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Do Pinnipeds Have Personality? Coding Harbor Seal (*Phoca vitulina*) and California Sea Lion (*Zalophus californianus*) Behavior Across Contexts

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DO PINNIPEDS HAVE PERSONALITY? CODING HABOR SEAL (*PHOCA VITULINA*) AND CALIFORNIA SEA LION (*ZALOPHUS CALIFORNIANUS*) BEHAVIOR ACROSS CONTEXTS.

by

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ABSTRACT

DO PINNIPEDS HAVE PERSONALITY? CODING HABOR SEAL (*PHOCA VITULINA*) AND CALIFORNIA SEA LION (*ZALOPHUS CALIFORNIANUS*) BEHAVIOR ACROSS CONTEXTS.

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Personality has now been studied in species as diverse as chimpanzees (King & Figueredo, 1997) and cuttlefish (Carere et al., 2015), but marine mammals remain vastly underrepresented in this area. A broad range of traits have been assessed only in the bottlenose dolphin (Highfilll & Kuczaj, 2007), while consistent individual differences in a few specific behaviors have been identified in grey seals (Robinson et al., 2015; Twiss & Franklin, 2010; Twiss, Culloch, & Pomeroy, 2011; Twiss, Cairns, Culloch, Richards, & Pomeroy, 2012;). Furthermore, the context component of definitions of personality is not often assessed, despite evidence that animals may show individual patterns of consistency (Kuczaj, Highfill, & Byerly, 2012). The current study therefore aimed to assess underlying personality factors and consistency across contexts in two unstudied marine mammal species, using behavioral coding.

Two California sea lion and three harbor seal personality factors were extracted using exploratory factor analysis. Two factors were broadly similar across species; the first, Boldness, resembled human Extraversion, and to some extent Openness. The second factor was labeled Routine Activity and contained some Conscientiousness-like traits. Excitable-Interest emerged as a third factor in seals but had low reliability. 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 species-level trends. This study, therefore, provides novel evidence for broad personality factors and both species- and individual-level patterns of contextual consistency in two pinniped species.

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Thank you to my friend and fellow graduate student, Mälin Lilley, for the painstaking hours spent coding my data for reliability (particularly of Shark bite).

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DEDICATION

This thesis is dedicated to Alex, without whom none of this would have been possible, and who loves Pirate almost as much as I do.

Thank you to my parents, for their unconditional support and encouragement in everything that I do.

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CHAPTER I - INTRODUCTION

Non-Human Animal Personality

Many definitions have been used to describe personality. In humans, this term tends to be used to refer to individual patterns of thinking, feeling, and behaving (Goldberg, 1990), which are consistent across contexts. These traits are also largely consistent across time, although there are some consistent patterns of change over the course of the human lifespan, until at least middle age (Roberts, Walton, & Viechtbauer, 2006). For non-human animals, terms such as temperament, behavioral syndromes, and personality have been used synonymously (Gosling & John, 1999), but perhaps the most common definition requires there to be individual differences in behavior that are consistent over time and context (Gosling, 2001). However, there are likely species-specific patterns of lifetime change in traits, for which there is some tentative evidence (Bell, Hankison, & Laskowski, 2009), as well as more complex behavioral patterns across contexts.

Behavioral coding has been the primary method used to examine animal personality (Gosling, 2001). Ethograms are used to identify species-specific behaviors, the frequencies of which are then recorded across multiple observations (Watters & Powell, 2012). Interpretations can then be made about underlying personality traits; for example, boldness could be manifested as a short latency to approach a novel object (Weiss & Adams, 2013). Behaviors are correlated to form factors, which are named based on the function of the behaviors they contain. Naturalistic coding tends to be a predominantly bottom-up method, as animals are observed behaving as they choose to without any human intervention, and behaviors are usually selected from species-specific ethograms (Freeman & Gosling, 2010). The alternative method, trait rating, involves human judges rating animals on their tendencies across a range of traits. As these traits are often selected from existing models, this method tends to facilitate cross-species comparisons (Gosling, 2001). However, the nature of behavioral coding makes it more likely that traits relevant to the focal species are included; this method, therefore, lends itself well to unstudied species for which relevant traits are likely not yet known.

Using these methods, research into consistent individual differences in behavior in non-human animals has largely concentrated on behaviors linked to 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 factor structure of a range of traits have increased, typically using the most widely accepted human model of personality, the Five Factor Model (Goldberg, 1990), as a theoretical framework. Such personality structures are now available for many species, including chimpanzees (King & Figueredo, 1997), cuttlefish (Carere et al., 2015), African elephants (Horback, Miller, & Kuczaj, 2013) and domestic dogs (Svartberg, Tapper, Temrin, Radesäter, & Thorman, 2005), among many others. Furthermore, as in human personality research, evidence that these personality structures are stable across populations is beginning to emerge. For example, the six personality factors found in chimpanzees (King & Figueredo, 1997) have been replicated across multiple populations (King, Weiss, & Farmer, 2005; Weiss, King, & Hopkins, 2007; Weiss, King, & Hopkins, 2009).

Animal studies have replicated all five of the human personality factors, some more commonly than others. The most extensive review to date found that Extraversion had been replicated most, with Neuroticism-like factors second and Agreeableness-related third (Gosling & John, 1999). Openness to Experience was slightly less general, but similar factors were still found in more than half of the studied species, and this lower generality may be at least partially attributable to methodological issues. Conscientiousness was substantially less general and was found only in chimpanzees and humans, as well as a combined factor with Openness to Experience in cats and dogs (Gosling & John, 1999). Since this review, a factor containing traits associated with Conscientiousness has been found in several other species, including bottlenose dolphins (Highfill & Kuczaj, 2007). Activity was found in two studies (Gosling & John, 1999), with the age difference at which it disappears in chimpanzees suggesting that it may only be a separate factor during childhood, as in humans (John, Caspi, Robins, Moffitt, & Stouthamer-Loeber, 1994). One 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. This refers to patterns of consistency in behavior across contexts for a group of individuals (Stamps & Groothuis, 2009). Practically, this leads to the expectation that the rank order of individuals' trait scores is retained across contexts, meaning 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. One of these is contextual plasticity, which describes patterns of behavior across different 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 animal. Such individual patterns of contextual plasticity have been identified in bottlenose dolphins. Personality ratings revealed that only some individuals were consistent in several personality traits across all contexts (with environment, with conspecifics, with humans), while other dolphins were consistent across some but not all, and one dolphin was rated differently in all three contexts (Kuczaj, Highfill, & Byerly, 2012). However, behavioral consistency across contexts is not often included in assessments of animal personality, 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, there has been remarkably little personality research in these animals. The bottlenose dolphin is currently the only species to have been assessed on a wide range of traits (Highfill & Kuczaj, 2007). In an initial assessment, traits rated reliably by human judges provided evidence for analogs of the five human factors. A second set of ratings made more than a year after this initial assessment, during which the subjects were displaced by Hurricane Katrina, demonstrated the stability of these personalities. Members of this species have also been reliably rated on a subset of traits across several contexts: interactions with humans, the environment, and other animals (Highfill et al., 2012), suggesting individual patterns of contextual consistency.

To date, there is no literature describing personality factors in any pinniped species. However, there is evidence of stable individual differences on a few specific behavioral axes in wild gray seals. Firstly, a possible indicator of the bold-shy axis was measured in male seals (Twiss & Franklin, 2010). Time spent alert was highly individually consistent across two consecutive breeding seasons. While the sample size in this study was small, this was in part due to the inclusion of only dominant, resident males who spent at least half of their time amongst females during the breeding season, therefore ruling out several possible confounding factors.

