

Department of Physics, Chemistry and Biology

Master Thesis

Personality assessment and interactions in eight
captive bottlenose dolphins (*Tursiops truncatus*)

Sabina Birgersson

LiTH-IFM- Ex--2415--SE

Supervisor: Mats Amundin, Linköpings universitet

Examiner: Matthias Laska, Linköpings universitet



Linköpings universitet

Department of Physics, Chemistry and Biology

Linköpings universitet

SE-581 83 Linköping, Sweden



Avdelning, Institution
Division, Department

Avdelningen för biologi
Institutionen för fysik och mätteknik

Datum
Date

2011-06-03

Språk

Language

- Svenska/Swedish
 Engelska/English

Rapporttyp

Report category

- Licentiatavhandling
 Examensarbete
 C-uppsats
 D-uppsats
 Övrig rapport

ISBN

LiTH-IFM- Ex--2415--SE

ISRN

Serietitel och serienummer

Title of series, numbering

ISSN

LiTH-IFM-Ex--2415--SE

URL för elektronisk version

Titel

Title

Personality assessment and interactions in eight captive bottlenose dolphins (*Tursiops truncatus*)

Författare

Author

Sabina Birgersson

Sammanfattning

Abstract

In recent years there has been an increased interest in measuring animal personality. It is argued that personality in animals is expressed through the behaviours they display. In this study personality has been investigated in a group of eight captive bottlenose dolphins (*Tursiops truncatus*). Data from focal samplings were analysed by using behavioural codings and the Five-factor model consisting of Openness to experience, Conscientiousness, Extraversion, Agreeableness and Neuroticism. The results revealed that the dolphins display both distinct personality differences as well as similarities in these factors. By calculating coefficients of association it was found that the dolphins also prefer the company of certain individuals over others. Knowledge of individual personality differences and its implications can be helpful in aspects such as management and reintroduction programs, evolution and genetics and in providing a complementary perspective to explain other behavioural and cognitive studies.

Nyckelord

Keyword

behaviour, bottlenose dolphin, five-factor model, individual differences, personality, *Tursiops truncatus*

Content

1 Abstract	1
2 Introduction.....	1
3 Material and Methods.....	3
3.1 Animals and management.....	3
3.2 Experimental set-up and recordings.....	5
3.3 Statistical analysis.....	7
4 Results	7
4.1 Personality profiles based on the Five-factor model.....	8
4.1.1 Ariel (female).....	8
4.1.2 Fenah (female).....	9
4.1.3 Luna (female).....	9
4.1.4 Lyra (female).....	10
4.1.5 Nephele (female).....	10
4.1.6 Pichi (male).....	11
4.1.7 Sting (male).....	12
4.1.8 Vicky (female).....	12
4.2 Comparisons between the dolphins within the same personality factor.....	13
4.2.1 Openness to experience (+).....	13
4.2.2 Extraversion (+).....	14
4.2.3 Agreeableness (+).....	14
4.2.4 Neuroticism (+).....	15
4.2.5 Neuroticism (-).....	16
4.3 Coefficient of association.....	16
4.4 Sociograms.....	17
5 Discussion.....	18
6 Acknowledgements.....	22
7 References.....	23

1. Abstract

In recent years there has been an increased interest in measuring animal personality. It is argued that personality in animals is expressed through the behaviours they display. In this study personality has been investigated in a group of eight captive bottlenose dolphins (*Tursiops truncatus*). Data from focal samplings were analysed by using behavioural codings and the Five-factor model consisting of Openness to experience, Conscientiousness, Extraversion, Agreeableness and Neuroticism. The results revealed that the dolphins display both distinct personality differences as well as similarities in these factors. By calculating coefficients of association it was found that the dolphins also prefer the company of certain individuals over others. Knowledge of individual personality differences and its implications can be helpful in aspects such as management and reintroduction programs, evolution and genetics and in providing a complementary perspective to explain other behavioural and cognitive studies.

Key words: behaviour, bottlenose dolphin, five-factor model, individual differences, personality, *Tursiops truncatus*

2. Introduction

Differences among individuals have fascinated humans over centuries. Darwin (1859) noted in his book “The origin of species” how individual differences in phenotypes play a big role in the today well known theory of evolution. Individual differences in personality have been explored in both the human and animal domain. However, compared to humans only some parts of the various personality phenomena have been studied in animals (Gosling, 2001). In literature there is no clear consistency in definition of personality among researchers, not even regarding the human domain (Gosling, 2001). Personality psychologists would likely describe personality as “psychological qualities that contribute to an individual’s enduring and distinctive patterns of feeling, thinking, and behaving” (Pervin & Crevone, 2010). This could be simplified by defining personality as patterns of behaviours that are constant over time and situations (Pervin & Crevone, 2010). Some animal oriented studies prefer to use the term “temperament” as a substitute of, or synonymously with, personality. A reason could be to make it sound less anthropomorphic. This may cause confusion since in human studies temperament has been defined as “the early appearing tendencies that interact with environmental influences to serve as the biological foundation for personality” (Bekoff, 2004). Even though animal subjects, compared to humans, have some advantages in studies (such as greater experimental control) the methods to explore animal personality are in some perspectives limited. We do not have the possibility to implement study methods used for human studies based on e.g. questionnaires or life-stories. However, it has been suggested that personality differences in animals can be expressed through the ways an animal behaves.

Studies investigating personality in animals have been carried out over a wide range of species from invertebrates, such as octopus, to vertebrates, such as primate species (see Gosling, 2001, for review). The criterion that behaviours reflecting personality should be consistent means that humans can predict how an individual would react to certain stimuli in regards to some traits. This has for example been shown in a study on rhesus macaques (*Macaca mulatta*) where it was

found that specific situations elicited a trait response that matched the predictions (Capitanio, 1999). Predictions in personality have most likely played a role in the process of domestication where pets and farm animals have been under high selective pressures. These selections appear to have produced various personality traits that also correlate with other physiological traits in animals, as has been found in domestic dogs (*Canis familiaris*) (Careau et al., 2010).

It has been, and is still, debated which the best method is in order to assess personality in animals. For the time being, there are two main approaches most commonly applied in previous personality studies. One is based on behavioural codings while the other is based on rating of personality traits (Vazire et al., 2007). While behavioural coding is more objective, with an observer interpreting the behaviours expressed, trait rating relies on human's ability to evaluate individuals based on experiences, which is more subjective. Both approaches can be considered to have pros and cons and it is a matter of tradeoffs. According to Vazire et al. (2007) trait ratings could even be more reliable and less subjective than people may think.

There are numerous terms and traits describing personality. Trials to list personality traits and sort them in clusters have been made by e.g. Cattell (1943). Thurstone (1934) found that five broad factors were sufficient to explain the analysed coefficients of 60 personality traits. Since these days the ways of exploring personality have developed and a model that relies on these five big groups has formed. Goldberg (1993) suggests that it is reasonable to conclude that all trait adjective analyses in humans will bring out a variant of the five-factor structure. Consequently this method, called the Five-factor model, has become very popular in personality studies in recent years and is regarded as one of the best ways to map personality (Gosling & John, 1999). The model is originally based on human psychology but has been taken into the animal domain as the studies of personality in non-human animals are progressing. The five factors, to which descriptive adjectives connected to personality could be divided into, are Openness to experience, Conscientiousness, Extraversion, Agreeableness and Neuroticism. Examples of traits in the Openness to experience factor are adventurous, imaginative and curious. Conscientiousness can consist of traits that e.g. show planned behaviour or self-discipline. Traits such as energetic and a tendency to seek stimulation belong to the factor Extraversion. Agreeableness is characterised by friendliness and a tendency to be co-operative. Finally Neuroticism consists of a tendency to experience uncomfortable emotions, such as aggression or anxiety.

It is important to interpret animal behaviours with care and not to become anthropomorphic. Hence, the Five-factor model has sometimes been modified to make it possible to apply on species other than humans. In a study conducted by Highfill & Kuczaj (2007) the Five-factor model was modified by listing adjectives within the factors that cohere more with dolphin behaviours. Factors can also be added. A study on chimpanzees (*Pan troglodytes*) revealed that they express traits that can fit into the human Five-factor model with an additional factor comprising of dominance behaviour (King & Figueredo 1997). In some cases researchers have instead excluded a factor. The factor Conscientiousness has been considered to only apply on humans and chimpanzees (Gosling & John, 1999). In a cross-species comparison test between humans (*Homo sapiens*) and dogs (*Canis familiaris*), this was also the factor not scored for in dogs (Gosling et al., 2003). There have been discussions on if and how comparisons between species could be carried out (Gosling, 2001). Naturally, personality comparisons within the same species are usually easier to assess than between species, depending on the behavioural repertoire expressed by the species. Nonetheless, comparisons between species can also be considered to be just as important.

When comparing great ape species with dolphin species it has been found that there are certain attributes found in both groups. Dolphins are highly social animals and have a large

amount of cognitive and intellectual abilities (Pack & Herman, 2006). One example of a complex ability shared by these species is self-recognition in mirrors (Reiss & Marino, 2001). Even though several studies on dolphins have been carried out focusing on behaviour and cognition, dolphin species are relatively underrepresented in regards to personality studies (Gosling, 2001). Yet, Highfill & Kuczaj (2010) state that complex behavioural differences displayed by dolphins indicate personality traits in various situations. For example, in cooperative feeding behaviour dolphins may use different strategies or take different roles in the hunting process (Gazda et al., 2005). It has also been observed how dolphin mothers vary in their style of disciplining their calves as well as variations in the separations and reunions with their calves (Hill et al., 2007). A study carried out by Lusseau & Conradt (2009) showed that dolphin individuals perform behaviours initiating or terminating travels with the group.

