation, and has an alpha exceeding 0.7 (Table 3).

Factor 2 was labeled Routine Activity, and contains three variables with positive loadings: pattern swim, alert, and surface swim, as well as two negatively loaded variables: resting and maintenance. This factor has an alpha value of 0.676, and explains 19.9% of the total variation (Table 3). Correlations between factors in both species were negligible, at -0.096 for harbor seals and 0.014 for California sea lions.

Mixed ANCOVAs

For both ANCOVAs, Levene's test was violated. However, the less conservative Hartley's F-max test was significant only for the recipient comparison for tactile behaviors. The violation of homogeneity of variance for this one comparison is interesting in itself, as it demonstrates the greater variability in tactile behaviors performed towards other animals compared to the environment. Furthermore, while this comparison

should be interpreted with some caution, ANOVAs are largely robust to this violation when samples are approximately equal (Glass, Peckham, & Sanders, 1972).

Tactile behavior contextual generality

Within subjects, there was a significant main effect of behavioral recipient on the frequency of tactile behaviors, $F(1,557) = 98.158$, $p < 0.001$, where environment, M (SEM) = 4.893 (0.291), was more frequently the recipient than other animals, M (SEM) = 1.350 (0.178). There was also a significant interaction between recipient and species, $F(1,557) = 12.371$, $p = 0.017$. Both covariates had significant interactions with behavioral recipient; age: $F(1,557) = 5.955$, $p = 0.015$; visitor presence: $F(1,557) = 5.75$, $p = 0.017$, reflecting the decrease in frequency of tactile behaviors with age and in the presence of visitors. Between subjects, there was a non-significant main effect of species, $F(1,557) = 1.173$, $p = 0.279$, with sea lions, M (SEM) = 3.312 (0.236), and seals, M (SEM) = 2.931 (0.250), performing approximately equal frequencies of tactile behaviors. Visitor presence was also not significant, $F(1,557) = 1.507$, $p = 0.22$, but age did significantly affect behavioral frequency, $F(1,557) = 37.715$, $p < 0.001$.

Within both species, there was a significant effect of recipient; sea lions: $F(1,295) = 26.66$, $p < 0.001$; seals: $F(1,264) = 97.61$, $p < 0.001$; tactile behaviors were performed significantly more towards the environment than towards other animals. Seals performed significantly more tactile behaviors towards the environment compared to sea lions, $F(1,560) = 7.38$, $p = 0.007$, while sea lions performed significantly more tactile behaviors towards other animals than did seals, $F(1,560) = 18.4$, $p < 0.001$ (Figure 1).
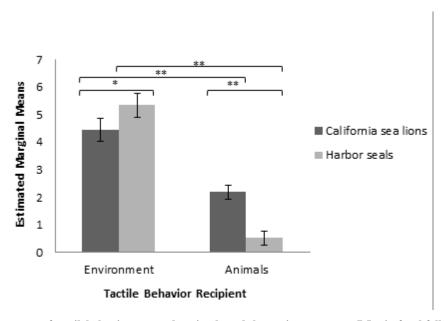

Figure 1. **Mean frequency of tactile behaviors towards animals and the environment per 7.5 min focal follow**. Error bars are ± SEM. Covariates evaluated at the following values: Visitor presence = 0.1365, Age = 5.0215. *$p < 0.01$, **$p < 0.001$.

Interactive behavior contextual generality

Across all interactive behaviors, there was a significant main effect of behavioral recipient, $F(1,557)$ = 10.16, p = 0.002, with behaviors performed more frequently towards the environment, M (SEM) = 4.893 (0.291), than other animals, M (SEM) = 3.164 (0.334). The interaction of recipient with visitor presence was significant $F(1,557)$ = 5.986, p = 0.015, as animals performed fewer interactive behaviors when visitors were present. The interaction of recipient with species was also significant, $F(1,557)$ = 36.415, $p < 0.001$. There was no significant interaction between age and behavioral recipient $F(1,559)$ = 0.324, p = 0.569. Between subjects, there was a significant main effect of species, $F(1,557)$ = 22.312, $p < 0.001$, as sea lions, M (SEM) = 5.063 (0.293), performed interactive behaviors more frequently than seals, M (SEM) = 2.993 (0.311). There was a significant effect of age, $F(1,557)$ = 57.865, $p < 0.001$, as the frequency of interactive behaviors decreased with age, but there was no effect of visitor presence $F(1,557)$ = 0.055, p = 0.815.