The subsequent two studies used a remote-control vehicle (RCV) for experimental testing of gray seals. Pup-checking behaviors by females and aggressive behaviors by males were assessed in response to RCV approach, across a short retest interval of four to twelve days (Twiss et al., 2011). All subjects had significantly repeatable individual responses to the RCV, with no effect of inter-test interval on repeatability. Next, the authors used the same RCV protocol to test females in the following year, in order to assess longer term behavioral consistency (Twiss, Cairns, Culloch, Richards, & Pomeroy, 2012). The responses of seven females were adequately repeatable, but with large individual differences in the extent of this repeatability. The authors suggest that this could be a result of their small sample size, but also identify that the overall trend of behavioral repeatability is to decrease with increased inter-test interval (Bell, Hankison, & Laskowski, 2009). There may also be lifetime trends of change in personality traits in these animals, as there are in humans, that are currently unknown. Pup-checking rates within the second breeding season were not individually consistent across undisturbed and RCV disturbed contexts. The authors attribute individual differences in the extent of reaction 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, individual differences in several behaviors have also been identified in the Scottish Isle of May gray seal colony (Robinson et al., 2015). Over the course of both pilot and main data collection, newly weaned seals were captured into two holding pens. Experimental testing involved placing into a third pen two pups who were either strangers or familiar with each other. Aggressive, affiliative and checking behaviors performed by pups in both conditions were all significantly affected by individual pup identities, demonstrating significant individual differences in each type of behavior across two contexts.

These studies provide substantial evidence for stable and consistent individual differences in several behaviors in gray seals, but an assessment of a broad range of traits in any pinniped species is lacking. Such an assessment would be ideally carried out with a wild population, in order to maximize ecological validity. However, in practice, it would be challenging and time-consuming to reliably identify a sufficient number of animals on enough occasions to collect a substantial amount of behavioral data. Assessment of a captive population may also allow individualized welfare provisions to be made. Furthermore, 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 not hauled out.

Why Study Animal Personality?

Finally, it is important to consider the benefits associated with studying animal personality. Perhaps most significantly, there are welfare implications associated with personality, which has applications for animals in a variety of settings, such as zoo, aquarium, research, farm, and domestic. It has been suggested that empirical personality assessments could be used to improve the assignment of captive animals to specific roles (Watters & Powell, 2012). For example, the roles that zoo animals usually fulfill involve different activities, such as breeding, education, and exhibit. It is, therefore, reasonable that some personality traits may be more beneficial for certain roles, which might increase the success of these programs (Watters & Powell, 2012). There is already some empirical evidence linking personality traits to a range of outcomes, including stereotypic behaviors in chimpanzees (Vandeleest, McCowan, & Capitanio, 2011) and parrots (Cussen, 2013), interactions with enrichment objects in snow leopards (Gartner & Powell, 2012) and chimpanzees (Yamanashi & Matsuzawa, 2010), the effect of visitors on gorillas (Stoinski, Jaicks & Drayton, 2012), breeding success in cheetahs (Wielebnowski, 1999), black rhinos (Carlstead, Mellen, & Kleiman, 1999) and giant pandas (Martin, 2014), and participation in research and training activities in chimpanzees (Herrelko, Vick, & Auchanan-Smith, 2012; Reamer et al., 2014). Nevertheless, there is still a need for further research to understand the relationships between personality and welfare outcomes, but such research requires the existence of data describing the personality of any species of interest.

In several cases, there are now personality studies available for multiple species within a taxonomic group, such as primates (Gosling & John, 1999). This breadth of knowledge permits comparisons between many closely related species, providing an insight into the evolution of personality, and increasing the validity of such cross-species comparisons. Understanding the personality structure of many species may allow inferences to be made about associations between particular life history features and certain personality traits or factors. Furthermore, it is advantageous to have data from many closely related species when studying personality in any previously unstudied species, in order to increase the likelihood of including species-relevant traits and excluding irrelevant ones.

Current Study

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 uses behavioral coding to provide the first comprehensive assessment of personality in two currently unstudied marine mammal species: California sea lions and harbor seals. At least one reliable personality factor is expected to emerge in each species, which will likely show parallels with one or more human personality factors. There is also predicted to be considerable overlap between the factor(s) elucidated across species, although some species-specific differences are expected. Patterns of both contextual generality and individual plasticity are also examined across two contexts: interactions towards other animals and towards the environment. Due to their more social life histories, California sea lions are expected to interact more with other animals compared to harbor seals. However, all individuals are not expected to conform to group-level patterns. Instead, individual differences are predicted to occur in the extent to which interactive behaviors are directed towards animals versus the environment, as well as in the total frequency with which these behaviors occur.

CHAPTER II - METHODS

Ethics Statement

All data collection procedures were approved by the IACUC at the University of Southern Mississippi.

Subjects

Subjects were nine California sea lions (*Zalophus californianus*) and seven harbor seals (*Phoca vitulina*) at Six Flags Discovery Kingdom, Vallejo (Table A1). Two of the sea lions gave birth during the data collection period, but their pups were not included in this study, due to the possible confound of patterns of change in personality traits over the course of their lifetime. Two of the harbor seals were excluded from overall analyses for the same reason, as they were born a month before data collection began. However, they were included for context analyses, as their inclusion did not change the direction or strength of results. Animals were housed across three locations: Seal Cove, Sea Lion Stadium, and Marine Research Center. Seal Cove is the public exhibit, while animals housed at the stadium were involved in the daily shows, and/or behavioral training. Two sea lions, Pebbles and Sarge, were housed at MRC for the purposes of rehabilitating a rescue animal, Shark bite, and one of the sea lion mothers and her pup were relocated here during the study to encourage nursing to occur.

Data Collection

Video recordings were made on 2 to 6 days per week from May 18^{th} to July $27^{th,}$ 2016. Focal follows (Altmann, 1974) were made of each animal for 7.5 minutes, twice a day. Session 1 focal follows were carried out between 7.30 and 12.30pm, and session 2 follows between 11.00am and 4.00pm, with a minimum of 30 minutes between the two sessions. Within each session, the three locations were filmed in a randomized order, with the filming order within each location also randomized. A total of 40 of each session were collected, resulting in 10 hours of focal follow data for each animal. Visitor presence or absence was recorded for each slot, excluding trainers and other facility staff.

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, Thyssen, Laevens, & Vervaeke, 2013; Wittmaack, Lahvis, Keith, & Self-Sullivan, 2015). Several novel and/or unexpected behaviors were observed during data collection, so were added to the ethogram: jaw open/close, hit, chew, push, touch, pool rest, haul to pool, pool to land, pushup, pool scan, bark, whine, mother-pup feeding, open mouth, object obstruction (Table A2). The frequency of each behavior during each slot was coded; as these frequencies were low for some behaviors, they were grouped into categories. 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 basis for grouping into a category were retained as separate categories, such as open mouth and jaw open/close. An exploratory factor analysis was conducted for each species, using direct oblimin rotation. One set of four focal follows per animal (7 hours of video recordings) were coded by a second observer, and a second set was recoded by the primary observer, in order to assess both inter- and intra-coder reliability.

For context analyses, four interactive behavioral categories were identified: social play, aggression, mating, and tactile. The frequency of behaviors in these categories directed towards seals, sea lions, humans, or the environment was coded for each focal follow. Mating behaviors occurred too infrequently for inclusion in analyses, as did any behaviors towards humans. Behaviors directed towards animals of the other species were infrequent, so the seal and sea lion recipient categories were collapsed into an overall animal category. Any focal follows that occurred while a mother was housed with this season's pup were excluded from these analyses, due to the level of interaction between mother and pup being abnormal compared to typical interactions between animals.

