Patrones de comportamiento y perfiles de personalidad en el delfín mular (*Tursiops truncatus*), y su utilidad como herramienta de manejo en cautividad

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TESIS DOCTORAL

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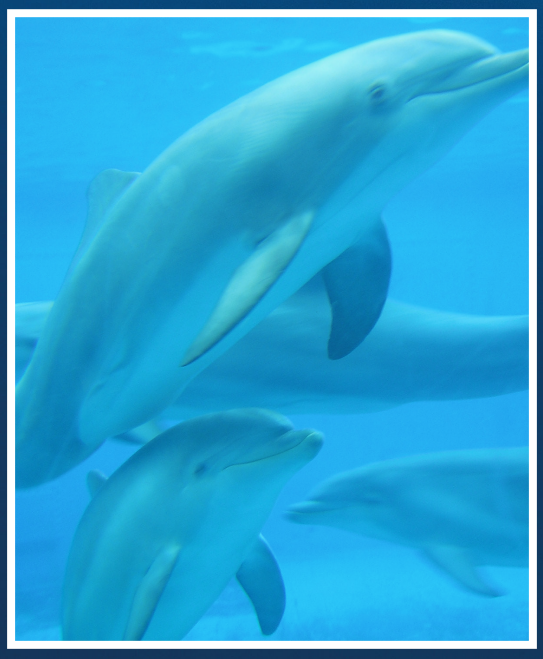

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Departamento de Biología Evolutiva, Ecología y Ciencias Ambientales
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Memoria presentada por **Carolina Quirós Garzón**
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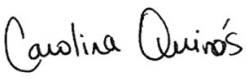

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A Enric y Martina,
mis dos amores

En memoria de Anak, Nereida, Nika,
Tumay, Inuk, Blau, Neo y Leia

"Conocer es la clave para cuidar, y con el cuidado hay esperanza de que las personas se motiven a tomar acciones positivas" (Sylvia Earle, 2009)

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ABSTRACT

The study of solitary and social behavioral patterns of animals under human care is useful for management practices, as the impacts of all the experiences perceived and expressed by individuals represent their welfare states. As animal welfare depends on how an individual copes with its living conditions and challenges, the identification of personality profiles contributes to a better understanding of individual needs and can be used to guarantee optimum welfare. Animal personality is defined as the behavioral differences between individuals of the same species, which are consistent over time and across contexts. Despite there is a great number of studies on activity budgets in cetaceans, few have established the range and threshold of frequent behavioral patterns, that are indicative of welfare states. There are also studies in cetacean personality, but very few have determined the correspondence between behavioral measures and questionnaire-based assessments, aiming at determining personality. The main objective of this thesis was to study the solitary and social behavior of a group of eight bottlenose dolphin (*Tursiops truncatus*) in captivity (Barcelona Zoo), during two reproductive cycles, to identify the behavioral and personality structures of the species, and explore how this knowledge can be used to improve welfare and success in *ex situ* conservation programs. Ethological observations were made during nine different reproductive stages, to study behavioral patterns in different environmental and social contexts, and detect personality structures. The proportion of behaviors that the study subjects engaged in solitary and interindividual interactions during their daily activity patterns, were explored using all-occurrence continuous follow sampling bouts and instantaneous scans. Behavioral structure was explored using a multivariate temporal pattern (T-pattern) analysis and personality structure was identified using a dimension reduction analysis. Both methods were then compared to test their effectiveness in identifying personality traits in social mammals. Two personality assessment methodologies, observed interactions (known as “codings”) and ratings of adjective items (known as “ratings”), were used and then compared, to validate the “codings” methodology for the species. Different social contexts significantly modulated mean frequencies of solitary and social behaviors. Findings suggest that the most frequent behaviors out of the total visible activity budget were solitary swimming (18% - 28%), close swimming (20%) and maternal close swimming (20% - 42%). Behavioral structures varied according to context, as structures were more complex during the pre-natal phase, suggesting that

endocrine and physiological changes during the advanced pregnancy stage may modulate behavioral patterns of mothers. Expectant females seemed uncomfortable during the pregnancy stage, possibly due to an inappropriate birthing environment, but their relationship improved when their calves were born. We found that a better approach to assess personality profiles is achieved by inferring dimensions, rather than studying multivariate T-patterns. In total, four personality factors were identified in this investigation: *Extraversion, Agreeableness, Neuroticism* and *Conscientiousness*. The factors inferred with both personality assessments correlated statistically and traits grouped similarly, which validates the "codings" methodology used in this investigation. Bottlenose dolphins exhibit different behaviors, even having equal characteristics like sex, age group, birth type, reproductive status, and living under the same environmental conditions and social groupings. This suggests that subjects respond in different ways to the same experiences, which is why it is useful to have knowledge of the personality of individuals, to predict their responses and to know the characteristics that help their adaptation to changes and living conditions in captivity. With this, we conclude that personality is a useful tool to improve the management of bottlenose dolphins under human professional care and to determine the social conditions that guarantee welfare and breeding success, which are crucial for *ex situ* conservation programs of endangered species.

ÍNDICE

INTRODUCCIÓN GENERAL

1. INTRODUCCIÓN GENERAL

1.1. Comportamiento animal

El comportamiento animal es la respuesta de un ser vivo a factores causales internos o externos (Tinbergen, 2020). Los animales reaccionan a las alteraciones en el ambiente modificando su comportamiento. Estos ajustes ayudan al animal a sobrellevar y prosperar en entornos cambiantes. El estudio del comportamiento implica buscar respuesta a la pregunta sobre qué estímulos o procesos externos o internos, provocan o facilitan la manifestación de ciertas respuestas conductuales en un individuo en un momento dado y de qué modo el individuo acaba desarrollando un determinado estilo de comportamiento, temperamento y personalidad.