One of the first systematic studies on dolphin personality was conducted by Highfill & Kuczaj (2007). That particular study was based on the Five-factor model and trait ratings by people that were considered to know the animals well. The study compared ratings of dolphins before and after the strike of Hurricane Katrina, which caused the dolphin individuals to be relocated. It was found that the dolphins were rated the same way both before and after the event and thus were consistent in their personality over time and across situations.

Since personality differences have been demonstrated to exist and be measurable in dolphins, as in the study by Highfill and Kuczaj (2007), by the means of trait ratings it is reasonable to believe that this also can be achieved through behavioural codings.

The aim of this study is to investigate whether differences in personality can be assessed in a group of eight captive bottlenose dolphins (*Tursiops truncatus*) based on behavioural codings and the Five-factor model. In social species, such as dolphins, it is also important to reflect on the context and the interactions. Hence, the aim is also to investigate how the individuals interact within the group. Creating sociograms and calculating the coefficient of association will give additional information to the individual personalities according to the Five-factor model.

3. Material and methods

3.1 Animals and management

In this study, eight bottlenose dolphins (*Tursiops truncatus*) residing at Kolmården Wildlife Park in Sweden were observed. The dolphinarium at Kolmården consisted of three pools that were all located indoors. Two of them (the Lagoon and the Show pool) were visible to visitors while the Middle pool was out of sight for visitors (Figure 1). The middle pool interconnected with the others. Gates between the pools enabled the possibility to close the pass ways. The Lagoon had a surface area of 900 m², the Show pool had a surface area of 800 m² and the Middle pool had a surface area of 180 m². Depth varied between three to six meters in the Lagoon and three to four meters in the Show pool. The pool complex held about 6400 m³ water with a salt halt of 3 ‰. Temperature was around 19 °C. The dolphin group consisted of two males and six females (Table 1) that were identified by body shape, tooth rakes and other marks.

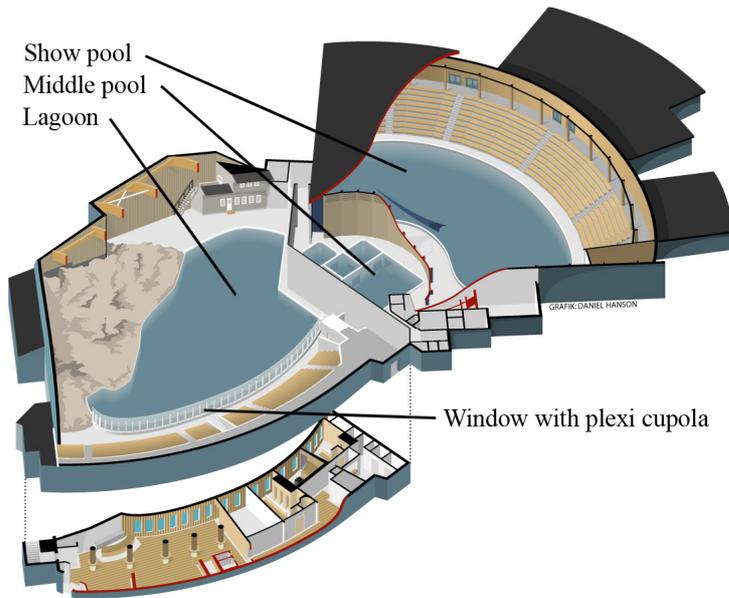


Figure 1: The dolphinarium with an overview over the Show pool, the Middle pool and the Lagoon. In this study the dolphins had free access to all pools.

Table 1: The dolphins included in the study, their background and relationships within the group.

Subject	Female (F)/ Male (M)	Born (y)	Born in: wild (W)/ dolphinarium (D)	Previous dolphinaria	Relationships to other dolphins in the group
Vicky	F	1973	W	USA	Mother of Ariel and Luna
Pichi	M	1982	W	France, Parc Asterix	Father of Sting and Fenah
Nephele	F	1983	W	Germany	None
Ariel	F	1996	D	None	Daughter of Vicky, sister of Luna, half sister of Lyra, mother of Sting
Lyra	F	1999	D	None	Half sister of Ariel and Luna, mother of Fenah
Luna	F	2001	D	None	Daughter of Vicky, sister of Ariel, half sister of Lyra
Fenah	F	2008	D	None	Daughter of Pichi and Lyra, half sister of Sting

Sting	M	2008	D	None	Son of Ariel and Pichi, half brother of Fenah
-------	---	------	---	------	---

3.2 Experimental set-up and recordings

At Kolmården Wildlife Park under water view could only be obtained in the Lagoon. A window with a plexi cupola attached to the glass provided a fish eye view over most of the Lagoon area. By this window videos were obtained and data was collected using focal follow sampling (Altmann, 1974). The dolphins were filmed mornings (around 6 am), lunchtimes (around noon) and evenings (around 6-8 pm). No interactions between the dolphins and their trainers or caretakers took place during the filming sessions. This was done with the intention of observing the animals performing as undisturbed and spontaneous behaviours as possible. In total, each dolphin was filmed for two hours divided in sessions of five minutes distributed to every dolphin. To obtain an overview of the situation in the pool every focal sampling was preceded with one minute film, scanning the area. Each dolphin was then filmed five minutes per session using a Sanyo Xacti DMX-CG110 camera. The focal sampling was done in a random order every session. The dolphins had free access to all pools during all observing sessions. As a reduced space possibly could create a social tension among the dolphins and thus cause an unusual situation the gates remained open. This way the dolphins had the opportunity to swim away from other dolphins if e.g. a conflict would occur. However, because of this a certain focal dolphin could be absent from the Lagoon, where the observations took place, when the turn came to film that particularly individual. To help this problem to some extent, only sessions where five or more dolphins were present most of their focal time were used. The idea was to include sessions in the data with at least over half of the dolphins present in each session. The focal sampling films were analyzed using the software Noldus - The Observer XT 7.0. In order to assess the personality in dolphins the Five-factor model, modified by Highfill & Kuczaj (2007), was used to code and interpret the behaviours recorded. It is important to note the context of performed behaviours since a specific behaviour could mean many things (e.g. producing bubbles could be playful or agonistic in interaction with another dolphin). The Five-factor model was modified to list traits more suitable for the dolphin behavioural repertoire. Each factor can consist of both positive and negative traits that have opposite meanings but are related to the same factor. For example in Openness to experience “curiosity” is a positive trait while “not exploratory” is negative. In the same way Neuroticism can consist of traits such as “aggressive” as the positive trait while being “calm” is a negative trait (Table 2). It is worth noting that this table was constructed with the intention to be suited for a study based on trait ratings. Since the presented study was based on behavioural codings without human interactions, some of the aspects were not taken into consideration in this study (e.g. most of the negative values except Neuroticism). The data included in this study was collected between September 8th and October 25th 2010.

Table 2: Traits used to measure dolphin personality based on the five-factor model. Defined and created by Highfill & Kuczaj (2007) and modified for the presented study.

Factor 1:	Factor 2:	Factor 3:	Factor 4:	Factor 5:
Openness to experience	Conscientiousness	Extraversion	Agreeableness	Neuroticism
(+) Creative, imaginative:	(+) Careful, cautious: Animal	(+) Assertive: Self-assured,	(+) Friendly, gentle:	(+) Jealous: Resentful or

Approaches situations and addresses problems in novel, creative ways (e.g. finds various ways to play with a toy).	exhibit care in its actions.	not easily intimidated.	Friendly, amicable, and congenial towards other animals. Responds to others in an easy, kind manner. Not hostile. Not antagonistic.	envious of another dolphin.
(+) Intelligent: Animal appears to learn easily. Quick to understand.	(+) Alert, vigilant: Ready, attentive, watchful; appears to pay attention to the surroundings.	(+) Playful: Engages in playful behaviour.	(+) Obedient, cooperative: Obeys; cooperative with instructions. Not defiant.	(+) Aggressive: Threatens or causes harm; high frequency of raking, biting, or hitting other animals.
(+) Curious: Appears to be interested in new situations or objects.	(+) Diligent, attentive: Animal monitors its actions and exhibits a willingness to please.	(+) Active, energetic: Moves around a lot. Locomotion can include swimming, leaping,	(+) Affiliative, companionable: Agreeable and sociable. Appears to like the company of others. Seek out social contact	(+) Temperamental: Displays frequent mood swings.
(-) Not exploratory or inquisitive: Does not seek out or investigate novel situations	(-) Lazy: Resistant to work or exertion.	(-) Timid: Hesitant, apprehensive, tentative.	with other animal or person. (-) Inflexible, incompilant: Stubborn or headstrong. Not willing to adapt or change.	(-) Relaxed, calm: Assured or at ease. Not tense or highly sensitive.
(-) Unoriginal, conforming: Not inventive or original; does not produce new and unusual	(-) Undependable, unreliable: Not easily relied or depended on. Not a “go-to” animal.	(-) Quiet, not vocal: Does not vocalize often.	(-) Demanding: Requires much effort or attention from other dolphins.	(-) Comfortable, complacent: Self-satisfied, content: Appears free from anxiety.

actions.				
(-) Simple: Engages in routine behaviours. Does not have a complex behavioural repertoire.	(-) Inconsistent, variable: Not consistent or predictable.	(-) Unexcitable: Not readily roused into action; relatively unresponsive to stimuli.	(-) Selfish: Self-centered or concerned chiefly with itself and its needs.	(-) Tolerant and easy-going: Inclined to be relaxed and tolerant.