Two mixed design ANCOVAs were performed; one compared the recipient of tactile behaviors only, while the other combined tactile, social play and aggressive behaviors into one overall interactive behavioral category. Social play and aggressive behaviors were not examined separately because only animals were recipients of these behaviors, so there were, therefore, no contexts to compare. For both analyses, behavioral recipient was the within-subjects variable, with species as the between subjects variable. Age and visitor presence were included as covariates, as the occurrence of play behaviors is known to change with age (Renouf, 1993), and visitor presence can affect overall behavior (Stevens et al., 2013).

CHAPTER III - RESULTS

Exploratory Factor Analyses

Observer Reliability

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

For harbor seals, the scree plot suggested that three factors be extracted (Figure A1), which was fairly consistent with the suggestion of two factors by MAP analysis (Figure A2). Given the theoretical expectation of around five factors, three, four, and five-factor versions of the analysis were run to test the most appropriate fit for the data. Both the four and five-factor models produced pattern matrices that made little theoretical sense and contained multiple cross-loading items. The three-factor model provided the best fit to the data, after the removal of several variables which did not load (likely due to low frequencies): blow air, jaw open/close, wallowing, mother-pup feeding, feeding, and object obstruction (Table 1). KMO measure of sampling adequacy was adequate (Field, 2013) at 0.537, and a significant Bartlett's test indicated that sphericity was not violated (Table A3).

Factor 1 contained six variables, all with positive loadings: tactile, move on land, movement in/out of water, alert, aggressive, and other vocal behaviors. With a loading of 0.34, aggression fell slightly below the 0.35 cut off, but was maintained for the sake of discussion, and changed the factor-alpha score by only 0.05 if removed. This factor explains 18.2% of total variance (Table A4) and has a Cronbach alpha of 0.625, a value approaching the recommendation of 0.7 as a reasonable value for a novel measure (Nunnally, 1978).

Table 1

Harbor Seal Pattern Matrix

Behaviors	**Factor 1**	**Factor 2**	**Factor 3**
Move on land	0.875		
Move in/out	0.775		
Alert	0.760		
Tactile	0.591		
Other vocals	0.372		
Aggression	0.340		
Pattern swim		0.744	
Surface swim		0.590	
Back swim		0.530	
Resting		-0.706	
Maintenance		-0.445	
Play alone			0.768
Random swim			0.703
Fast dive			0.615
Open mouth			0.398
Social play			0.355

Two behavioral variables loaded negatively on factor 2, maintenance and resting, while three loaded positively, pattern swim, back swim, and surface swim. 13.3% of total variation was explained by this factor (Table A4), with an alpha of 0.551. Finally, factor 3 contained five variables with positive loadings: play alone, social play, random swim, fast dive, and open mouth. This factor explains 10.7% of the variation (Table A4), and has an alpha of 0.364. Despite the direct oblimin rotation method allowing inter-factor correlations, these were very low, with a maximum of -0.096 between factors 2 and 3 (Table A5).

California Sea Lions

The California sea lion EFA scree plot suggested that two factors should be extracted (Figure A3), which was consistent with MAP analysis (Figure A4). Given that theory would suggest a larger number of factors, two, three, and four-factor versions of the analysis were run to find the best fitting model. The three and four-factor analyses did not conform to a simple structure, as they continued to include cross-loading items, as well as making little theoretical sense. In contrast, the two factor analysis produced a clear simple structure with no cross-loading items (Table 2), although several variables were removed due to low loadings below 0.3, several of which were likely due to low frequencies: mating, wallowing, fast dive, back swim, mother-pup feeding, feeding, object obstruction, whine, bark, other vocals. The KMO measure indicated adequate sampling (Field, 2013), at 0.648, and sphericity was not violated (Table A6).

Table 2

California Sea Lion Pattern Matrix

Behavior	**Factor 1**	**Factor 2**
Open mouth	0.839	
Move in/out	0.830	
Social play	0.786	
Move on land	0.697	
Random swim	0.622	
Tactile	0.618	
Aggression	0.579	
Jaw open/close	0.395	
Pattern swim		0.809
Alert		0.806
Surface swim		0.705
Play alone		0.440
Resting		-0.636
Maintenance		-0.491

Factor 1 consists of eight variables with positive loadings: open mouth, movement in/out, social play, movement on land, random swim, tactile, aggression, and jaw open/close. This factor had a high alpha of 0.779 and explains 28.5% of the total variation (Table A7). Factor 2 contains four variables with positive loadings: pattern swim, alert, surface swim, and play alone, as well as two negatively loading variables:

resting and maintenance. This factor also has a good alpha value, 0.701, and explains 19.5% of the total variation (Table A7). The correlation between these two factors was negligible, at only 0.011 (Table A8).

Mixed ANCOVAs & Simple Effects

For both ANOVAs, Levine's test was violated (Table A8 and A9). However, for three of four comparisons, Hartley's F-max test was non-significant, indicating that variances were only substantially heterogeneous for the recipient comparison for tactile behaviors (Table A8 and A9). Comparisons between these groups should, therefore, be interpreted with caution.

Tactile Behaviors

Within subjects, behavioral recipient had a significant effect on the frequency of tactile behaviors [$F(1,557)=98.158$, $p<0.001$]. 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: $F(1,557)=5.75$, $p=0.017$]; this reflected the greater frequency with which younger animals performed tactile behaviors towards the environment compared to older animals, and that animals performed more tactile behaviors towards each recipient when visitors were absent.

Between subjects, species did not significantly affect the frequency of tactile behaviors [$F(1,557)=1.173$), $p=0.279$]. Visitor presence was also not significant [$F(1,557)=1.507$, $p=0.22$], but age did significantly affect behavioral frequency, indicating that younger animals performed tactile behaviors with greater frequency than older individuals [$F(1,557)=37.715$, $p<0.001$].

Simple effects analyses revealed within species and recipient patterns. Within each species, tactile behaviors were performed significantly more towards the environment than towards other animals [sea lions: $F(1, 295)=26.66$, $p<0.001$; seals: $F(1, 264)=97.61$, $p<0.001$]. 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 [$F(1, 560)=18.4$, $p<0.001$]; these patterns are illustrated by Figure 1.

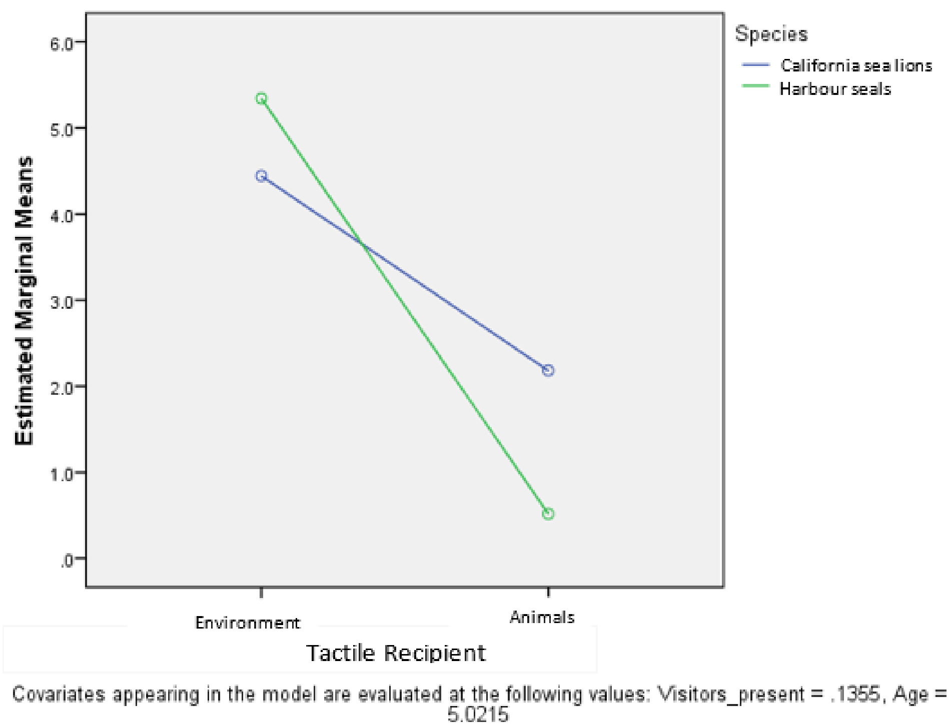

Figure 1. Frequency of Tactile Behaviors Towards Animals and the Environment.