Los estudios basados en la observación del comportamiento no son ni invasivos, ni costosos, y generan conocimientos que se pueden aplicar en el cuidado de los animales (atención médica, entrenamiento, manejo), en su bienestar (según necesidades físicas, psicológicas sociales, y necesidades relacionadas con el ambiente, tales como el hábitat, instalaciones y transporte), y en la conservación de la vida silvestre (Pirotta et al., 2016). Así, el conocimiento adquirido a partir de estudios de comportamiento ayuda a los gestores en zoológicos, a científicos y a conservacionistas a predecir cómo se comportará un individuo en el futuro, por ejemplo, al ser trasladado a otra instalación, a otro grupo social o a otro centro zoológico. El comportamiento se puede medir con indicadores estáticos, como las frecuencias de los patrones de actividad, o con indicadores dinámicos que registran secuencias y duraciones para estudiar la relación estructural entre los actores de las interacciones mostrando la estabilidad de la estructura del comportamiento y posible existencia de diferencias. Para detectar patrones de comportamiento a partir de las secuencias y duraciones, se precisan metodologías y herramientas especiales para hacer visibles los perfiles de personalidad (Magnusson, 1996).

Las diferencias interindividuales en el comportamiento ocurren como un mecanismo adaptativo debido a varios factores como la vida temprana y las experiencias pasadas, la genética y los estados de salud (Manteca & Deag, 1993). Los perfiles de comportamiento aparecen cuando se aprecian diferencias en el comportamiento entre individuos de una especie a lo largo de diferentes contextos (Sih et al., 2004), y se podrían denominar ‘síndromes de comportamiento’, ‘temperamento’ o ‘personalidad’ (Bell,

2007). Las medidas de personalidad se relacionan con el comportamiento, si el comportamiento se agrega a lo largo del tiempo (Epstein, 1979). Estudios recientes en epigenética comportamental han demostrado que la expresión de los genes está influenciada por las experiencias y el entorno, y que produce diferencias interindividuales tanto en el comportamiento como en los perfiles de personalidad (Powledge, 2011). Esto puede explicar por qué individuos de la misma especie, sexo y edad, se comportan de manera diferente en situaciones similares (Gosling & John, 1999) y cómo la personalidad juega un papel clave en la expresión del comportamiento de un individuo (Dudzinski et al., 2012).

1.2. Personalidad animal

El concepto de personalidad animal se basa en la existencia de patrones de comportamiento individuales que permanecen constantes tanto a lo largo del tiempo como a través de situaciones diferentes (consistencia intraindividual; Koski, 2011), y que marcan diferencias comportamentales y fisiológicas entre sujetos de la misma especie (variabilidad interindividual; Pervin & John, 1997; Carere & Maestripieri, 2013). Dicha variabilidad puede estar provocada por factores genéticos (Weiss et al., 2000; Weiss et al., 2009) o ambientales (físicos: King et al., 2005; sociales: Krause et al., 2010; Koski, 2011; Kuczaj et al., 2012), y tener consecuencias ecológicas importantes, lo cual nos permite conocer la evolución de la vida social y las estrategias de supervivencia de las especies (Dudzinski & Frohoff, 2008). Darwin, cuando observó que no todos los individuos de la misma especie están hechos con el mismo molde, sugirió que los animales exhiben diferencias interindividuales en sus rasgos de comportamiento y que dichos rasgos pueden evolucionar de la misma manera que los caracteres físicos (Highfill & Kuczaj, 2010), y reconoció que la importancia de las diferencias interindividuales se debe a que proporcionan material para que la selección natural se acumule (Kuczaj et al., 2012). En las últimas dos décadas, y debido a que se empezaron a observar diferencias de comportamiento intrapoblacionales (Carere & Maestripieri, 2013), ha habido un creciente interés por los estudios de personalidad y su importancia evolutiva (Barnard et al., 2016). Desde entonces, un gran número de estudios ha demostrado que individuos de la misma especie, independiente del sexo o la edad, difieren en su comportamiento, incluso bajo condiciones estandarizadas de laboratorio. Dichas diferencias interindividuales pueden ser medidas fácilmente cuando los individuos tienen que afrontar retos sociales y no

sociales (peces y reptiles: Overli et al., 2007; mamíferos: Coppens et al., 2010), por lo que la personalidad animal pone de manifiesto los estilos de afrontamiento o predisposiciones. Los rasgos de comportamiento que representan la personalidad están generalmente intercorrelacionados, por lo cual los individuos suelen tener agrupaciones de estos rasgos (Wilson et al., 1994; Gosling & John, 1999; Gosling, 2001; Sih et al., 2004; Nettle & Penke, 2010; Stamps & Groothuis, 2010). Se han realizado estudios de personalidad en una amplia variedad de especies pertenecientes a diferentes taxones (ver revisión bibliográfica en Gosling, 2001), desde invertebrados, como cnidarios (Hensley et al., 2012) y artrópodos (Schuett et al., 2011), hasta vertebrados como peces (Nakayama et al., 2012; Khan & Echevarria, 2017; Hasenjager et al., 2020), reptiles (Carter et al., 2012; Waters et al., 2017), aves (Guillette et al., 2015; Riyahi et al., 2016; Quintavalle et al., 2019) y mamíferos (primates: Stevenson-Hinde and Zunz, 1978; Gold & Maple, 1994; Úbeda & Llorente, 2015; Masilkova et al., 2020; cetáceos: Highfill & Kuczaj, 2007; Úbeda et al., 2019; Hill et al., 2019; Díaz, 2020; Morton et al., 2021; Evans et al., 2021; felinos: Goswami et al., 2020; roedores: Forkosh et al., 2019; otros grupos: Horback et al., 2013; Andres-Bray et al., 2020).