3.3 Statistical analysis

To establish personality profiles the durations of various behaviours within the same factor were pooled. Then the mean values per session with standard deviations were calculated. Statistical analysis for significance was carried out using the program IBM SPSS Statistics 19. To investigate if there was a significant difference between data sets Kruskal-Wallis tests were conducted. If a statistical significance was found the post hoc test Bonferroni was used to find out between which data sets there was a significant difference. These tests were carried out both between the factors for each dolphin individual and within the same factor between the dolphin individuals.

The personality profiles only describe to some extent what the dolphins do, but not who they are interacting with. In order to explore interactions between the individuals the coefficient of association was also calculated using Half-Weight Index (HWI). In the equation, X is the total duration where dolphin a and b were associated. Ya is the total duration where dolphin a was seen but not dolphin b and Yb is the total duration dolphin b was seen without dolphin a.

$$HWI = X/(X+0.5(Ya+Yb))$$

A dolphin was considered to associate with other dolphins if they were within one body length from each other. A dolphin could sometimes be seen swimming together with two dolphins, one on each side. In these situations both dolphins were scored for.

To illustrate some of the ways the dolphins interacted sociograms for affiliative behaviour, agonistic behaviour and sexual behaviour were constructed based on the total durations in seconds of these behaviours.

4. Results

Due to the circumstances at Kolmården dolphinarium where the dolphins had access to all pools the focal dolphin could sometimes be absent during the recording. To give some perspectives to the results provided, the percentages of the time when the dolphins were present and observable are illustrated in Table 3.

Table 3: The time in percentage and minutes the dolphins were present in the Lagoon and observable.

Dolphin	Percentage of time the dolphins were observable	Time in minutes the dolphins were observable during a total of two hours
---------	---	--

Ariel	74.7 %	89.6 min
Fenah	70.3 %	84.4 min
Luna	89.8 %	107.8 min
Lyra	81.8 %	98.2 min
Nephele	89.4 %	107.3 min
Pichi	57.1 %	68.5 min
Sting	75.3 %	90.4 min
Vicky	87.2 %	104.6 min

4.1 Personality profiles based on the Five-factor model

The personality factors Openness to experience, Extraversion, Agreeableness and Neuroticism, with positive and negative traits, will sometimes be referred to in the text as O+, E+, A+, N+ and N-.

To assess personality in the eight captive bottlenose dolphins, graphs were constructed to illustrate the mean value of the scored traits in each factor according to the Five-factor model. Further, statistical comparisons were carried out both between the factors within the same personality profile and between the dolphins within the same factor. The graphs illustrate the mean durations in seconds per session together with standard deviations.

4.1.1 Ariel (female)

Ariel scored in the factors O+, E+, A+ and N- (Figure 2). This means that she displayed behaviours indicating curiosity, playfulness, affiliation and relaxed swimming alone behaviours. Comparison between factors through the Kruskal-Wallis test showed that there are significant differences ($\chi^2 = 30.280$, $df = 3$, $p < 0.001$). The Bonferroni test revealed that Ariel spends significantly more time expressing behaviours in association with A+, such as affiliation, compared to O+ ($p < 0.001$), E+ ($p < 0.001$) and N- ($p = 0.011$). Ariel also spends significantly more time alone and calm (N-) as opposed to energetic and playful (E+) ($p = 0.031$).

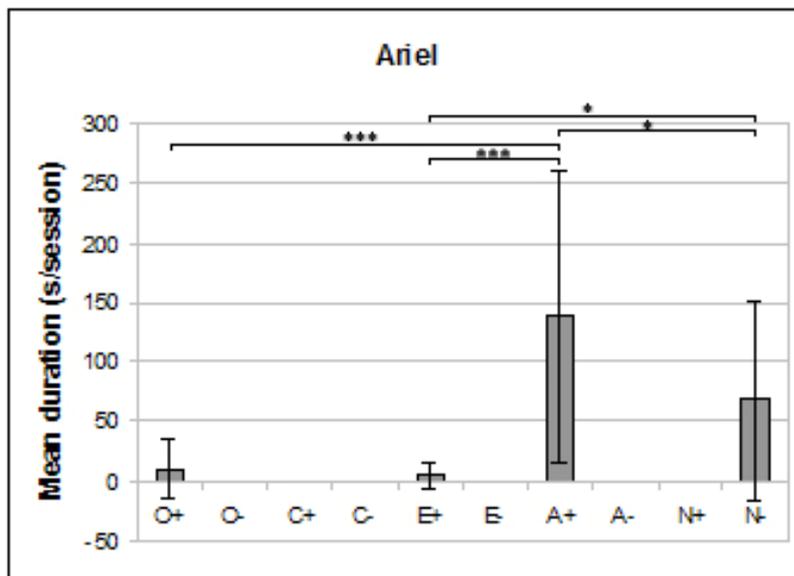


Figure 2. The mean duration in seconds Ariel displayed behaviours within each factor per 5-minute session. Mean (\pm SD) (***) = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$)

4.1.2 Fenah (female)

Fenah scored in the factors O+, E+, A+, N+ and N- (Figure 3). This indicates that Fenah expressed behaviours associated to curiosity, playfulness, affiliation, agonistic and calmness. The Kruskal-Wallis test shows that significant differences can be found ($\chi^2 = 44.153$, $df = 4$, $p < 0.001$). According to the Bonferroni test Fenah spends significantly more time being affiliative compared to the other factors ($p < 0.001$ for all).

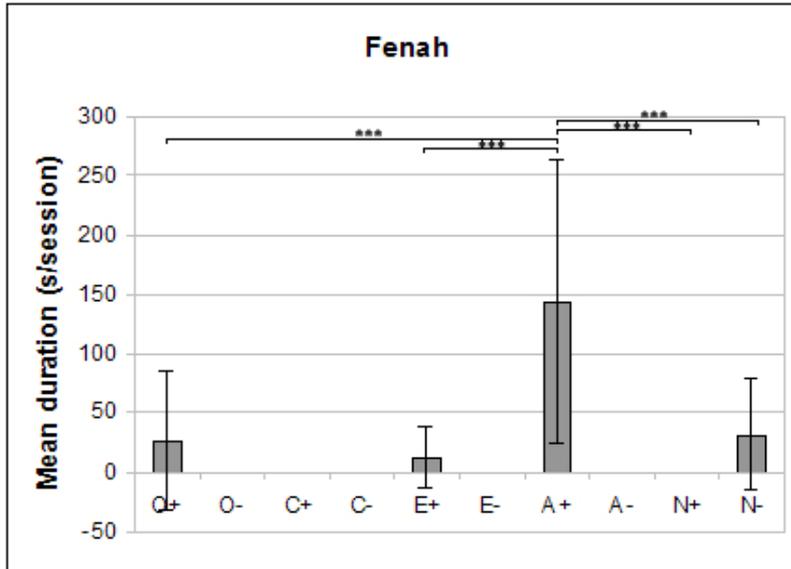


Figure 3. The mean duration in seconds Fenah displayed behaviours within each factor per 5-minute session. Mean (\pm SD) (***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$)

4.1.3 Luna (female)

Luna scored in three factors, E+, A+ and N- (Figure 4). This means that Luna was seen carrying out behaviours indicating affiliation, playfulness and calmness. The Kruskal-Wallis test indicates that differences can be found ($\chi^2 = 24.516$, $df = 2$, $p < 0.001$) and Bonferroni shows that Luna spends significantly more time being affiliative than being playful or swimming calmly by herself ($p < 0.001$ for both).

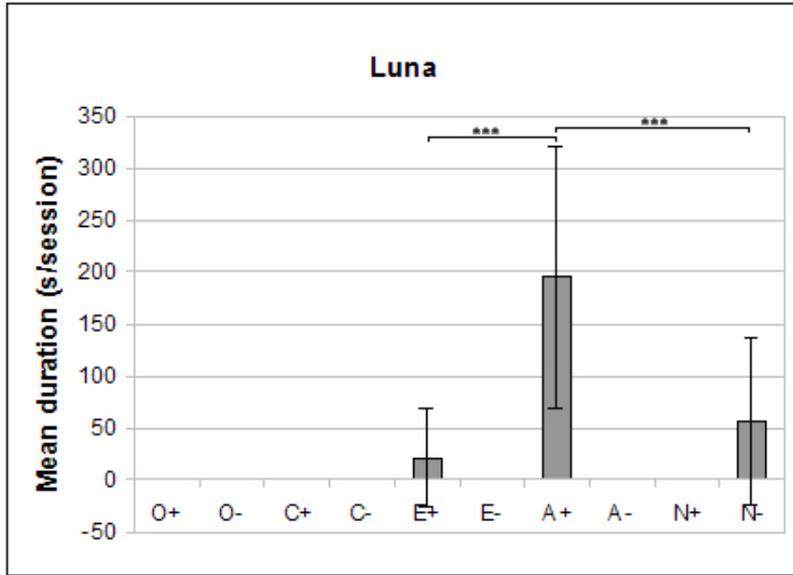


Figure 4. The mean duration in seconds Luna displayed behaviours within each factor per 5-minute session. Mean (\pm SD) (***) = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$)

4.1.4 Lyra (female)

O+, E+, A+, N+ and N- were the factors Lyra scored in (Figure 5). This means that she was observed to express behaviours such as curiosity, playfulness, affiliation, agonistic and relaxed swimming by herself. The Kruskal-Wallis test shows that significant differences can be found ($\chi^2 = 67.736$, $df = 4$, $p < 0.001$). Bonferroni reveals that Lyra spends most of her time being either affiliative or swimming by herself compared to the other factors ($p < 0.001$ for all). There is no significant difference between A+ and N-.