Overall Interactive Behaviors

Across all interactive behaviors, behavioral recipient had a significant within subjects effect on behavioral frequency [$F(1,557)=10.16$, $p=0.002$]. The interaction of recipient with visitor presence was significant [$F(1,557)=5.986$, $p=0.015$], meaning that animals performed fewer interactive behaviors towards each recipient 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 [$F(1,559)=0.324$, $p=0.569$], indicating that there was not a significant tendency for interactive behavioral frequency towards animals or the environment to change with age.

Between subjects, species differed significantly in the frequency of interactive behaviors [$F(1,557)=22.312$, $p<0.001$]. There was a significant effect of age [$F(1,557)=57.865$, $p<0.001$], but not of visitor presence [$F(1,557)=0.055$, $p=0.815$]; this indicated that younger animals performed more interactive behaviors than older ones and that the total frequency with which the animals performed interactive behaviors did not differ when visitors were present versus absent.

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 [$F(1,557)=48.76$, $p<0.001$], as illustrated by Figure 2.

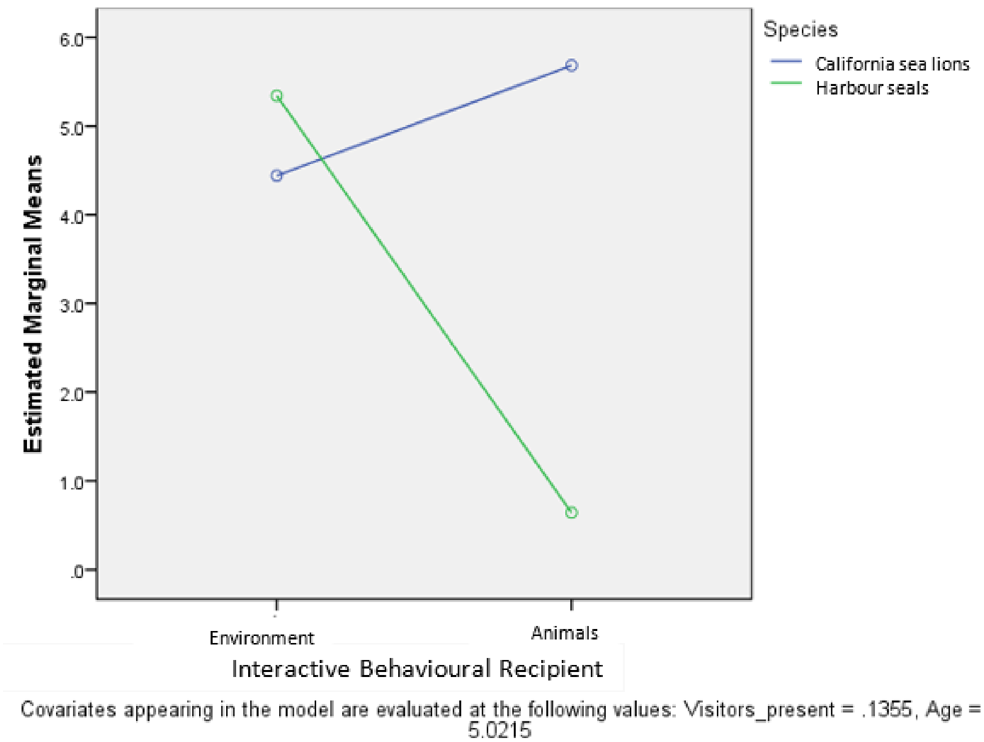

Figure 2. Frequency of Overall Interactive Behaviors Towards Animals and the Environment.

CHAPTER IV – DISCUSSION

Factor Interpretations

Several personality factors were extracted for harbor seals and California sea lions, two of which are largely consistent across species. The first of these can be interpreted as Boldness, which contained several facets of human Extraversion, and accounted for the most variation in behavior for both species. This factor includes movement in and out of the water and travelling on land, both of which are active and suggest boldness or confidence; animals of both species tended to use the water as a safe base from which to explore, getting out of the water less frequently when visitors were present, as well as more cautious animals being less likely to leave the water if another animal had not already done so. Aggression also loaded on each species' first factor, but interpretations based on this should be made with caution, as these behaviors occurred infrequently over the study period. When aggressive behaviors did occur, for sea lions they tended to be initiated when one animal who had been participating in social play tried to move on to another activity. For seals, aggression has a low loading on the factor, but it is nevertheless interesting that it related similarly to other behaviors across both species. Lastly, tactile behaviors loaded strongly on this factor, suggesting exploration, and to some extent sociability, although tactile behaviors were primarily directed towards the environment.

Several behaviors were not shared across species. In seals, this factor also contained alert behaviors and other vocalizations, while the sea lion factor included open mouth, jaw open close, social play and random swim behaviors. The vocalizations exhibited by seals were likely aggressive in nature, but could not be categorized as such based on the operational definitions used for coding. Alert behaviors involve active scanning, whether in the water or on land, which is consistent with the active, exploratory nature of this factor. Three of the four behaviors unique to this factor in sea lions - open mouth, social play, and random swim - instead load onto the third factor in seals, perhaps suggesting slight species-specific differences in the range of traits associated with each factor. Open mouth behaviors most often occurred as part of a period of social play, both of which are consistent with bold, interactive traits; however, the loading of these behaviors on this factor in sea lions, but not seals, suggests that social interactions may play a greater role in this personality dimension in sea lions. Overall, the nature of behaviors loading on the first factor in both species suggests bold, confident, interactive, and active traits, therefore showing broad similarities with the human factor of Extraversion (Goldberg, 1990). The loading of tactile behaviors possibly also suggests exploration and curiosity, paralleling a facet of human Openness (Goldberg, 1990). However, the primary interpretation of this factor is consistent with existing animal personality literature, in which Extraversion has been replicated most frequently (Gosling & John, 1999).

The second factor for both species can be characterized as Routine Activity, containing behaviors indicative of predictability. Strongly loaded at the positive end of this factor is pattern swim and surface swim; surface swims usually occurred as animals breathed between pattern swims, thus both being indicative of routine, repetitive swimming. Consistent with this, back swimming also loaded positively for seals, which tended to be part of transitions in and out of pattern swims. Positively loaded items unique to sea lions were alert behaviors and playing alone. The correlation of alone play with other routine behaviors might seem inconsistent; however, further examination of the raw data reveals that more than half of the play behaviors performed were leaps, where animals jump fully out of the water while swimming on a trajectory, often during pattern swimming. These loadings, therefore, suggest that this end of the factor is more high energy for sea lions compared to seals. Resting and maintenance behaviors loaded at the negative end of the factor in both species, indicating inactivity and self-grooming. These interpretations of behaviors loading onto the positive pole of this factor share similarities with the human factor of Conscientiousness, such as predictability and dependability (Goldberg, 1990). However, behaviors in the negative direction are less consistent with this factor, as they are indicative of inactivity and laziness rather than erraticism. Thus, this factor is labeled Routine Activity but does contain some traits consistent with human Conscientiousness.