1.2.1. Métodos de evaluación de la personalidad

Los dos modelos de evaluación de la personalidad animal son: el de codificación ("codings"), basado en codificaciones objetivas del comportamiento, y el de calificación ("ratings"), basado en calificaciones subjetivas de los rasgos de personalidad (Gosling, 2001; Vazire et al., 2007). Con la codificación, los datos se obtienen realizando observaciones directas, mientras que con la calificación los datos se obtienen mediante encuestas cualitativas realizadas por cuidadores, entrenadores y personal que conoce a los sujetos, a partir de observaciones indirectas. Mediante la codificación se registran las pautas observadas, utilizando etogramas en diferentes sesiones de observación. También se pueden obtener datos sobre la conducta realizando experimentos que permiten observar cómo los animales reaccionan frente a determinados estímulos y cómo se enfrentan a circunstancias específicas (Tkaczynski et al., 2019). Las pruebas cognitivas y de enriquecimiento ambiental son buenos ejemplos para identificar rasgos de personalidad en individuos. En resumen, mediante la codificación un equipo de observadores entrenados identifica y registra los comportamientos expresados por los animales que "a

posteriori" se agrupan para mostrar rasgos diferenciados que describen perfiles de personalidad.

A partir de las calificaciones ("ratings") los factores de personalidad se obtienen agrupando adjetivos que se relacionan entre sí, utilizando cuestionarios y una escala de valoración (escala de Likert). Estos cuestionarios son rellenados por expertos familiarizados con los sujetos de estudio, que en cautividad suelen ser los cuidadores o entrenadores, que conocen bien a los sujetos, y que pueden observar una amplia variedad de comportamientos proporcionando una información detallada de los rasgos de personalidad durante un largo periodo de tiempo (Highfill & Kuczaj, 2007). Los estudios de Clegg (2018) demuestran empíricamente que los cuidadores evalúan de manera precisa el bienestar, el comportamiento y la personalidad de los animales a su cargo. No obstante, puesto que depende de la percepción de los calificadores, para minimizar sesgos subjetivos se realizan múltiples calificaciones de diferentes personas para los mismos individuos, y las calificaciones deben tener una fiabilidad interobservacional elevada para garantizar su validez. Las calificaciones precisan de muestras más grandes de individuos para atribuir valores a los rasgos de personalidad (Watters & Powell, 2012). La Tabla 1 muestra las características de ambos modelos de evaluación, con sus ventajas y desventajas.

1.2.2. Modelos de personalidad

Los expertos en comportamiento animal proponen diversos modelos para organizar los rasgos de personalidad, según los objetivos y la especie de estudio. En ecología del comportamiento se proponen cinco rasgos descriptivos: 1) el continuo de *Timidez-Atrevimiento*, 2) el continuo de *Exploración-Evitación* (evitación de la novedad), 3) *Actividad*, 4) *Sociabilidad,* y 5) *Agresividad*. En comportamiento se propone el Modelo de los Cinco Factores (Five Factor Model, FFM), que agrupa factores con rasgos de comportamiento relacionados entre sí: 1) *Apertura a la experiencia* ("*Openness to Experience"),* 2) *Consciencia ("Conscientiousness"), 3) Extroversión ("Extraversion"), 4) Amabilidad ("Agreeableness") y 5) Neuroticismo ("Neuroticism";* Goldberg, 1993).

Tabla 1. Características, ventajas (✓) y desventajas (✗) de los dos modelos de evaluación utilizados en estudios de personalidad animal (Modificado de: Barnard et al., 2016; Freeman, 2011; Manteca & Deag, 1993; Tkaczynski et al., 2019).

	Medidas de comportamiento	
Calificaciones de adjetivos	**Observaciones naturalistas**	**Pruebas experimentales**
✗ Subjetivo (la evaluación es filtrada por la percepción que tiene el calificador del animal).	✓ Objetivo.	✓ Objetivo.
✗ No refleja comportamientos que ocurren naturalmente (bajos niveles de validez ecológica).	✓ Refleja comportamientos que ocurren naturalmente.	✗ No refleja comportamientos que ocurren naturalmente (bajos niveles de validez ecológica).
✓ Las evaluaciones con cuestionarios son más rápidas.	✗ Requiere tiempo.	✗ Requiere tiempo.
✓ Permite hacer comparaciones entre especies de manera estandarizada.	✓ Permite hacer comparaciones entre especies de manera estandarizada.	✗ Dificultad para hacer las mismas pruebas para diferentes especies.
✓ Basado en observaciones hechas a largo plazo, por lo cual pueden aportar información desde una base y perspectiva más amplia (incluso sobre la totalidad de la vida del individuo), por lo cual puede aportar información más precisa.	✗ Basado en observaciones hechas a corto plazo y momentáneo (en un momento específico).	✗ Basado en observaciones hechas a corto plazo y momentáneo (en un momento específico).
✓ Se puede obtener información de aspectos sutiles que no representen los comportamientos solos.	✗ Se obtiene información solo de aspectos que se observan.	✗ Se obtiene información solo de aspectos que se observan.
✓ Los evaluadores ya están entrenados y hacen las calificaciones basados en su conocimiento del animal a través de diferentes contextos y situaciones.	✗ Los observadores deben estar entrenados y deben conocer el comportamiento de la especie de estudio.	✗ Los observadores deben estar entrenados y deben conocer el comportamiento de la especie de estudio.
✗ Si los evaluadores entrenados no tienen disponibilidad para contestar las encuestas, nadie más puede hacer las calificaciones de ciertos individuos.	✓ Los observadores se pueden entrenar para evaluar los comportamientos.	✓ Los observadores se pueden entrenar para evaluar los comportamientos.
✗ Solo puede hacerse con individuos en cautividad, o con individuos en libertad de los cuales se tenga un conocimiento previo de su comportamiento.	✓ Puede hacerse con individuos en cautividad y en libertad, sin necesidad de tener una relación o conocimiento previo de su comportamiento.	✓ Puede hacerse con individuos en cautividad y en libertad, sin necesidad de tener una relación o conocimiento previo de su comportamiento.