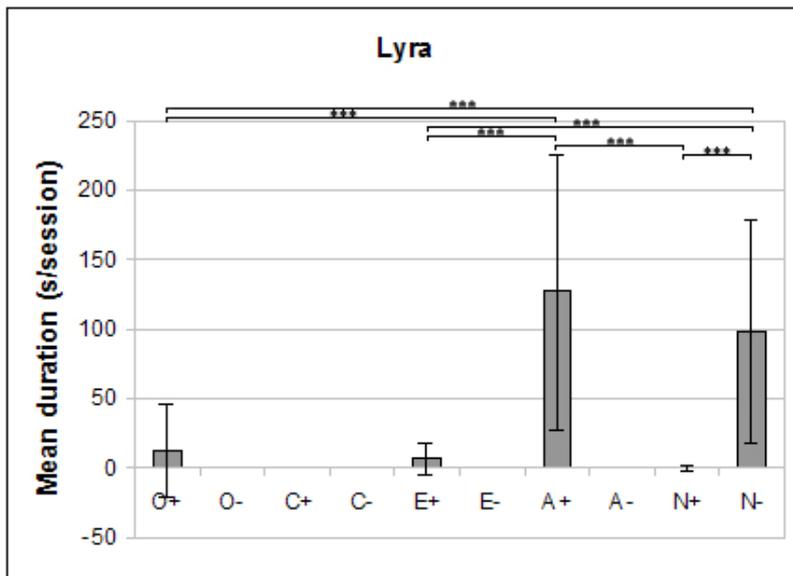


Figure 5. The mean duration in seconds Lyra displayed behaviours within each factor per 5-minute session. Mean (\pm SD) (***) = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$)

4.1.5 Nephele (female)

Nephele scored in O+, E+, A+ and N- (Figure 6). This result implies that Nephele expresses behaviours such as curiosity, playfulness, affiliation and calmly swimming alone.

Kruskal-Wallis test tells us that significant differences can be found among the factors ($\chi^2 = 57.342$, $df = 3$, $p < 0.001$). As is shown in the Bonferroni test Nephele spends most of her time calmly swimming alone compared to the other factors ($p < 0.001$). Significant differences could also be found indicating that Nephele spends more time in affiliation (A+) compared to curiosity or playfulness (O+ and E+) ($p < 0.01$).

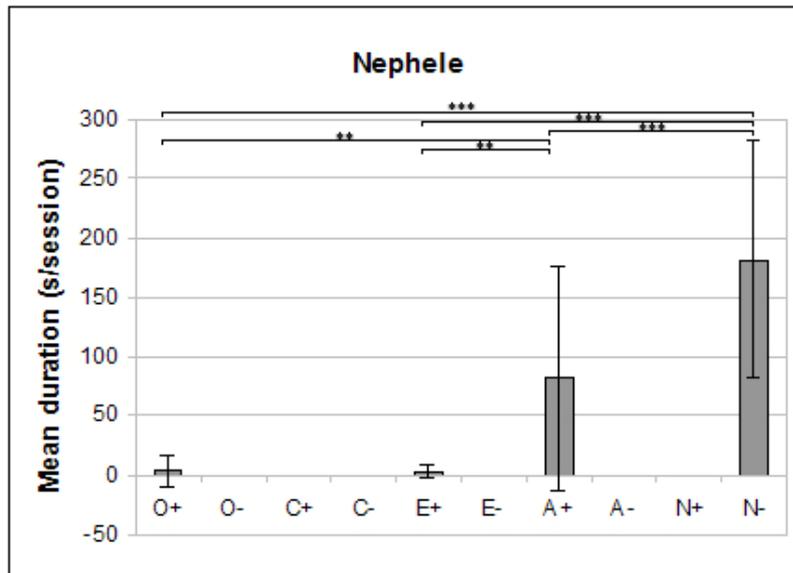


Figure 6. The mean duration in seconds Nephele displayed behaviours within each factor per 5-minute session. Mean ($\pm SD$) (**= $p < 0.01$, ***= $p < 0.001$, *= $p < 0.05$)

4.1.6 Pichi (male)

Pichi scored in the factors O+, A+ and N- (Figure 7). This means that he display behaviours such as curiosity, affiliation and calmly swimming alone. The Kruskal-Wallis test shows differences can be found between the factors ($\chi^2 = 25.860$, $df = 2$, $p < 0.001$).

Only the factor N- is significantly higher compared to the others according to Bonferroni test ($p < 0.001$). That means Pichi spends more time swimming calmly alone than in expressing affiliation or curiosity.

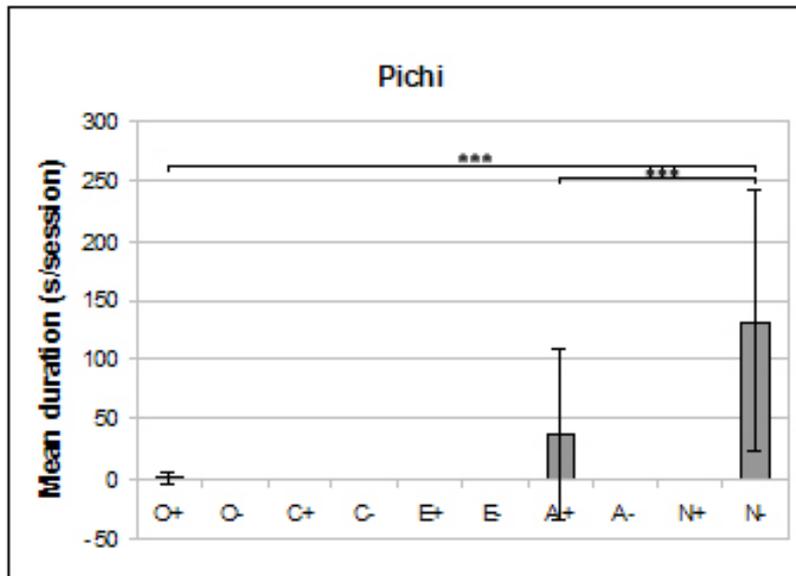


Figure 7. The mean duration in seconds Pichi displayed behaviours within each factor per 5-minute session. Mean (\pm SD) (***) = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$)

4.1.7 Sting (male)

The factors O+, E+, A+, N+ and N- were the ones Sting scored in (Figure 8). This means that Sting was seen displaying behaviours indicating curiosity, playfulness, affiliation, agonistic and swimming calmly alone. Differences can be found between these factors according to the Kruskal-Wallis test ($\chi^2 = 52.458$, $df = 4$, $p < 0.001$). The Bonferroni test shows that Sting spends significantly more time in affiliation compared to the other factors ($p < 0.001$ for all).

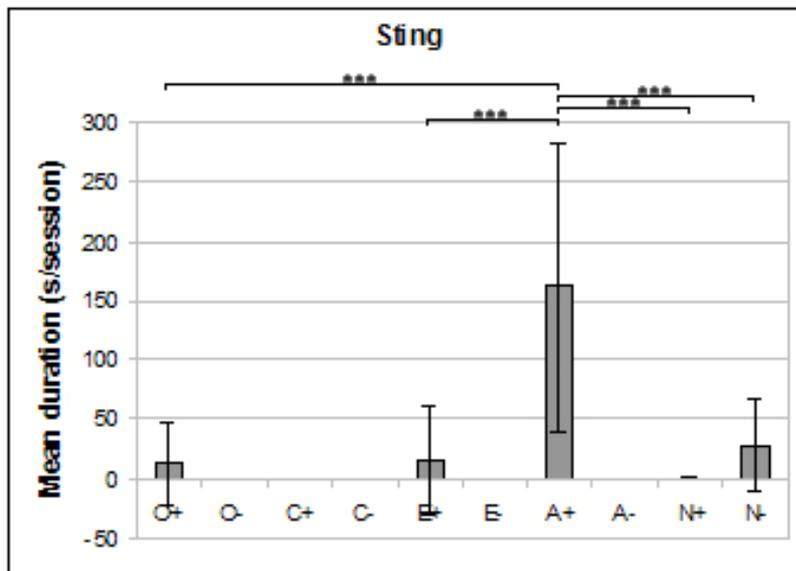


Figure 8. The mean duration in seconds Sting displayed behaviours within each factor per 5-minute session. Mean (\pm SD) (***) = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$)

4.1.8. Vicky (female)

Finally, Vicky scored in E+, A+ and N- (Figure 9). This means that Vicky was expressing behaviours indicating playfulness, affiliation and relaxed swimming alone. Kruskal-Wallis test confirms that significant differences can be found ($\chi^2 = 34.335$, $df = 2$, $p < 0.001$). Bonferroni test shows that Vicky spends significantly more time expressing affiliation compared to playfulness and swimming alone ($p < 0.001$ for both).