A third factor unique to harbor seals was identified. This factor contained five behaviors with positive loadings, although two of these are low (Table 1). Play alone loaded most strongly on this factor, which, in contrast with sea lions, consisted largely of pirouetting and waving behaviors (73% of total frequency). Random swimming and fast diving also both loaded strongly, both of which are indicative of somewhat erratic behavior. Random swimming also suggests interest, as it tended to occur as a transition between play or scanning behaviors. Although the final two behaviors on this factor had low loadings, they are consistent with this interpretation. Open mouth behaviors tended to be performed around social play, which was predominantly made up of nose to nose and hugging behaviors by Maile and Freya towards their pups before they were weaned and following performed most often by Lily and Pip towards Maile or Freya. While all of these behaviors are interactive, they do not require much physical contact or active interaction; they therefore also suggest interest rather than purely playfulness. This factor can, therefore, be characterized as Excitable-Interest, although its low reliability indicates that future replication is required to justify its retention.

Contextual Consistency

Three categories of interactive behaviors were examined: tactile, social play, and aggressive. Tactile behaviors were performed in both contexts, towards other animals and the environment, while social play and aggressive behaviors were only performed towards other animals. Analysis of cross-context patterns for each behavioral category could therefore only be conducted for tactile behaviors. However, overall patterns across contexts were still able to be examined, by using the frequency of tactile behaviors directed towards the environment, compared to the total summed frequency of all tactile, social play, and aggressive behaviors directed towards other animals.

These analyses revealed species-specific, group-level patterns of contextual generality. When tactile behaviors alone were examined, both species more frequently directed these behaviors, such as nosing and biting, towards the environment rather than towards other animals. However, this difference was much more dramatic for seals (Figure 1). When frequencies for each individual were examined, both pups (Pirate and Luna) demonstrated this pattern most dramatically (Figure 4); an analysis run excluding them confirmed that they were not solely responsible for the species-level trend, as this result remained highly significant.

The addition of two further behavioral categories, social play, and aggression, produced the same result in seals, who still interacted dramatically more towards the environment than other animals. In other words, even though social play and aggressive behaviors could only be performed towards other animals, seals still interacted most with the environment. This can be explained by the low overall frequency of social play and aggressive behaviors observed: 122 occurrences of the former and 7 of the latter. However, sea lions showed the opposite pattern, overall directing more interactive behaviors (social play, aggressive, and tactile) towards animals. Therefore, the addition of social play and aggressive behaviors made an appreciable difference only in California sea lions. It is worth noting that social play is largely responsible for this trend, as it occurred more than five times as frequently as aggressive behaviors. These species-level patterns are consistent with the overall more social nature of California sea lions compared to harbor seals, but these frequencies also demonstrate that this population of animals shows low levels of aggression overall.

Individual patterns of contextual consistency were also seen. Within harbor seals, all individuals conform to the group-level pattern, for all interactive behaviors (Figure 3) and for tactile behaviors alone (Figure 4). However, there are substantial individual differences in the total frequency of interactive behaviors, as well as the frequency with which these behaviors were directed towards the environment. For example, while all individuals performed social play, tactile, and aggressive behaviors towards other animals with similarly low frequencies, there is great variability in the frequency of tactile behaviors directed towards the environment (Figure 3). Both Pirate and Luna direct the highest frequency of behaviors towards the environment, with Dyson and Freya performing the least. This is largely consistent with age, given that the former seals are only a few months old, while the latter are the oldest. However, the intermediate animals range in age from one to ten years old, suggesting that there is still some individual variation in the frequency of environment-directed tactile behaviors that is not explained by age.

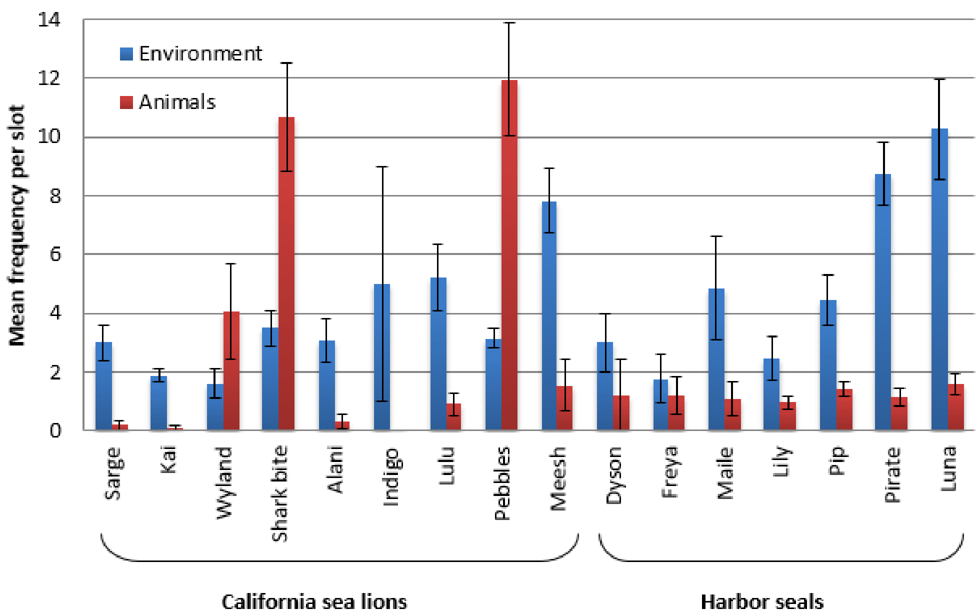

Figure 3. Mean frequency of all interactive behaviors by each individual directed towards animals and the environment, with standard error bars.

Sea lions also demonstrated individual patterns of contextual plasticity. Three animals deviate from the overall trend for tactile behaviors but are responsible for the species-level pattern when social play and aggressive behaviors are included. Pebbles, Shark bite, and Wyland all directed tactile behaviors towards animals and the environment with approximately equal frequency, while the remaining sea lions interacted more with the environment (Figure 4). However, these three animals performed social play and aggressive behaviors frequently, so across all three behavioral categories they interacted dramatically more with other animals (Figure 3). In contrast, all other sea lions still performed more interactive behaviors towards the environment, meaning that they directed little to no tactile, social play, or aggressive behaviors towards other animals. Two of the young females, Lulu & Meesh, are the only individuals to exhibit intermediate frequencies of animal-directed behaviors. These individual patterns, therefore, do not seem to be solely attributable to age; the higher frequencies of animal-directed behaviors are not particularly surprising in Pebbles and Shark bite, as they are only two years old, but Meesh is a year younger than this and shows the opposite pattern. Wyland also prefers to interact with other animals, despite being a thirteen-year-old adult male, although he does show lower overall frequencies of interactive behaviors than the younger animals. As in the harbor seals, there are therefore substantial individual differences in frequencies of these interactive behaviors. For example, Lulu and Kai are housed together and both interact more with the environment than with other animals, but Lulu exhibited substantially more environment-directed tactile behaviors than Kai.