Los individuos con niveles altos del factor *Apertura a la experiencia* son aventureros, imaginativos y curiosos. Los que muestran niveles altos del factor *Consciencia,* muestran un buen control de los impulsos, son cuidadosos, prudentes, comprometidos y autodisciplinados. Los que tienen niveles altos del factor *Extroversión* son energéticos, activos, sociales y buscan la atención, mientras que los individuos con niveles bajos de *Extroversión* son introvertidos, más solitarios, y muestran bajos niveles de contacto con otros conespecíficos. Los sujetos con niveles altos de *Amabilidad* son cooperativos, cariñosos, populares y amistosos. Los que muestran niveles altos de *Neuroticismo,* son más agresivos, nerviosos e irritables, mientras que los que tienen niveles bajos están menos preocupados y más relajados (Digman, 1990; Goldberg, 1993).

El Modelo FFM es el más utilizado en investigación de personalidad en humanos (Digman, 1990) y su uso es frecuente en el estudio de la personalidad animal (Gosling & John, 1999). Los primeros estudios de personalidad animal utilizando el mismo método de evaluación de calificación, se llevaron a cabo en primates no humanos en la década de los 60s, cuando se comenzaron a encontrar similitudes entre los factores inferidos en primates con aquellos frecuentemente encontrados en humanos (macaco Rhesus, *Macaca mulatta*: Locke et al., 1964; Chamove et al., 1972; chimpancés, *Pan troglodytes*: Van Hooff, 1971), aunque no siempre aparecen todas las características. Stevenson-Hinde y Zunz (1978), utilizando el FFM, sólo encontró tres factores de personalidad en macacos Rhesus. En chimpancés (*Pan troglodytes*), estudios posteriores como el de King y Figueredo (1997) proponen agregar otro factor para agrupar rasgos relacionados con la dominancia en primates, encajando de este modo en el FFM. A partir de esta propuesta, el FFM ha sido modificado para ser aplicado en el estudio de personalidad en diferentes especies.

Más recientemente, se han realizado estudios que basan los perfiles de personalidad a partir de la reacción de los sujetos a objetos novedosos, y los comparan con evaluaciones realizadas mediante cuestionarios (calificaciones) a cuidadores en zoológicos (por ejemplo, en el leopardo de las nieves, *Panthera uncia*: Gartner & Powell, 2012). Otros estudios comenzaron a combinar ambos modelos de evaluación (calificaciones *vs* codificaciones) demostrando que la evaluación de la personalidad a partir del repertorio conductual es un indicador válido para el seguimiento del comportamiento a largo plazo, y que es capaz de identificar compatibilidad social, entrenamiento operante o individualización del enriquecimiento ambiental (Horback at al., 2013). Konečná et al. (2008) combinaron calificaciones a partir de cuestionarios

basados en los FFM con las observaciones de la conducta en el langur común (*Semnopithecus entellus*) en condiciones de libertad, y obtuvieron resultados similares por ambos modelos de evaluación de la personalidad.

1.2.3. Aplicaciones de los estudios de personalidad

Cómo los animales interactúan con su ambiente viene influido por la personalidad. Puesto que las experiencias subjetivas de los animales no se pueden medir directamente, los patrones de comportamiento pueden ser indicadores de cómo los individuos reaccionan y se adaptan a su medio (Diener et al., 1999; King & Landau, 2003; Gartner & Weiss, 2013; Mellor et al., 2015). La personalidad permite conocer las preferencias y necesidades sociales y ambientales de los individuos, y puede ayudar a predecir el comportamiento de los individuos en cualquier contexto (Barnard et al., 2016), lo que es de interés para el manejo en cautividad. Los estudios de personalidad han sido útiles para formar grupos sociales adecuados, para mantener la diversidad comportamental y para ubicar a los animales en nuevos grupos e instalaciones donde conseguir un máximo bienestar (Gold & Maple, 1994; Stoinski et al., 2004; Vazire and Gosling, 2004; Powell, 2010; Barnard et al., 2016). Por ejemplo, los machos de gorila (*Gorilla gorilla*) con niveles altos del factor *Comprensión*, muestran más comportamientos afiliativos y menos agresivos, haciendo que sean más aptos para ser alojados en grupos sociales de solteros (Kuhar et al., 2006). El conocimiento de la personalidad facilita el manejo correcto de los animales en cautividad y mejora su bienestar (Kuczaj et al., 2013), permitiendo que cuidadores y gestores de centros zoológicos actúen basándose en las necesidades individuales. El conocimiento de la personalidad también sirve para seleccionar a los individuos más aptos para el entrenamiento, y para detectar tempranamente problemas de comportamiento (Barnard et al., 2016). Las diferencias individuales, como la personalidad y la jerarquía social, también pueden ser tomadas en cuenta al aplicar programas de enriquecimiento ambiental, teniendo en cuenta la personalidad de los individuos para adaptar dichos programas según las preferencias individuales de alimento, aromas y habilidades sociales (Soriano et al., 2015; Clegg, 2018).