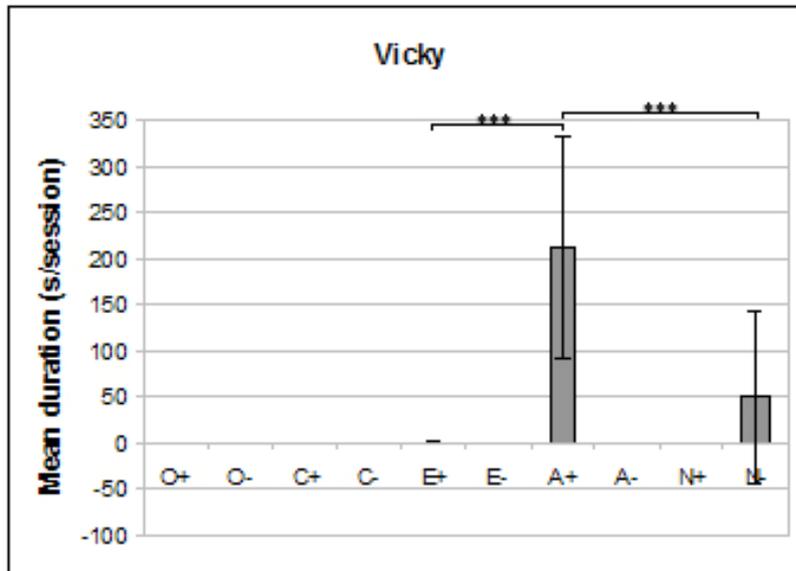


Figure 9. The mean duration in seconds Vicky displayed behaviours within each factor per 5-minute session. Mean ($\pm SD$) (***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$)

4.2 Comparisons between the dolphins within the same personality factor

As the statistical differences between the factors were established for each dolphin it is of interest to evaluate the scores among the individuals in the group within the same factor. In total the dolphin group scored in five different factors: Openness to experience (O+), Extraversion (E+), Agreeableness (A+) and the positive and negative traits of Neuroticism (N+ and N-).

4.2.1 Openness to experience (+)

The dolphins scoring in the O+ factor were Ariel, Fenah, Lyra, Nephele, Pichi and Sting (Figure 10). In other words, these individuals were the ones observed to display curiosity. However, no significant differences between these individuals could be found based on the Kruskal-Wallis test ($\chi^2 = 7.821$, $df = 5$, $p = 0.166$).

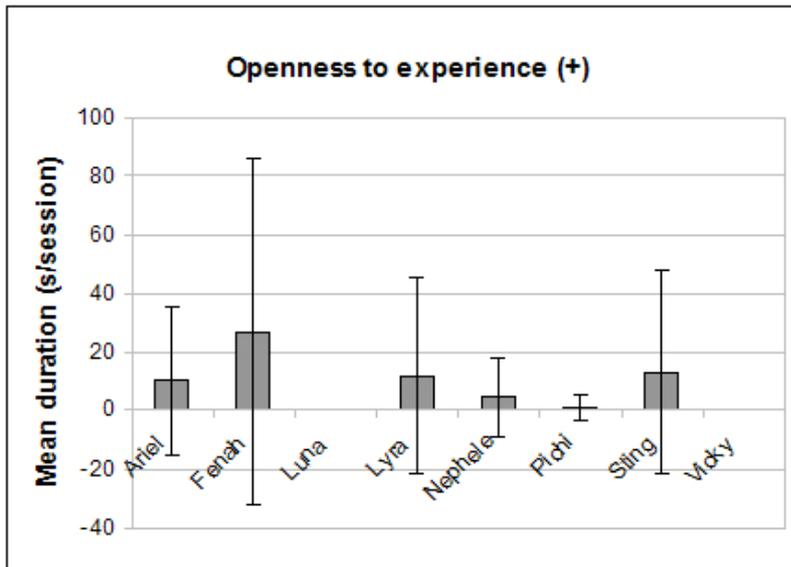


Figure 10. The mean duration in seconds the dolphins displayed behaviours within the factor Openness to experience (+) per 5-minute session. Mean (\pm SD) (***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$)

4.2.2 Extraversion (+)

The dolphins scoring in E+ were Ariel, Fenah, Luna, Lyra, Nephela, Sting and Vicky (Figure 11). This means that all dolphins except Pichi were observed to display playful behaviours. No significant difference among these individuals could be detected with the Kruskal-Wallis test ($\chi^2 = 7.734$, $df = 6$, $p = 0.258$).

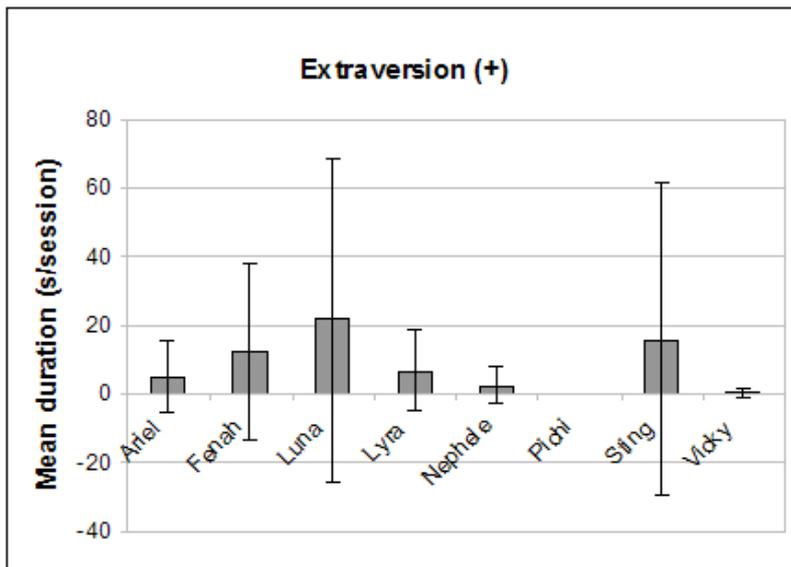


Figure 11. The mean duration in seconds the dolphins displayed behaviours within the factor Extraversion (+) per 5-minute session. Mean (\pm SD) (***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$)

4.2.3 Agreeableness (+)

All dolphins were observed to conduct behaviours in association with the A+ factor, (Figure 12). That is, all dolphins were seen displaying affiliative behaviours, such as swimming together

with others. The Kruskal-Wallis test reveals that differences between the dolphins can be expected ($\chi^2 = 37.185$, $df = 7$, $p < 0.001$). After conducting a Bonferroni test it is shown that Fenah spends significantly more time displaying affiliation compared to Pichi ($p < 0.05$). Luna spends significantly more time displaying affiliation compared to Pichi ($p < 0.001$) and Nephele ($p < 0.05$). Vicky was observed to display significantly more affiliation compared to Nephele ($p < 0.01$) and Pichi ($p < 0.001$). Finally, Sting spends more time conducting affiliative behaviours compared to Pichi ($p < 0.01$).

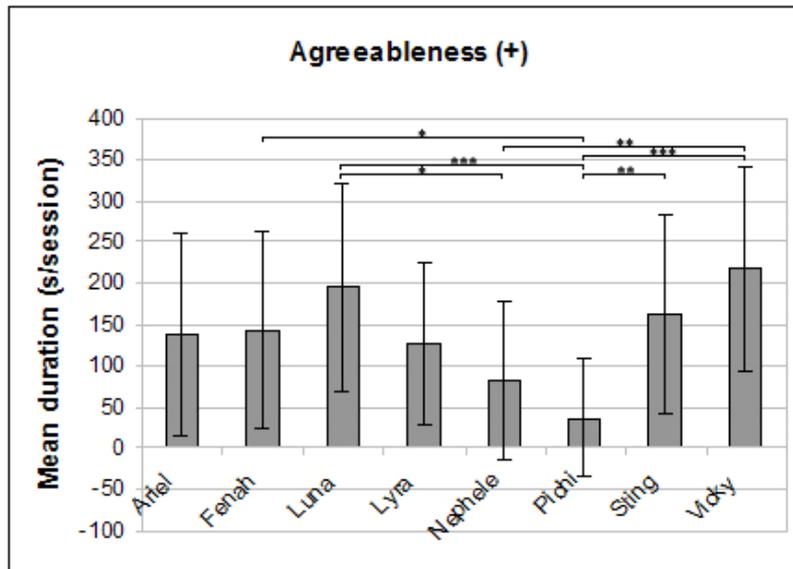


Figure 12. The mean duration in seconds the dolphins displayed behaviours within the factor Agreeableness (+) per 5-minute session. Mean (\pm SD) (***= $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$)

4.2.4 Neuroticism (+)

Behaviours within the factor N+ were rare and were only observed in Fenah, Lyra and Sting (Figure 13). This means that aggressive and agonistic behaviours only appeared on rare occasions in these individuals. However, the observed behaviours did not elicit any significant difference among these three individuals ($\chi^2 = 1.181$, $df = 2$, $p = 0.554$).