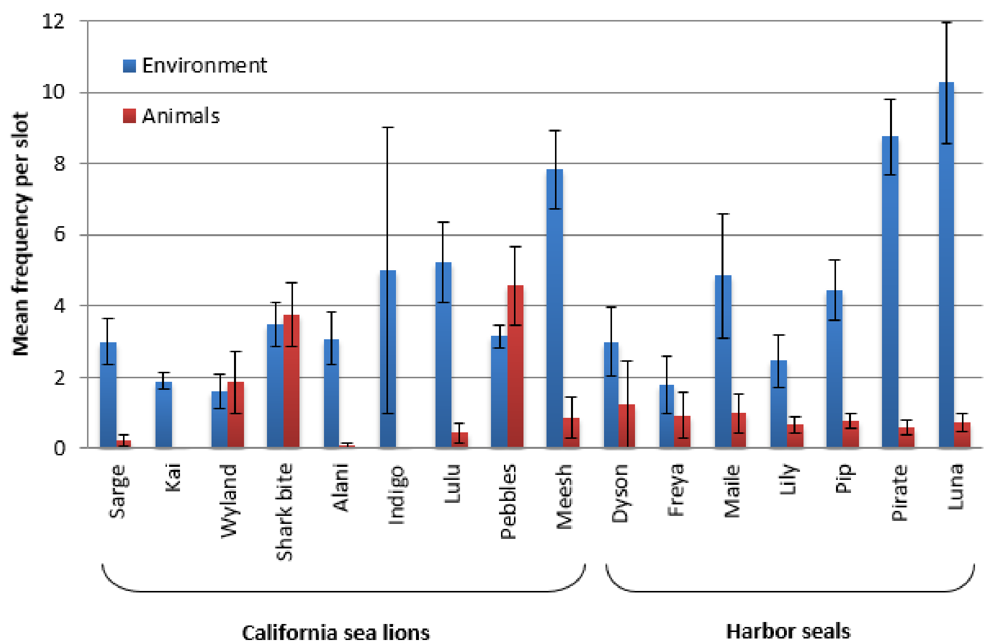

Figure 4. Mean frequency of tactile behaviors by each individual directed towards animals and the environment, with standard error bars.

General Discussion

California sea lions and harbor seals can now both be added to the growing list of species known to have personality. The Boldness factor found in both species broadly resembled Extraversion, which is consistent with its cross-species generality in previous studies (Gosling & John, 1999). A Routine Activity factor also emerged in both species, containing some Conscientiousness-like traits. Excited-Interest emerged as a third factor only in seals, but with low reliability. Future research is now needed to validate the existence of these factors, or not, across a greater number of individuals, as well as in wild populations of these species.

Species and individual level differences were found in the extent to which animals performed interactive behaviors in two contexts: towards other animals versus the environment. It was originally planned to include interactions with seals and with sea lions as separate contexts. However, behaviors were too rarely directed at members of the opposite species to allow such separation, a finding which is interesting in itself. Not only did inter-species interactions rarely occur for positive behaviors, such as social play, but aggressive interactions were also barely observed, with a frequency of only nine over the entire data collection period. Interactions with humans were also intended to be included as a fourth context, but only two such behaviors were observed over the duration of data collection. This may partially be due to focal follows not being conducted during any situations when animals were being asked to perform trained behaviors, to attempt to capture data only when animals were able to behave completely as they chose. However, focal follows were still conducted when trainers were in enclosures carrying out other activities, such as cleaning or feeding other animals. Individuals, therefore, had the opportunity to engage in unreinforced, interactive behaviors towards humans, but seemingly chose not to.

Direct comparisons cannot be made with previous studies of gray seal individual differences across contexts (Twiss et al., 2012), due to the different contexts measured. This is also likely to be the case with future studies, depending on the specific research question of interest, given that the possible range of contexts over which animals could be tested is almost incomprehensible. However, where contexts of interest are similar to those in existing literature, it would be useful for future research to use consistent context definitions, in order to facilitate such comparisons.

Age had a significant effect as a covariate in context analyses, and visual examination of individual patterns confirm that interaction frequencies tended to decrease with age, although some animals did not conform to this pattern (Figures 3 and 4). The individual scores for seals on both Boldness and Excited-Interest decreased with age overall (Figure A5), suggesting possible lifetime patterns of change in these factors, although no such trends can be seen in the sea lion factor scores (Figure A6). Repeated measures of these animals at future time points would be required to confirm the existence of these lifetime patterns of change. Whether there are such patterns in California sea lions and harbor seals across the personality factors found here, therefore, remains an open question for future research.

The results of this study have possible implications for the welfare of harbor seals and California sea lions. In particular, both are common rescue species in the USA, as well as other countries around the world; for example, California sea lions are the most commonly rescued species by the Marine Mammal Center in California, with around 1400 individuals rescued since the center's founding in 1975 ("California Sea Lion", 2016), and approximately 400 harbor seals were rescued between 2000 and 2011 in just one region of the UK (Seal Conservation Society, 2012). Given that 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 be used to optimize these environments. For example, Shark bite was adjusting to the facility during data collection, after stranding and being rescued for a third time, making him un-releasable. Trainers at the facility mentioned that the animals he was housed with, Pebbles and Sarge, were selected based on behavioral tendencies that were thought to be amenable to his acclimatization. With information about the personality of facility animals, housing decisions such as these could be made based on certain traits, such as

Boldness scores, or behaviors, such as aggression, rather than on anecdotal reports of their behavior.

Furthermore, individual factor scores could be used to suggest individualized housing provisions. For example, individuals who interacted more frequently with other animals, such as Pebbles and Shark bite, may experience the greatest reduction in welfare if separated from other animals. It may also be beneficial to ensure that animals who frequently interacted with the environment, such as Meesh and Luna, always have access to a range of enrichment objects. There may also be interactions between personality and preferences for different types of enrichment, such as solid objects versus chewable toys. Animals of both species with high scores on the Routine Activity factor, such as Wyland, may also be most vulnerable to unpredictable changes in housing. Future research is required to investigate whether a lack of access to such individually-relevant housing features actually does reduce welfare and vice versa. Finally, the extremely low frequency of aggressive interactions between species, or indeed interactions of any kind, supports the conclusion that there is no obvious welfare disadvantage, or advantage, to housing California sea lions and harbor seals together, at least in terms of cross-species interactions.

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 evidence of underlying personality dimensions in two such species, harbor seals and California sea lions. However, substantial future research is required to assess the generalizability of these dimensions 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.

APPENDIX A – Subjects & Ethogram

Table A1.

Subject Animal Demographic Information

Animal	**Age (years)**	**Sex**	**Species**	**Parents**
Dyson	13	M	Seal	N/A
Freya	11	F	Seal	N/A
Maile	10	F	Seal	N/A
Lily	2	F	Seal	Maile & Dyson
Pip	1	F	Seal	Maile & Dyson
Luna	0.2	F	Seal	Maile & Dyson
Pirate	0.2	M	Seal	Freya & Dyson
Sarge	20	M	Sea lion	N/A
Kai	20	M	Sea lion	N/A
Wyland	13	M	Sea lion	N/A
Shark bite	2	M	Sea lion	N/A
Alani	20	F	Sea lion	N/A
Indigo	9	F	Sea lion	N/A
Lulu	4	F	Sea lion	Alani & Sarge
Pebbles	2	F	Sea lion	Alani & Sarge
Meesh	1	F	Sea lion	Alani & Sarge

Table A2.