La personalidad también es un predictor importante de la salud física y mental de los animales, por estar relacionada con las reacciones comportamentales al estrés (Wielebnowski et al., 2002) y con la respuesta inmune (Ironson et al., 2008; Deary et al., 2010; Capitanio, 2011). Algunos factores de personalidad como el *Neuroticismo* y la

Consciencia están asociados con enfermedades; el factor *Neuroticismo* está asociado con la ansiedad y la depresión, y el factor *Consciencia* está asociado con la longevidad (Atherton et al., 2014). Si se identifican qué rasgos de personalidad se relacionan con la salud, se puede trabajar con aquellos rasgos para mejorar la salud y el bienestar de los individuos. Si se determina sistemáticamente la personalidad de cada individuo, se pueden identificar fácilmente indicadores de ansiedad, dolor, o cualquier otra emoción desagradable que afecten el bienestar del animal.

El conocimiento de la personalidad también tiene aplicaciones en los programas conservación *ex situ* garantizando el bienestar de individuos que participan en dichos programas, mejorando el éxito reproductivo. Cuando se forman grupos con fines reproductivos, se buscan las condiciones sociales apropiadas para que los animales se reproduzcan con éxito, y se determinan qué individuos son más compatibles para que haya atracción para formar parejas y éxito reproductivo incluyendo los individuos son más eficientes para criar a sus crías con éxito (Soriano et al., 2015). Carlstead (1999) descubrió que las parejas reproductoras exitosas de rinoceronte negro (*Diceros bicornis*) en su mayoría consistían en una pareja de un macho sumiso y una hembra dominante. Wielebnowski (1999) descubrió que los individuos tensos y temerosos de guepardos (*Acinonyx jubatus*) tenían menos éxito para reproducirse y criar a sus crías, debido a la dificultad que tienen para adaptarse a entornos cautivos. Después de descubrir este problema, encontraron soluciones colocando a los sujetos con estos rasgos de personalidad, en áreas aisladas, proporcionando escondites para reducir los comportamientos tensos y temerosos, aumentado así el éxito reproductivo de los individuos.

La conservación de la naturaleza está vinculada a la capacidad de respuesta de las especies a los cambios ambientales (Highfill & Kuczaj, 2010), como por ejemplo los causados por el cambio climático o por la degradación ambiental. Los estudios de personalidad pueden ayudar a determinar la capacidad de adaptación de los animales a cambios en el hábitat que afectan directamente a su supervivencia. Existe un consenso creciente de que la personalidad juega un papel importante en la selección natural (Wolf et al., 2007), pero aún se debe investigar más sobre el tema (Kuczaj et al., 2013). La personalidad tiene una relevancia emergente en el desarrollo de programas de conservación de la naturaleza que trabajan por la desfragmentación de los hábitats, por la reintroducción en poblaciones silvestres de individuos criados en cautividad, o en la translocación de individuos de unas áreas a otras. En programas de recuperación y

reintroducción, se monitorea el éxito reproductivo y la tasa de supervivencia en relación con las variaciones interindividuales. Si se tiene en cuenta la información sobre la personalidad de los individuos en la toma de decisiones (por ejemplo acerca de cuándo liberar a un individuo), se puede mejorar el éxito de un proyecto de reintroducción (Carere & Maestripieri, 2013). En cuanto a la rehabilitación y liberación de animales que han sido recuperados o criados en cautividad, el conocimiento de la personalidad ayuda a determinar qué rasgos y qué individuos, son los mejores candidatos para una liberación exitosa debido a que las estrategias territoriales y de forrajeo también pueden estar vinculadas a la personalidad. Los individuos que tienen más probabilidades de sobrevivir en libertad, después de haber estado cautivos por cualquier motivo, son aquellos que tienen la capacidad de adaptarse mejor a nuevos entornos, protegerse de los depredadores y buscar alimento (Carere & Maestripieri, 2013).

1.3. Bienestar animal

El bienestar animal es el estado en que se encuentran los animales que disfrutan de unas condiciones de vida adecuadas a sus necesidades y gozan de buena salud. Existe una amplia gama de experiencias que se relacionan con las opciones y los retos a los que se enfrentan los animales. Por ejemplo, el animal tiene un bienestar óptimo cuando tiene opciones de qué y dónde comer, interactuar, o no, con otros animales, habitar diferentes ambientes que proporcionan una variedad de comodidades. Los retos a los que se enfrenta el animal pueden ser físicos o cognitivos, y están en consonancia a las habilidades y necesidades individuales. Los retos se concretan en por ejemplo, la búsqueda de alimento y la recompensa de su obtención (Mellor et al., 2015). Para evaluar el bienestar de forma efectiva y sistemática se utiliza el "Modelo de los Cinco Dominios" (Mellor et al., 2020), constituido por los siguientes dominios: 1) nutrición, 2) ambiente físico, 3) salud, 4) interacciones de comportamiento, y 5) estado mental. En los primeros cuatro dominios se agrupan factores que generan experiencias subjetivas positivas o negativas específicas, denominadas afectos, los cuales se agrupan en el quinto dominio y contribuyen al estado mental del animal (Figura 1).