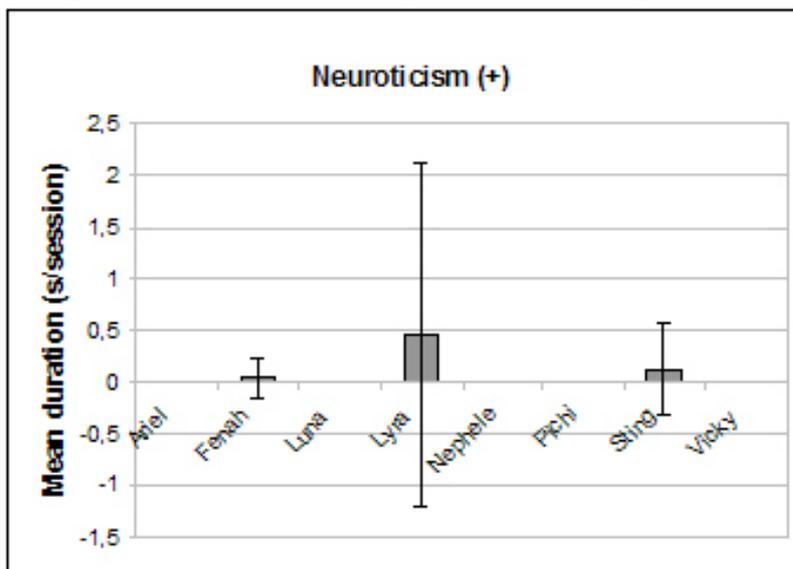


Figure 13. The mean duration in seconds the dolphins displayed behaviours within the factor Neuroticism (+) per 5-minute session. Mean (\pm SD) (***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$)

4.2.5 Neuroticism (-)

All dolphins expressed behaviours in association with the N- factor (Figure 14). That means that all dolphins were seen swimming alone from time to time in a relaxed manner. Significant differences could be found among the individuals according to the Kruskal-Wallis test ($\chi^2 = 46.438$, $df = 7$, $p < 0.001$). Bonferroni test revealed several differences of significance involving Pichi or Nephele. Nephele was seen spending more time calmly swimming alone compared to Ariel ($p < 0.001$), Fenah ($p < 0.001$), Luna ($p < 0.001$), Lyra ($p < 0.05$), Sting ($p < 0.001$) and Vicky ($p < 0.001$). Also Pichi was observed to spend significantly more time swimming calmly alone compared to Fenah ($p < 0.001$), Luna ($p < 0.05$), Sting ($p < 0.001$) and Vicky ($p < 0.05$).

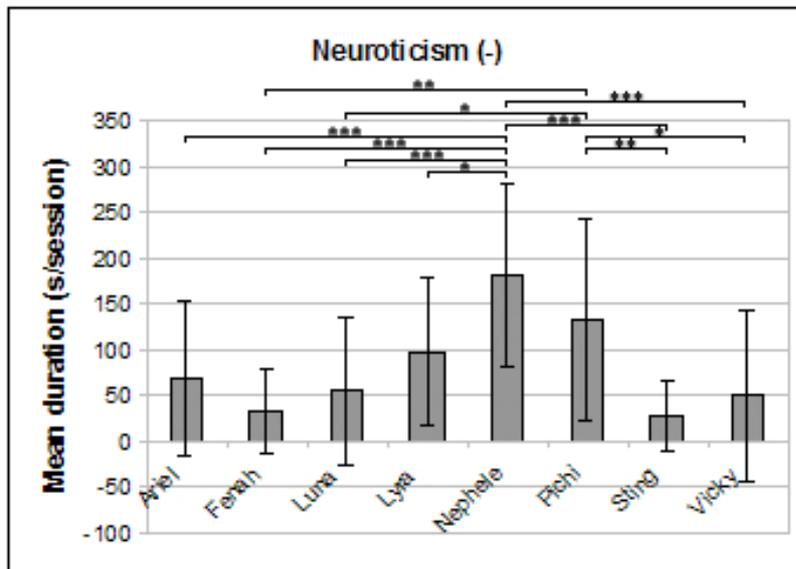


Figure 14. The mean duration in seconds the dolphins displayed behaviours within the factor Neuroticism (-) per 5-minute session. Mean (\pm SD) (***= $p < 0.001$, **= $p < 0.01$, *= $p < 0.05$)

4.3 Coefficient of association

The Five-factor model graphs illustrate how much time the dolphins are engaged with various behaviours within the factors. To demonstrate who the dolphins are interacting with coefficients of associations were calculated using the Half Weighted Index (HWI) formula. The result is shown in Figure 15. Vicky and Luna formed the strongest dyad (HWI = 0.85), followed by Ariel and Sting (HWI = 0.70) and Lyra and Fenah (HWI = 0.59).

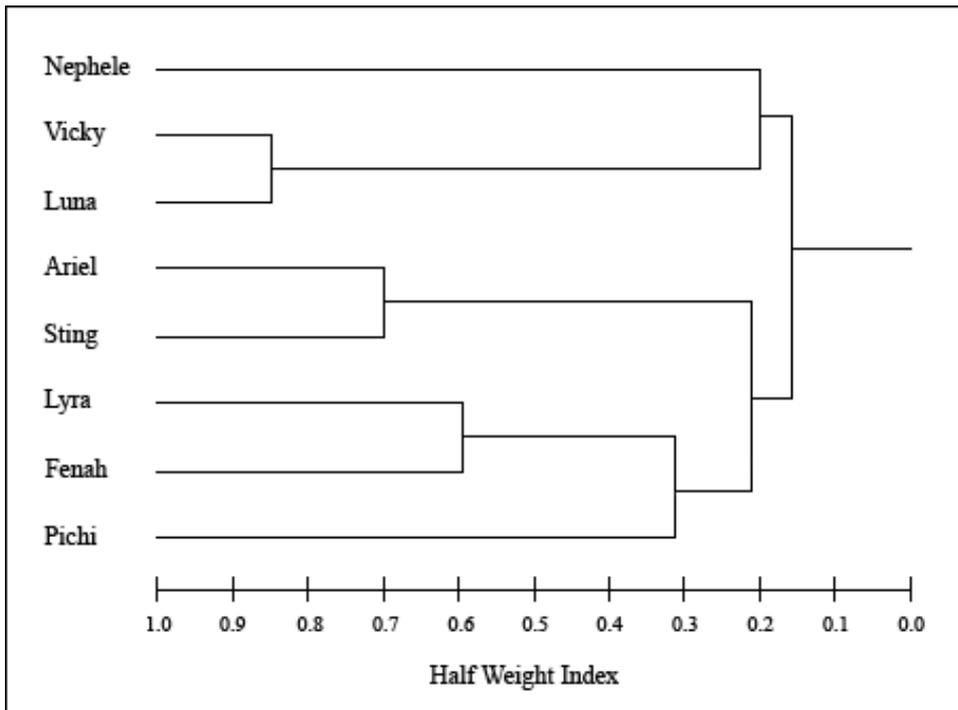


Figure 15. Coefficient of association with half-weight index shows how the dolphins associate with each other. (1 = always seen together, 0 = never seen together)

4.4 Sociograms

The sociograms present an overview on how the dolphins in this study were interacting in three different aspects. Agonistic behaviours were only observed among Lyra, Sting and Fenah (Figure 16) and sexual behaviours were only recorded in Lyra and Sting directed to Sting, Fenah, Pichi and Ariel (Figure 17). All dolphins were involved in affiliative behaviour as illustrated in Figure 18. There were big variations in the amount of time the dolphins spent together in affiliation. Some dolphins were never observed to direct affiliative behaviour to certain individuals, while some were barely seen apart.

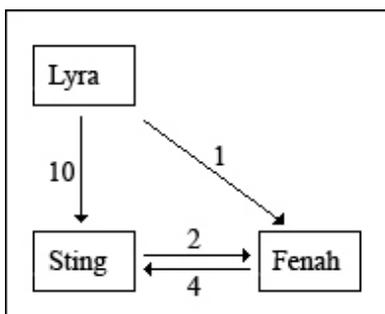


Figure 16. Sociogram over agonistic behaviour. Numbers represents the total duration in seconds agonistic behaviour was recorded among dolphin individuals.

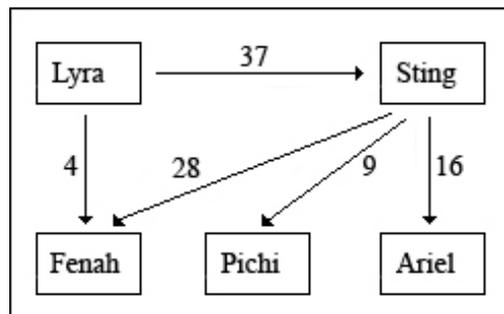


Figure 17. Sociogram over sexual behaviour. Numbers represents the total duration in seconds sexual behaviour was recorded among dolphin individuals.

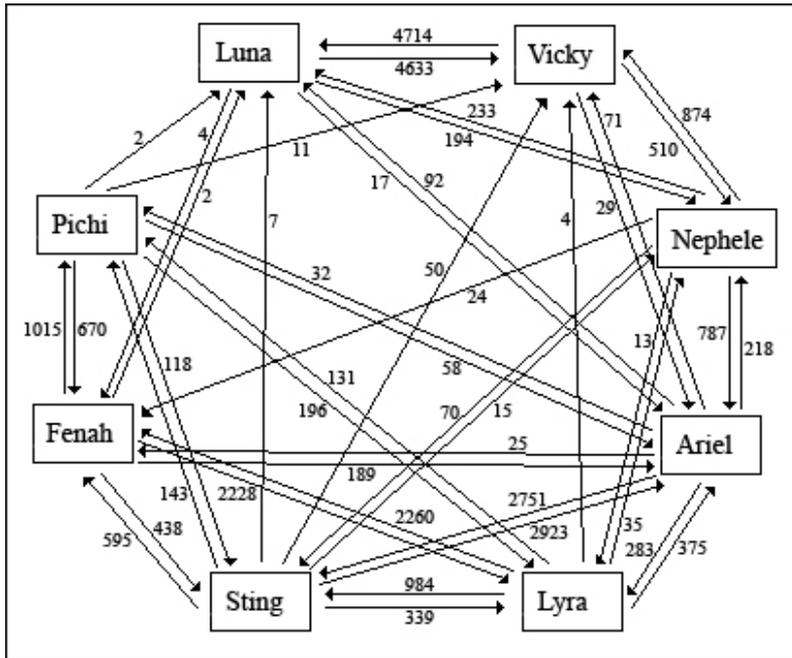


Figure 18: Sociogram over affiliative behaviour. Numbers represent the total durations in seconds affiliative behaviour was recorded among dolphin individuals.