There was no significant difference in the frequency of interactive behaviors towards each recipient type for sea lions, $F(1,295)$ = 2.38, p = 0.124, whereas seals performed interactive behaviors significantly more towards the environment than towards other animals, $F(1,264)$ = 34.50, $p < 0.001$. Seals performed significantly more interactive behaviors towards the environment than sea lions did, $F(1,557)$ = 7.38, p = 0.007, while sea lions performed significantly more interactive behaviors towards animals compared to seals, $F(1,557)$ = 48.76, $p < 0.001$ (Figure 2).
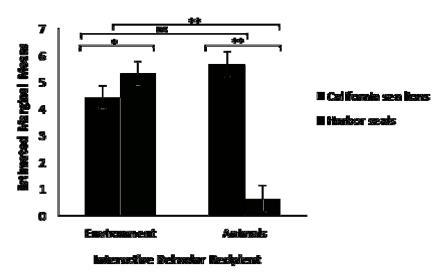

Figure 2. **Mean frequency of all interactive behaviors towards animal and the environment per 7.5 min focal follow**. Error bars are ± SEM. Covariates evaluated at the following values: Visitor presence = 0.1356, Age = 5.0215. *$p < 0.01$, **$p < 0.001$.

Individual contextual consistency

Visual examination of the frequency of interactive behaviors performed by each animal revealed a large amount of individual variation. All seven harbor seals exhibited the group-level pattern of more frequent interactions with the environment, across both tactile behaviors alone and all interactive behaviors, but some seals exhibited much greater frequencies of these behaviors overall (Figures 3 & 4). For sea lions, three individuals were responsible for driving the group-level patterns of contextual consistency: 17, 11, and 10. The other six sea lions interacted more frequently with the environment than other animals (Figure 3), even when social play and aggressive behaviors were included (Figure 4). As in the harbor seals, there is clearly a large amount of variation in the frequency with which individual sea lions perform interactive behaviors.
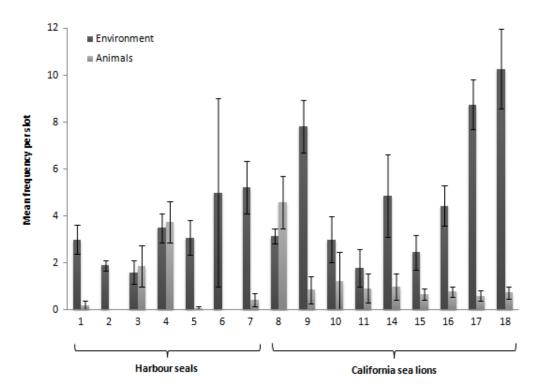

Figure 3. **Mean frequency of tactile behaviors directed towards animal and the environment per 7.5 min focal follow**. Error bars are ± SEM.
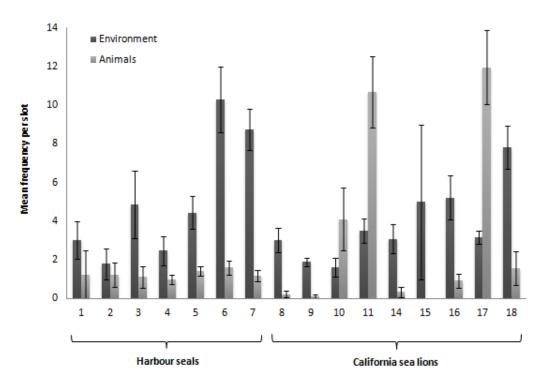
Figure 4. **Mean frequency of all interactive behaviors directed towards animals and the environment per 7.5 min focal follow.** Error bars are ± SEM.