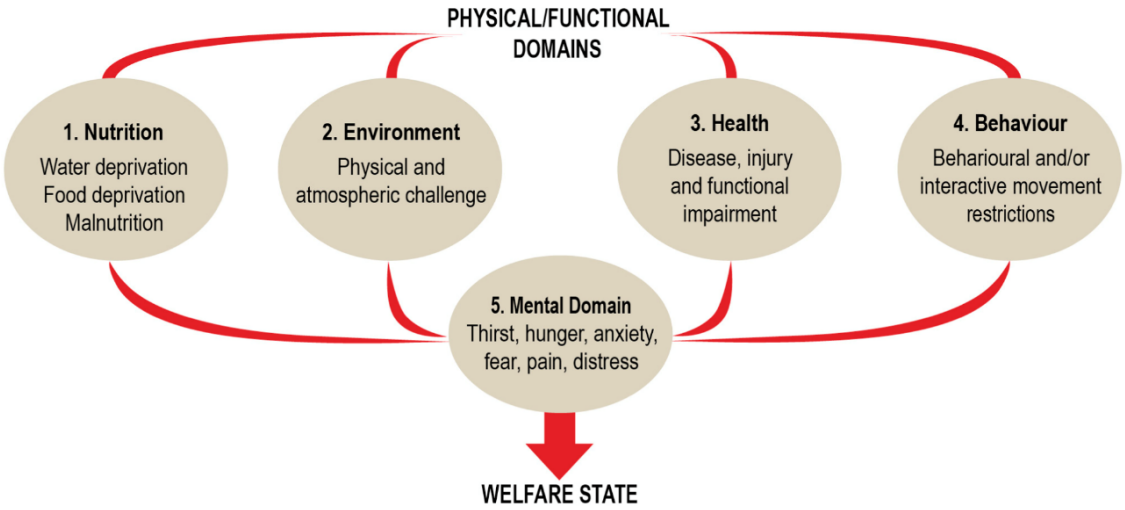

Figura 1. El Modelo de los Cinco Dominios de la evaluación de bienestar animal según Mellor et al. (2020)

Los primeros tres dominios se centran en desequilibrios internos o perturbaciones que puedan tener origen en la nutrición, el ambiente y la salud, los cuales alteran o interrumpen características particulares de la estabilidad interna del cuerpo. Cada característica alterada o interrumpida genera entradas sensoriales que son procesadas por el cerebro para formar afectos negativos específicos, y estos están asociados con comportamientos que actúan para restaurar la estabilidad interna del cuerpo, llamados afectos críticos para la supervivencia. El cuarto dominio se centra en la evidencia comportamental de animales que buscan, conscientemente, objetivos específicos al interactuar con el ambiente, con otros animales, y con humanos. En este dominio los afectos son producidos por entradas sensoriales obtenidas desde afuera del cuerpo, y por lo tanto captura las respuestas a factores relacionados con situaciones. El quinto dominio concede una evaluación final del estado general de bienestar del animal, entendido como lo que es probable que el sujeto perciba subjetivamente. Este modelo refleja la importancia de tener un amplio conocimiento de los patrones y perfiles de comportamiento para la evaluación del bienestar animal, ya que éstos funcionan como indicadores de las percepciones de los animales a circunstancias externas (Mellor et al., 2020).

Las evaluaciones y medidas del comportamiento, específicamente las interacciones sociales, pueden proporcionar tanta o más información sobre el bienestar que las medidas fisiológicas y de salud, ya que los comportamientos son mejores indicadores del estado emocional del animal (Waples & Gales, 2002; Joseph et al., 2010).

Un enfoque más reciente, pero menos común, se basa en la afirmación de que las diferencias interindividuales en la personalidad y en el estado de ánimo pueden afectar significativamente el sesgo cognitivo (Clegg, 2018). Entre los comportamientos que han sido propuestos como indicadores de buen bienestar, están el comportamiento afiliativo (Boissy et al., 2007), la variabilidad en el repertorio comportamental dentro del patrón de actividad del animal, las variaciones espontáneas en el patrón de actividad diario, y la frecuencia de juego y exploración (Galhardo et al., 1996). Es por esto que el bienestar puede ser reducido cuando hay una expresión de comportamientos afiliativos en bajas frecuencias (Tamaki et al., 2006). Es más probable que el comportamiento de juego ocurra en ausencia de amenazas y necesidades utilitarias (Bel'kovich et al., 1991), y está relacionado con emociones positivas en algunas especies (Held & Špinka, 2011), por lo cual puede ser un indicador de buen bienestar (Clegg et al., 2017). Por otra parte, el bienestar se compromete cuando se presentan comportamientos agonísticos en altas frecuencias (Galhardo et al., 1996). Además, en animales silvestres los comportamientos anormales (como niveles altos de agresividad) son inexistentes, en cambio se observa en muchas especies en cautividad (ver ejemplos en Miller et al., 2011). El estudio del patrón de actividad en animales mantenidos en cautividad aporta información sobre la presencia de comportamientos anormales (Bell, 2007) y, por consiguiente, ser imprescindible para encontrar soluciones sobre cómo reducirlos. El desafío más importante de tener animales bajo el cuidado profesional humano, es mantener los más altos estándares de bienestar.