5. Discussion

The results show that the behaviours expressed by the eight dolphins mainly indicate affiliation and calmness. This corresponds to the factors Agreeableness (positive traits) and Neuroticism (negative traits). These are also the only factors where significant differences could be found between some of the individuals. There were generally low or sometimes even absent scores in playful (Extraversion (+)), curious (Openness to experience (+)) and agonistic (Neuroticism (+)) behaviours compared to affiliation and swimming calmly alone for the whole dolphin group. The females Fenah, Luna and Vicky and the younger male Sting displayed significantly more behaviours in association to the factor Agreeableness (+) (affiliation) compared to either the female Nephele or the oldest male Pichi or both. Nephele was seen swimming alone significantly more compared to all dolphins except Pichi who was also seen swimming alone significantly more compared to Fenah, Luna, Sting and Vicky. While most dolphins have either Agreeableness (+) or Neuroticism (-) as their most dominant factor Lyra show no significant difference between the two.

In the sense of the Five-factor model the factor Agreeableness is probably the most represented in previous dolphin studies. Agreeableness contains traits of affiliation which have been recorded in various forms. Observations of e.g. synchronized swimming (Connor et al., 2006), bounding by touch (Paulos et al., 2007) and flipper rubbing (Sakai et al., 2006) have all been stated to be a sign of affiliation. Based on these facts synchronized swimming, pectoral fin contact and body contact were the main behaviours contributing to the factor Agreeableness (+) in the presented study. The factor Openness to experience (+) was based essentially on curious behaviours such as exploring the bottom or observing people or objects on the other side of the windows.

The females Vicky and Luna did not score in this factor at all and no significant difference was found between the individuals that did score in this factor.

Extraversion (+) consisted of various behaviours indicating play or active behaviours such as leaping out of water or beaching. Pichi, the old male, was never recorded to display such behaviours and no significant difference could be found among the rest of the dolphins.

Neuroticism (+) was scored on behaviours such as biting, chasing (non-playful) or head jerks directed to others. However, these behaviours were rare and when they occurred the total duration averaged around one second. Only the female Lyra and the two young dolphins Sting and Fenah were recorded to perform these behaviours during the observations, though none of them were significantly more agonistic than the others. Before the study was conducted the dolphin trainers had observed some aggression in Pichi directed to Nephele. However, during the study no aggression was observed between the two. Pichi and Nephele were not seen to interact at all during the focal samplings. Scott et al. (2005) found that aggression is more likely to be expressed by males than females. However, they were not as likely to direct aggression to pregnant females or females with dependant calves as opposed to cycling females. The same study implied that females are highly tolerant. Since the group in the presented study consisted of a majority of females with individuals that additionally had calves, this could possibly have been a contributing factor to the calm and stable situation. This finding suggests that the group of dolphins at Kolmården is tolerant and that the dolphins express very little aggressive behaviour towards each other.

The most common behaviour in the Neuroticism (-) factor was swimming alone (over one body length from any other dolphin). This was scored as Neuroticism (-) since all the dolphins seemed relaxed and content with the situation.

As seen in the results, none of the dolphins observed scored in the factor Conscientiousness or the negative traits of the factors except Neuroticism.

The lack of certain trait displays does not necessarily mean that the factor does not exist. It has been stated that to prove a dimension does not exist it would be needed to be actively looked for (Gosling & John, 1999). The reason that the dolphins in this study did not score in Conscientiousness as they did in the study by Highfill & Kuczaj (2007) is simply explained by the use of different methods. The study presented here is completely based on the behaviours occurring spontaneously with no interaction with humans other than the observer filming by the window or people that on rare occasions passed by a window. Traits in the factor Conscientiousness might be traits that can be expected particularly from human interactions such as training sessions. In trait ratings people with a general knowledge and experience from the individuals can take e.g. training sessions into consideration for a broader view.

In the coefficient of association graph (Figure 15) it is illustrated who the dolphins are usually seen together with. This includes all types of behaviours such as affiliation, agonistic, play, sexual etc. The sociograms (Figure 16-18) gives a deeper understanding of the type of interactions the dolphins display. Figure 18 reveals that a big portion of the interactions seen in the dolphin group are of affiliative nature. Based on this the coefficient of association graph illustrates mainly who is expressing affiliation with who. The dolphins in the strongest dyads in the Coefficient of association graph thus tend to be the individuals with the highest scores in Agreeableness (+). Similarly, since Neuroticism

(-) is mainly based on swimming alone behaviour this can also be reflected in the Coefficient of association graph. This shows that Pichi and Nephele, who scored highest in this factor, are the two individuals with the weakest associations to others. Even though the graph suggests that Pichi is associating with the Lyra-Fenah dyad he is associating mainly with Fenah, as can be seen in the affiliative sociogram (Figure 18). In the same way, Nephele is mainly associating with Vicky in the Vicky-Luna dyad.

Something that the three dyads illustrated in the coefficient of association graph have in common is that they consist of mothers with calves. As Fenah and Sting are relatively young (two years by the time of observation) this situation may change as they grow older. Yet it is worth noting that Luna is several years older compared to Fenah and Sting (nine years old by the time of observation), still Luna contributes to the strongest dyad. In a study conducted by Mann et al. (2000) it was found that the weaning ages of bottlenose dolphins range between 2.7 and 8.0 years. This could explain the strong associations between mothers and calves in this study, especially between Ariel and Sting as well as between Lyra and Fenah.

It is important to take the context into consideration when evaluating personality. Logically, behavioural differences expressed by individuals can be the result of other factors apart from personality (Bekoff, 2004). Age and sex are some examples of how behaviours can vary both within and across species. For example, the factor Neuroticism has been noted to display big variations between the sexes in spotted hyenas (*Crocuta crocuta*) while only a slight difference was found between the sexes in humans (Gosling & John, 1999). In the case of dolphins, studies have shown that dolphin males often team up with other adult males. These alliances cooperate in the competition for access to females (Connor et al., 2001). Since Pichi is the only adult male in the group at Kolmården it could be a reason why he was often seen to be swimming alone. Perhaps if there had been another adult male in the group he would have scored higher in Agreeableness (+). Seasonal fluctuations and time of the day may also affect how individuals behave in terms of e.g. mating or resting behaviour.

The dolphins were not always present during the focal samplings creating an uneven distribution of total time observable. The total time the focal animal was observable thus ranged from 68.5 to 107.8 minutes. The fact that the dolphins visited the other pools from time to time could eventually say something about their personality as well. Perhaps the dolphins are avoiding certain individuals that at the moment were in the Lagoon, or maybe there are other activities or interests in the other pools that attract the dolphin's attention. In the sessions used for this study Pichi was absent nearly 43 % of his focal sampling time. The reason for his absence is unknown. It could be speculated that he tried to avoid certain individuals. It might be worth noting that Pichi is deaf and thus it could also be speculated that he, relying on his vision instead of hearing, preferred to visit the other pools often to see if something was going on there.

Due to practical implementations, the dolphins were essentially filmed mornings (around 6 am) and evenings (around 6 to 8 pm). It is likely that these periods of the day were calmer and more relaxed. The daily activity was not investigated for this particular dolphin group, however in a study exploring resting behaviours in captive dolphins, the most active time period during the day was found to be the afternoon (Sekiguchi & Kohshima, 2003).

In personality studies not all traits are equally easy to assess (Gosling, 2001). From a cross-species comparison study the factors Extraversion, Agreeableness and Neuroticism have been stated to be the easiest to assess in animals (Gosling & John, 1999). To obtain the most reliable personality assessment it has been considered that the use of both behavioural codings (both in spontaneously occurring situations and controlled experimental situations) and trait ratings should provide the best idea of an animal's personality.

It is of interest to investigate the personality of animals for many reasons. As has been discussed by Watters and Powell (2011), this knowledge can be of use both theoretically and practically on an educational level as well as population management in zoos. In cognitive and behavioural studies it can be important to pay attention to the role of personality and how it may affect the results. For example, in an experimental study to investigate the existence of active or passive coping in domestic piglets (*Sus scrofa domestica*) it was found that 60 % of the variations could be explained by three possible personality traits, i.e. aggression, exploration and sociability (Forkman et al., 1995). Establishing the personality can help researchers understand more about the nature and needs of the species and individuals observed. Findings from personality studies can then be practically useful in the aspects of welfare of individual animals and environmental enrichment. In the case of the dolphins, differences in personality can also be of interest to the trainers or caretakers in their work as well as for veterinarians. In a study conducted by Delfour & Beyer (2011) it was found that the use of environmental enrichment objects varied depending on the dolphin's individual behaviours. While certain objects caused interest and manipulation in some dolphins other objects did not elicit a response. Knowing what the individuals prefer will improve the use of environmental enrichment objects. Investigating the personalities of each individual will give a better understanding why some individuals might be more curious and playful with certain objects while others might be more hesitant.