Ethogram

Category	**Behavior**	**Description**
Play alone	Pirouette	360° spin one or more times in horizontal or vertical plane
	Bubble chase	Expels bubbles underwater, may chase to surface
	Wave	Waving motion with foreflipper
	Chew flipper	Bites/chews own foreflipper
	Circle	Swims in tight circle(s) chasing own hind flippers
	Torpedo	Swims quickly around tank, creating wave
	Thrash	Thrash entire body at surface of water
	Leap	Leap clear out of water whilst swimming on a trajectory
Social play	Roll	2 animals rolling over each other in close contact, often including nipping, hugging, and brief chases
	Nose to nose	Touch snout or vibrissae to that of another animal
	Hugging	Animal swims/floats beside another animal, putting foreflippers around other’s torso
	Chase	Fast swim chasing another animal
	Fin bite	Biting hind or fore flipper of another animal, typically during play behaviors such as chasing, or whilst swimming behind another animal

Table A2 (continued).

	Follow	Swim very close behind another individual's hind flippers, submerged or at surface, without urgency of chase
	Loop	2 animals swim in a tight circle with nose to other animal's flippers
Blow air		Hard blow out of nose, head at least partially out of water
Maintenance	Rub	Rub any body part against another body part
	Scratch	Scratch any body part with foreflipper or teeth
	Stretch neck	Stretch head up and backwards, eyes often closed
Mating	Holding	Holding another animal down below focal animal's body, often after mounting
	Mounting	Attempt (successful or unsuccessful) to mount another animal
	Breeding vocalization	
	Breeding display	Not directly towards another individual
Feeding		Eating any edible item (fish, jello)
Jaw open/Close		Open mouth past ~20 degrees and immediately close it again, nothing visible in mouth

Table A2 (continued).

Tactile	Nose	Actively touch with nose
	Feel with whiskers	Actively touch with whiskers
	Biting	Bites down on any objects, no chewing
	Touch	Actively touch with any body part, without any other tactile behaviors (e.g. rubbing, nosing)
	Rub	Rub any body part against object or animal
	Scratch	Uses foreflipper to scratch object or animal
	Hit	Use body part to hit something, no rubbing and more speed than touch
	Chew	Chews by opening and closing mouth on something
	Push	Use body part to actively push object or animal
Resting	Land rest	No other behaviors, no active scanning
	Bottling	Floating vertically in water, no active propulsion or scanning
	Logging	Floating horizontally in water, no active propulsion or scanning
	Headrest	Rest head on land edge, no attempt to get out
	Pool rest	Resting in pool, no other behaviors
	Yawn	Appears to yawn, open mouth wide without any biting or immediate closure

Table A2 (continued).

Pattern swim		Swim in repetitive pattern for one or more complete rotations, including sections interrupted by repetitive surface or scan swims
Random swim		Swimming other pattern swimming, not in repetitive pattern
Fast dive		Fast/urgent dive and swim, may splash hind flippers, often in pursuit of fish
Back swim		Propulsion while on back with nose out of water
Surface swim		Swim at surface without active scanning, head may be partially submerged
Move on land		Any movement on land resulting in traveling
Move in/out	Haul to water	Movement from land to completely in water
	Half haul to water	Movement from half haul to completely in water
	Haul out	Movement from water to completely out of water
	Half haul	Active movement from water to partially out of water
	Haul to half haul	Movement from completely out of water to half in and out of water
	Bounding	Leap out of water onto land
	Pool haul	Movement from land into shallow pool
	Pool to land	Movement from shallow pool onto land

Table A2 (continued).

Wallow		Lays down in shallows and moves or rolls around, but without rubbing or directed traveling
Alert	Swim scan	Swims with eyes open and head above water, actively looking around
	Land scan	Eyes open and actively looking around while on land or half hauled
	Pushup	Places foreflippers on land in shallows without actively moving out of water actively looks around
	Pool scan	Active scanning while in shallow pool
Aggression	Lunge bite	Lunges to bite another animal (successfully or unsuccessfully)
	Roll with thrashing	2 animals rolling over each other in close contact with clear thrashing at surface
	Hissing	Makes hissing sounds, usually through mostly closed mouth
	Growl	Growling noise directed at another animal
	Other vocalizations	Any other vocalization directed at another animal and preceded or followed by another aggressive behavior

Table A2 (continued).

Open mouth	Animal opens mouth past ~30 degrees without immediately closing it, may be directed at another animal and accompanied by pushing, touching and nosing
Bark	Clear barking vocalization (only sea lions)
Whine	Open mouthed whining sound (only sea lions)
Other vocalizations	Any other vocalizations not included in other vocal categories
Mother-pup nursing	Pup is suckling from mother
Object obstruction	Animal goes under/into object such that at least head is obscured and observer cannot tell what behavior is being performed
Out of sight	Animal is completely out of sight

APPENDIX B – Results: Figures & Tables

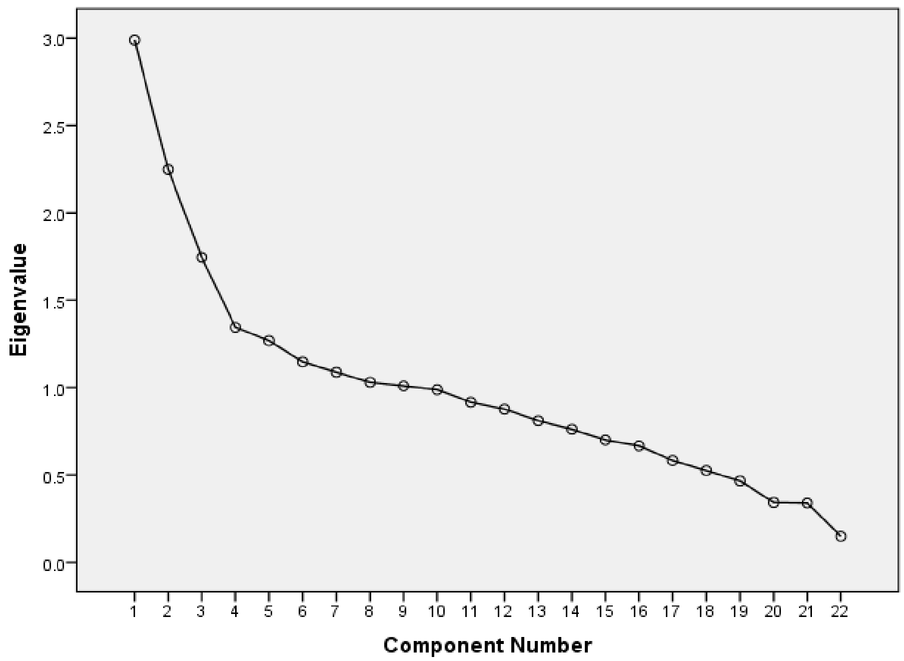

Figure A1. Harbor seal scree plot.

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The Number of Components According to the Original (1976) MAP Test is
  3

The Number of Components According to the Revised (2000) MAP Test is
  2
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Figure A2. Harbor seal MAP analysis.

Table A3.

Harbor seal KMO and Bartlett's test.

KMO Measure of Sampling Adequacy		0.537
Bartlett's Test of Sphericity	Approx. Chi-Square	1475.495
	df	120
	Sig.	<0.001

Table A4.

Variance explained by harbor seal personality factors.

Variance explained	**Factor 1**	**Factor 2**	**Factor 3**
% of Variance	18.2	13.3	10.7
Cumulative %	18.2	31.5	42.2

Table A5.

Harbor seal personality factor correlations.