1.4. Estudios en cautividad

Las instituciones zoológicas han evolucionado para desempeñar una labor como organizaciones implicadas en la conservación y equilibran las complejas demandas que requiere asumir un papel en la desaceleración de las tasas de extinción de la biodiversidad. Debido a esto, existe una necesidad de continuar mejorando el cuidado y el bienestar de los animales, dada la responsabilidad única de tenerlos bajo su cuidado profesional (Faust, 2019). La ventaja de hacer estudios con animales en centros zoológicos es porque la cautividad es un medio controlado, donde se puede observar el abanico de conductas que presentan los animales, y que en libertad no se logran detectar. Cada individuo puede presentar una gran variedad de comportamientos complejos y sutiles, y además se pueden explorar las señales visuales que utilizan los animales para socializar entre ellos. Es de

esta forma como la observación en cautividad se convierte en una herramienta para obtener información sobre la vida social y el comportamiento, en general, de las especies (Dudzinski & Frohoff, 2008).

En cautividad, también se puede estudiar cómo los factores sociales y ambientales afectan a los perfiles de personalidad de las diferentes especies, así como explorar la capacidad que tiene cada individuo para adaptarse a las condiciones de una instalación, a diferentes ambientes y a diferentes grupos sociales. Realizar un estudio en un medio controlado ofrece la ventaja de tener información exacta de cada individuo sobre su edad, sexo, procedencia, jerarquía y composición del grupo en el que vive, un tipo de información que no siempre está disponible para individuos en libertad. Además, los estudios que se realizan en varios centros zoológicos permiten conocer la prevalencia de fenómenos como una infestación de parásitos, o una anomalía dietética en particular, cotejando la información por si algo que aparece en un zoológico es inusual o común, o cómo está de extendido un comportamiento en particular (Hosey et al., 2009). Los cuidadores pueden aportar información clave respecto a los hábitos de los animales, sobre sus capacidades de entrenamiento, sus historias, la jerarquía social, las interacciones dentro de un grupo y sobre su personalidad (Clegg, 2018). Estos estudios se realizan con el fin de mejorar su vida en cautividad ya que, cuanto mejor se conozca a los animales y las dinámicas de su actividad social, mejor se les entenderá y mejor se les cuidará. Otro factor que se puede analizar en este tipo de estudios es la influencia de los humanos sobre los animales estudiados, y las interacciones que se establecen entre especies.

1.5. Especie de estudio: el delfín mular

Desde hace tres décadas se sabe que las acciones humanas están degradando los ecosistemas de la Tierra, eliminando genes, especies y rasgos biológicos a un ritmo alarmante (Cardinale et al., 2012). Los problemas medioambientales graves como el cambio climático, la contaminación, la sobreexplotación, la destrucción de los hábitats, las especies invasoras, los cambios en el uso de la tierra, entre otros, han llevado a la actual crisis y pérdida de biodiversidad siendo un gran reto para la humanidad. Prevenir la pérdida de biodiversidad y promover la conservación de la vida salvaje es un compromiso internacional que se ha convertido en dos de los Objetivos de Desarrollo Sostenible (ODS), representados por los números: 14) “Vida submarina”, y 15) “Vida de ecosistemas terrestres”. Junto con las crecientes amenazas a la vida salvaje en su hábitat,

se constata un incremento en el interés por desarrollar programas de protección de especies en peligro de extinción *in situ* (es decir, en el hábitat natural de la especie). Sin embargo, para las especies cuyo hábitat está gravemente amenazado, el panorama es tan crítico que las organizaciones internacionales reconocen que las acciones de conservación *in situ* deben combinarse con enfoques *ex situ*, como por ejemplo la cría en cautividad en centros zoológicos (Conde et al., 2011). Así, la comunidad de centros zoológicos y acuarios del mundo se han convertido en el tercer mayor contribuyente a la conservación de la naturaleza en todo el mundo, después de The Nature Conservancy (TNC) y el Fondo Mundial para la Naturaleza (WWF), ya que desarrollan proyectos de conservación, como programas de investigación y educación (Gusset & Dick, 2011). Los zoos y acuarios del mundo están comprometidos con los objetivos enfocados en la protección de la naturaleza, realizando programas de conservación *ex situ*, garantizando el óptimo bienestar de los individuos que participan en dichos programas (Barongi et al., 2015).

Según la Lista Roja de Especies Amenazada de la Unión Internacional para la Conservación de la Naturaleza (IUCN), 28% del total de especies que han sido evaluadas están en peligro de extinción, de los cuales 27% son mamíferos (IUCN, 2022). Las amenazas antropogénicas que afectan mares y océanos, también han llevado a un gran número de especies marinas al peligro de extinción. Debido a estas amenazas el 37% de especies de mamíferos marinos están en riesgo de extinción (Davidson et al., 2011), y el 26% de especies de cetáceos están amenazadas, de las cuales cinco están clasificadas en peligro crítico de extinción: el delfín chino de río (*Lipotes vexillifer*), el delfín giboso atlántico (*Sousa teuszii*), la vaquita marina (*Phocoena sinus*), la ballena franca glacial (*Eubalaena glacialis*) y el rorcual de Rice (*Balaenoptera ricei*); 12 están en peligro de extinción y 7 son vulnerables (IUCN-SSG CSG, 2022). Por esta razón, se deben realizar esfuerzos para trabajar por la conservación de este grupo de mamíferos marinos, garantizando el óptimo bienestar en cautividad y su supervivencia en libertad. Los estudios de comportamiento amplían el conocimiento de las especies que participan en programas de conservación, y su estudio en cautividad permite la observación de las secuencias, duraciones de las interacciones sociales (Samuel & Gifford, 1997; Tizzi et al., 2010).