Discussion

Personality Dimensions

  Two broadly similar personality factors emerged in both species. The first of these was labelled Boldness, as the behaviors loading on this factor suggest an active, confident, and investigative individual. In both species, movement in and out of the water and movement on land had strong positive loadings, and, as well as being highly active behaviors, appear to indicate boldness and confidence; the water tended to be used as a safe base from which animals explored, with some individuals consistently waiting for others to move onto land before doing so themselves. These active, confident traits parallel the bold-shy dimension, as well as facets of the human Extraversion factor (Goldberg, 1990), which is consistent with the latter factor's cross-species generality in previous studies (Gosling & John, 1999). Exploratory and curious tendencies are also implied by the positive loading of tactile behaviors, which may be related to Openness (Goldberg, 1990). Interestingly, the trait rating Extraversion/Impulsivity factor found in California sea lions also combines traits from Openness and Extraversion (Ciardelli et al., 2017). California sea lions performed more tactile behaviors towards other animals, which may reflect a species-specific social component; this would be consistent with the more social nature of this species compared to harbor seals (Bigg, 1981). This is further supported by the loadings of social play, open mouth behaviors, and aggression on the sea lion factor. These additional social and excitable elements increase the resemblance between sea lion Boldness and human Extraversion (Goldberg, 1990). There is also a potential developmental trajectory for harbor seal Boldness, as visual

examination of factor scores show a potential decrease with age. Future study is required to determine whether or not this is a valid pattern, particularly given the small number of seals sampled here, as well as the lack of such a pattern in sea lion Boldness scores.

The second factor in both species was labelled Routine Activity, as the positively loaded variables indicate a tendency to perform highly routine behavior. This is inherent in the operational definition of pattern swimming, and surface and back swimming both tended to occur when breaths were taken between loops. Such tendencies show some parallels with dependable and predictable facets of human Conscientiousness (Goldberg, 1990), although this is a tentative interpretation at this stage. There appears to be a greater role for environmental awareness and/or curiosity in the sea lion factor, given the presence of alert behaviors. The loading of resting behavior at the negative pole could be relevant to several factors, depending on its interpretation as indicative of inactivity, laziness, lethargy, or calmness. The self-grooming represented by maintenance in sea lions suggests an additional element of self-care. This factor therefore appears to represent a continuum between active routine behaviors and inactivity, with only the positive pole showing any potential parallels with Conscientiousness.

Contextual Consistency

The same pattern of group-level contextual consistency was seen for harbor seals across tactile behaviors alone, and when combined with social play and aggression. Seals continued to direct substantially more behaviors towards the environment, which can be explained by the low overall frequencies observed of social play and aggressive behaviors. However, California sea lions showed the opposite pattern, overall directing more interactive behaviors towards other animals. In their case, social play behaviors are largely responsible for this group-level pattern. These findings are consistent with the less social nature of harbor seals (Bigg, 1981), and also demonstrates the extremely low occurrence of aggression in this population. Interestingly, the only trait rating assessment of California sea lions found that aggressive traits were dispersed across elucidated factors, and suggested that fewer contexts may arise in stable, captive groups that require aggressive behaviors to be performed (Ciardelli et al., 2017).

As predicted, there was substantial individual-level variation masked by the group-level analyses, therefore providing support for assessing more aspects of contextual consistency than just group level generality (Stamps & Groothuis, 2009). Interestingly, the harbor seals all conformed to the group-level patterns, for both tactile behaviors alone and for all interactive behaviors. However, while all individuals performed animal-directed behaviors with approximately equal (and low) frequencies, there was great variation in the frequency of environment-directed behaviors. The broad pattern seen is somewhat consistent with age, as the young pups interact with the environment most, and the two oldest seals least. However, animals exhibiting intermediate frequencies range in age from one to ten years old, suggesting that there is still some variation not explained by age.

The California sea lions showed even greater individual variation than the seals. Three animals –10, 11, 17 – deviate from the group-level trend for tactile behaviors, as they interacted with the environment and other animals with approximately equal frequency. However, they are responsible for the overall pattern when social play and aggression are included, as they are the only individuals to perform social play and aggression with any appreciable frequency, thus interacting more with other animals than with the environment overall. Two young females, animals 16 and 18, exhibited intermediate frequencies of animal-directed behaviors, but all other sea lions performed more interactive behaviors towards the environment. As in the harbor seals, these

individual patterns do not seem to be solely attributable to age. While animals 11 and 17 are only two years old, animal 18 is a year younger and shows the opposite pattern of interactions. Animal 10 also prefers to interact with other animals, despite being a mature adult male, although he does show lower overall frequencies of interactive behaviors. Age may therefore have greater predictive power for the overall frequency of interactions, while individuals seem to differ in their preferred recipient.