Factor	**1**	**2**
2	-0.076	
3	0.014	-0.096

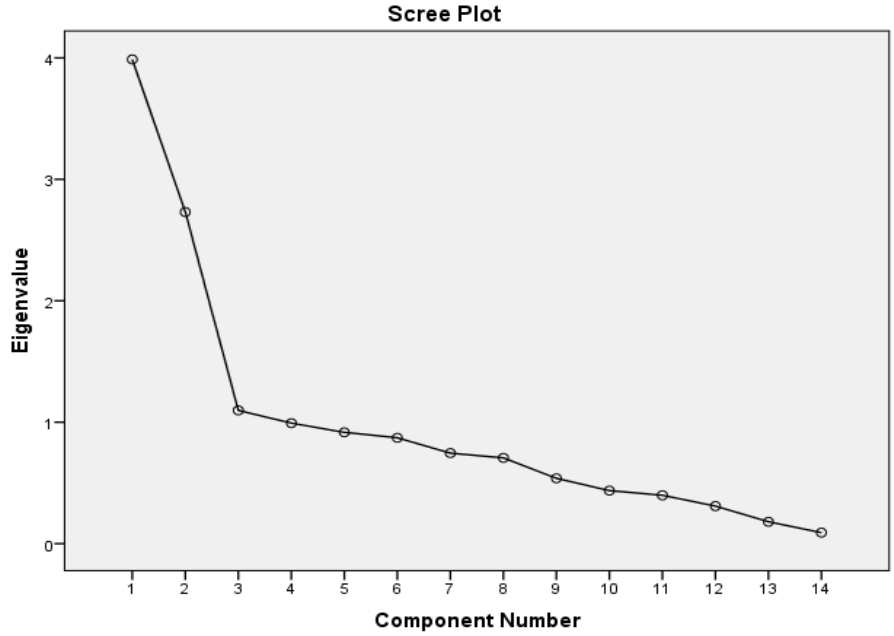

Figure A3. California sea lion scree plot.

```
The Number of Components According to the Original (1976) MAP Test is
  2

The Number of Components According to the Revised (2000) MAP Test is
  2
```

Figure A4. California sea lion MAP analysis.

Table A6.

California sea lion KMO and Bartlett's test.

KMO Measure of Sampling Adequacy		0.648
Bartlett's Test of Sphericity	**Approx. Chi-Square**	4318.890
	df	91
	Sig.	<0.001

Table A7.

Variance explained by California sea lion factors.

Variance explained	Factor 1	Factor 2
% of Variance	28.5	19.5
Cumulative %	28.5	48.0

Table A8.

California sea lion factor correlation.

Factor	1
2	0.011

Table A9.

Tactile behavior ANOVA homogeneity of variance tests.

Test	Groups	F	df 1	df 2	Sig/critical value
Levene's	Environment	7.987	1	559	0.005
	Animals	34.813	1	559	<0.001
Hartley's	Recipient	12.16	2	295	3.873
	Species	1.194	2	295	3.873

Table A10.

Overall interactive behavior ANOVA homogeneity of variance tests.

Test	Groups	F	df 1	df 2	Sig/critical value
Levene's	Environment	7.987	1	599	0.005
	Animals	83.761	1	599	<0.001
Hartley's	Recipient	2.172	2	295	3.873
	Species	1.92	2	295	3.873

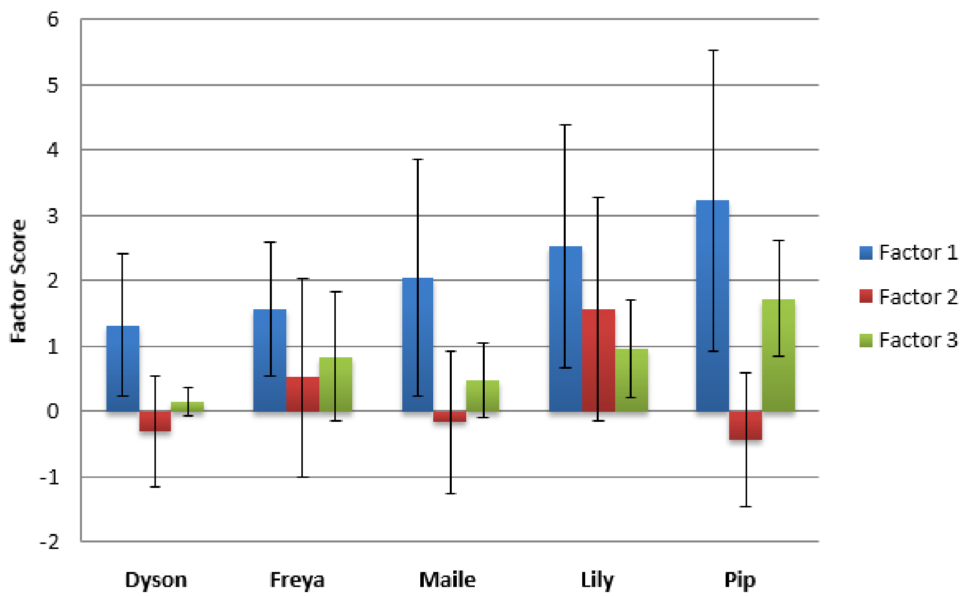

Figure A5. Harbor seal factor scores, with standard error bars.

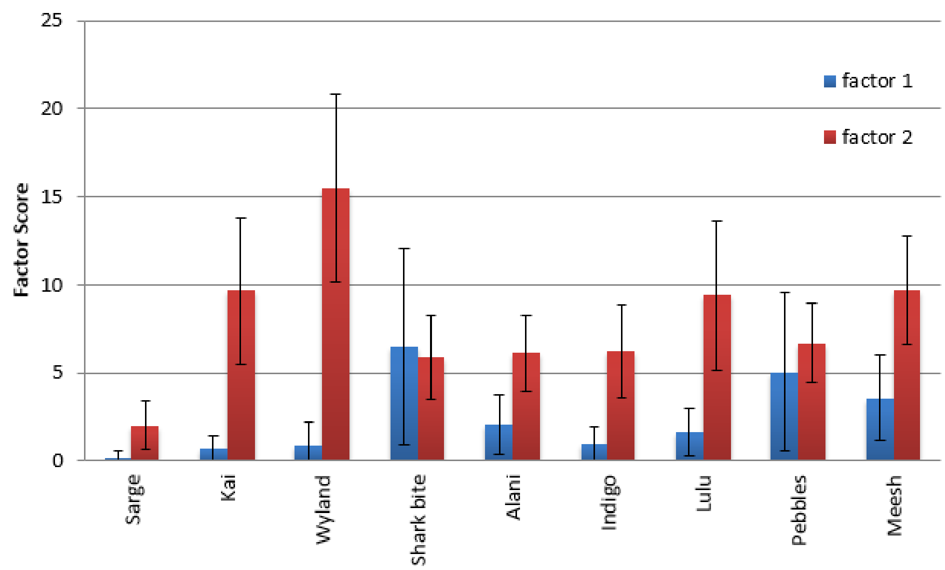

Figure A6. California sea lion factor scores, with standard error bars.

APPENDIX C – IACUC Approval Letter

THE UNIVERSITY OF
SOUTHERN MISSISSIPPI

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE

118 College Drive #5116 | Hattiesburg, MS 39406-0001
Phone: 601.266.6791 | Fax: 601.266.4377 | iacuc@usm.edu | www.usm.edu/iacuc

NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:	**16041404**
PROJECT TITLE:	**Assessing Personality in California Sea Lions and Harbor Seals Using Trait Rating and Coding, Incorporating Ratings of Affective States**
PROPOSED PROJECT DATES:	**04/2016 – 09/2018**
PROJECT TYPE:	**New**
PRINCIPAL INVESTIGATOR(S):	**David Echevarria**
DEPARTMENT:	**Psychology**
FUNDING AGENCY/SPONSOR:	**N/A**
IACUC COMMITTEE ACTION:	**Full Committee Approval**
PROTOCOL EXPIRATON DATE:	**September 30, 2018**

Frank Moore, PhD
IACUC Chair

4/14/2016
Date

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