Future conservation and reintroduction programmes are other aspects where results from personality studies may provide a helpful tool. For instance, it has been found that cheetahs (*Acinonyx jubatus*) with tense or fearful traits have a lower reproductive success compared to more bold individuals (Wielebnowski, 1999). From a management and conservation point of view, the shyer cheetahs may then need more places where they can hide away from stimuli causing fear in order to successfully be able to breed.

It has not yet been investigated what role personality may play in reintroduction programs and breeding in dolphins (Highfill, 2010). It could be helpful to establish through coefficients of association analysis how the dolphins interact with each other before separating two dolphins.

Another growing interest in personality studies is the connection to genetics. It has been suggested that differences in personality can have an adaptive value (Wilson, 1998). For example, the results from a study conducted by Weiss et al. (2002) indicates that subjective well-being in chimpanzees (*Pan troglodytes*) is heritable. Réale et al. (2007) argue that differences in personality traits (such as aggressiveness, anti-predator behaviour and exploratory behaviour) may have an impact on several aspects of evolution and animal ecology both on a population level as well as on an individual level. Since personality traits may be inherited and affect reproductive success it is also reasonable to believe that personality play an important role in evolutionary aspects. This will then

affect animal's future abilities to survive and adapt to a changing environment. At the same time it is essential to keep in mind that even though differences can be detected among individuals not all are of importance (Highfill, 2010).

To move on with the presented study it could be of interest to conduct a trait rating test as well as observe the dolphin's behaviours in connection to e.g. training sessions. This would give additional perspectives to the results that are based on behavioural codings. It is also important to consider synergy between laboratory studies and studies conducted in the field (Pack, 2010). Ideally, observations and comparisons of both wild and captive dolphins would complement to the understanding of personality in dolphins.

Another interesting aspect to this would be to investigate the consistency of personalities of the eight dolphins across a longer period of time. The presented study could then be continued in a couple of years.

A question that arises is whether two hours or slightly less per individual is enough to establish a reliable personality based on behavioural codings. Statistically, certain results in this study were found to be significant. However, in future work this could be an interesting parameter to investigate further. How long time of observations does it take before a reliable personality can be assessed? How does this time vary across species? Also, collecting the data for two hours straight or in smaller sessions over a longer period of time could very likely provide different results depending on the situation in that particular moment data is collected.

Based on the results in the presented study, one could ask if the dolphins that tend to associate the most have similar personality profiles. Vicky and Luna in the strongest dyad both seem to have similar profiles (Figure 4 and 9). None of them scored in the factor Openness to experience as did the other dolphins. Moreover, Vicky and Luna have no significant differences between the remaining factors scored for. This could possibly be of interest to investigate further in future studies.

The research field of personality in animals provides various aspects where we still have much to explore and learn. It will also be important in future studies to be consistent with terminology among researchers. For instance, Watters and Powell (2011) suggested that surveys for trait ratings should be standardized in a way that cross-species comparisons would be easier to assess along with the advantage of having the possibility to build up a larger sample size.

It is the idea that the results from the presented study in the future will contribute to a larger extent in comparing personality profiles for captive dolphins in various European countries. Personality studies from several dolphinariums will help create a larger sample size and hopefully offer researchers a more comprehensive knowledge about the bottlenose dolphin as a species.

In conclusion, the presented study has shown that personality exists and can be assessed by behavioural codings and the Five-factor model. Although to be able to rely on the personality profiles and understand the whole context sociograms and coefficients of association are also needed. The dolphin individuals at Kolmården are mainly calm and affiliative.

5. Acknowledgements

I would like to direct many thanks to Mats Amundin, Fabienne Delfour, Birgitta Mercera, the staff at Kolmården dolphinarium and the students involved in the ongoing international project in assessing dolphin personality, for advice and support in carrying out the presented study as well as providing feedback and helping out with practical issues.

6. References

Altmann, J., 1974. Observational study of behaviour: Sampling methods. *Behavior* 49, 227-267.

Bekoff, M. (Ed.), 2004. *Encyclopedia of animal behavior*, Vol. 2. Greenwood Press, London, pp. 818.

Capitanio, J. P., 1999. Personality dimensions in adult male rhesus macaques: Prediction of behaviors across time and situation. *American Journal of Primatology* 47, 299-320.

Careau, V., Réale, D., Humphries, M. M., Thomas, D. W., 2010. The pace of life under artificial selection: Personality, energy expenditure, and longevity are correlated in domestic dogs. *The American Naturalist* 175(6), 753-758.

Cattell, R. B., 1943. The description of personality: Basic traits resolved into clusters. *Journal of Abnormal and Social Psychology* 38, 476-506.

Connor, R. C., Heithaus, M. R., Barre, L. M., 2001. Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society of London B: Biological Sciences* 268, 263-267.

Connor, R. C., Smolker, R., Bejder, L., 2006. Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour* 72, 1371-1378.

Delfour, F., Beyer, H., 2011. Assessing the effectiveness of environmental enrichment in bottlenose dolphins (*Tursiops truncatus*). *Zoo biology* 29, 1-14.

Forkman, B., Furuhaug, I. L., Jensen, P., 1995. Personality, coping patterns, and aggression in piglets. *Applied Animals Behaviour Science* 45, 31-42.

Gazda, S. K., Connor, R. C., Edgar, R. K., Cox, F., 2005. A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society B: Biological sciences* 272, 135-140.

Goldberg, L. R., 1993. The structure of phenotypic personality traits. *American Psychologist* 48, 26-34.

Gosling, S. D., 2001. From mice to men: What can we learn about personality from animal research? *Psychological Bulletin* 1, 45-86.

Gosling, S. D., John, O. P., 1999. Personality dimensions in nonhuman animals: A cross-species review. *American Psychological Society* 8, 69-75.

Gosling, S. D., Kwan, V. S. Y., John, O. P., 2003. A dog's got personality: A cross-species comparative approach to personality judgements in dogs and humans. *Journal of personality and social psychology* 6, 1161-1169.

Highfill, L. E., Kuczaj, S. A., 2007. Do bottlenose dolphins (*Tursiops truncatus*) have distinct and stable personalities? *Aquatic mammals* 33(3), 380-389.

Highfill, L. E., Kuczaj, S. A., 2010. How studies of wild and captive dolphins contribute to our understanding of individual differences and personality. *International Journal of Comparative Psychology* 23, 269-277.

Hill, H. M., Greer, T., Solangi, M., Kuczaj, S. A., 2007. All mothers are not the same: Maternal styles in bottlenose dolphins (*Tursiops truncatus*). *International Journal of Comparative Psychology* 20, 35-54.

King, J. E., Figueredo, A. J., 1997. The five-factor model plus dominance in chimpanzee personality. *Journal of Research in Personality* 31, 257-271.

Lusseau, D., Conradt, L., 2009. The emergence of unshared consensus decisions in bottlenose dolphins. *Behavioural Ecology and Sociobiology* 63, 1067-1077.

Mann, J., Connor, R. C., Barre, L. M., Heithaus, M. R., 2000. Female reproductive success in bottlenose dolphins (*Tursiops sp.*): life history, habitat, provisioning, and group-size effects. *Behavioural Ecology* 11, 210-219.

Pack, A. A., Herman, L. M., 2006. Dolphin social cognition and joint attention: Our current understanding. *Aquatic Mammals* 32(4), 443-460.

Pack, A. A., 2010. The synergy of laboratory and field studies of dolphin behavior and cognition. *International Journal of Comparative Psychology* 23, 538-565.

Paulos, R. D., Dudzinski, K. M., Kuczaj, S. A., 2007. The role of touch in select social interactions of Atlantic spotted dolphin (*Stenella frontalis*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). *Japan ethological society and springer* 26, 153-164.

Pervin, L. A., Crevone, D., 2010. *Personality: Theory and research* (11th ed.). John Wiley & Sons, New York, pp. 7-9.

- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., Dingemanse, N. J., 2007. Integrating animal temperament within ecology and evolution. *Biological reviews* 82, 291-318.
- Reiss, D., Marino, L., 2001. Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *PNAS* 98(10), 5937-5942.
- Sakai, M., Hishii, T., Takeda, S., Kohshima, S., 2006. Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Marine mammal science* 22(4), 966-978.
- Scott, E. M., Mann, J. Watson-Capps, J. J., Sargeant, B. L., Connor, R. C., 2005. Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour* 142, 21-44.
- Sekiguchi, Y., Kohshima, S., 2003. Resting behaviors of captive bottlenose dolphins (*Tursiops truncatus*). *Physiology and behavior* 79, 643-653.
- Thurstone, L. L., 1934. The vectors of mind. *The Psychological Review* 41(1), 1-32.
- Vazire, S., Gosling, S. D., Dickey, A. S., Schapiro, S. J., 2007. Measuring personality in non-human animals. In Robins R. W., Fraley, R. C., Krueger, R. (Eds.), *Handbook of research methods in personality psychology*. Guilford Press, New York, pp. 190-206.
- Watters, J. V., Powell, D. M., 2011. Measuring animal personality for use in population management in zoos: Suggested methods and rationale. *Zoo biology* 29, 1-12.
- Weiss, A., King, J. E., Enns, R. M., 2002. Subjective well-being is heritable and genetically correlated with dominance in chimpanzees (*Pan troglodytes*). *Journal of Personality and Social Psychology* 83(5), 1141-1149.
- Wielebnowski, N. C., 1999. Behavioral differences as predictors of breeding status in captive cheetahs. *Zoo biology* 18, 335-349.
- Wilson, D. S., 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 353, 199-205.