The recipients chosen by this population are also interesting. Not only did inter-species interactions occur rarely for positive behaviors, such as social play, but aggressive interactions were also barely observed. These animals seemingly chose not to physically interact with humans, with such interactions occurring only twice throughout the study period. Although focal follows were not conducted during situations when animals were being asked to perform trained behaviors, they did span times when trainers were in enclosures, such as when cleaning or feeding other animals. These pinnipeds therefore had the opportunity to engage in unreinforced, interactive behaviors towards familiar humans, but seemingly chose not to.

General Discussion

California sea lions and harbor seals can now both be added to the list of species which demonstrate individual differences along behavioral personality dimensions. Future research is needed to validate the existence of these factors across a greater number of individuals, as well as in wild populations of these species. Nevertheless, these findings support the seemingly broad evolutionary conservation of the Bold-shy dimension and Extraversion-like traits (Gosling & John, 1999). The loading of some behaviors potentially indicative of Conscientiousness-like traits suggests that elements of this factor may exist, in some form, in more species than just humans and chimpanzees (Gosling & John, 1999), although this conclusion is extremely tentative, given that such a dimension was not found in ratings of California sea lions (Ciardelli et al., 2017). As ratings of Conscientiousness traits have proven reliable in bottlenose dolphins (Highfill & Kuczaj, 2007), an avenue for future research could be to examine whether there may be selection pressures shared by some marine mammal species and primates that have shaped this aspect of personality.

These results also have possible implications for the welfare of these species. Both are common rescue species in several countries worldwide (e.g., Seal Conservation Society, 2012). Rescued animals must be provided with suitable environments and care while being rehabilitated, and may be unable to be returned to the wild. Greater knowledge of factors such as personality may therefore be useful for optimizing these environments. Furthermore, for those animals unable to be returned to the wild, information about their personality could help inform housing decisions. For example, certain personality traits may make some animals better suited than others for acclimatizing rescued animals to their environment. Using personality assessments in this way may facilitate more effective acclimatization than relying on anecdotal reports of behavior.

It is not novel to suggest that individuals living permanently in managed care facilities may benefit from personality-based housing provisions (e.g., Gartner & Powell, 2012). For instance, individuals who interacted more frequently with other animals may experience the greatest reduction in welfare if separated from other animals. Furthermore, there may be unexplored interactions between personality and enrichment preferences. Animals scoring higher on the exploratory facet of Boldness may show shorter latencies to approach and interact with objects, but may also become bored of these objects faster, and require enrichment objects to be changed more frequently. Alternatively, in some species there is evidence to suggest that more extraverted individuals may show greater resilience to reduced enrichment options (Cussen & Mench, 2015).

At this point, these suggestions are largely speculative, and future research is required to investigate whether a lack of access to such individual-relevant housing features actually does reduce pinniped welfare, and vice versa.

Conclusions

Animal personality research has progressed dramatically in recent years, but many questions remain to be answered, and many species remain unstudied. This study provides the first comprehensive evidence of behavioral personality dimensions in two such species, harbor seals and California sea lions. However, substantial future research is required to validate these dimensions with other methods, as well as to assess their generalizability to other pinniped populations, both captive and wild. Nevertheless, even findings that are not externally valid can still be used to benefit the studied individuals, such as by individualizing housing and management provisions. Future research also cannot assume that all animals in a population exhibit group-typical patterns of behavior across contexts. For example, if this study had not examined individual-level contextual plasticity, one might have concluded that the overall trend for all of the studied California sea lions was to interact more with other animals than with the environment, when in reality this pattern only held true for one-third of the subjects. Overall, this novel personality assessment of two marine mammal species can now hopefully facilitate research that examines the connections between pinniped personality and a range of important outcomes, including rehabilitation and animal welfare.

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Financial conflict of interest: No stated conflicts.
Conflict of interest: No stated conflicts.