Las especies, longevas y sociales, son buenos modelos para estudiar patrones de comportamiento y rasgos de personalidad. La especie de estudio de esta tesis es el delfín mular (*Tursiops truncatus*; Montagu, 1821), un odontoceto de la familia Delphinidae, que es un buen modelo para realizar estudios comportamentales, debido a su carácter gregario

y su amplio repertorio conductual. Es la especie de cetáceo más conocida y estudiada, debido a la facilidad de avistamientos en su amplia área de distribución y por ser la más común en cautividad (Clegg et al., 2017).

1.5.1. Distribución y estado de conservación

El delfín mular habita aguas cálidas y templadas de todo el mundo, con temperaturas de la superficie del agua entre 10ºC y 32ºC, y se puede encontrar en zonas costeras, aguas pelágicas, mares abiertos, bahías, estuarios y puertos (Figura 2). Los delfines mulares suelen ser residentes en zonas costeras y alrededor de islas oceánicas, pero también pueden realizar movimientos ocasionales largos o migraciones estacionales, especialmente las poblaciones que se encuentran cerca de los extremos del rango geográfico de la especie (Wells & Scott, 1999; Wells & Scott, 2018; Wells et al., 2019).

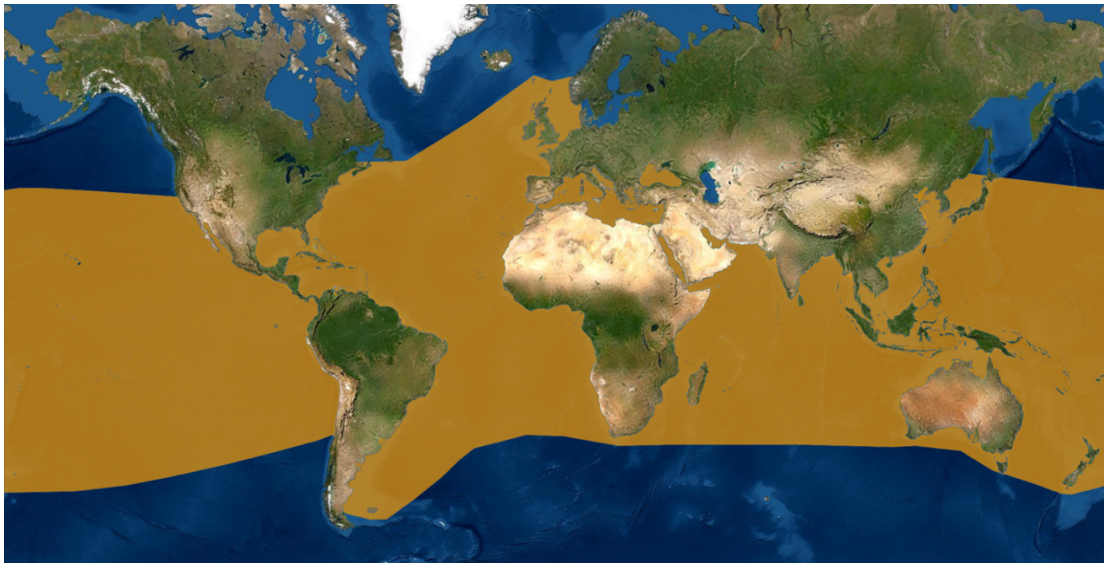

Figura 2. Rango geográfico del delfín mular (IUCN, 2019)

El delfín mular está catalogado como Preocupación Menor a nivel global (Wells et al., 2019) y como Vulnerable en el Mar Mediterráneo (Bearzi et al., 2012). Las amenazas de origen antrópico son: la contaminación, la captura accidental, la caza furtiva, la escasez de alimento por sobrepesca de sus presas, la degradación del hábitat, el cambio climático y la perturbación por turismo y tráfico marítimo, que interfieren con procesos vitales como forrajeo, reproducción y cría, entre otras (Wells, 2010; Wells et al., 2019).

1.5.2. Biología

Los delfines mulares son cetáceos odontocetos medianos, con forma de torpedo, cuerpo robusto, ojos a los costados de la cabeza, una aleta dorsal curvada y alta, y una marcada distinción entre el melón y su corto y ancho hocico. La longitud corporal es de 2.5 m a 3.8 m, el peso entre 150 kg a 650 kg, y el color del cuerpo es gradiente de gris claro a negro lateralmente, siendo la zona dorsal más oscura, y la zona lateral y ventral más clara (Wells & Scott, 2018; Figura 3).

Figura 3. Delfín mular (NOAA Fisheries, 2022)

El delfín mular alcanza la madurez sexual de los 5 a los 14 años y tiene una longevidad que varía entre 40 y 60 años (Wells & Scott, 2018). Las hembras tienen varias crías de diversos machos a lo largo de sus vidas, la gestación dura un año y tienen sólo una cría por parto. Las madres amamantan a las crías durante 18-24 meses, pero la inversión materna se extiende hasta los 3-6 años, en ocasiones coincidiendo con el nacimiento de la siguiente cría (Wells & Scott, 1999).

Se alimenta principalmente de peces (como caballas, jureles, merluzas, congrios), cefalópodos (como sepias, pulpos, calamares), crustáceos (como camarones y cangrejos), entre otros (Zofío & Vega, 2000). Utiliza la ecolocalización para cazar, comunicarse y navegar, tienen buena visión y audición, y carecen de lóbulos olfativos (Wells & Scott, 1999). Su cerebro tiene un telencéfalo (parte pensante) masivo (Marino et al., 2000) y tiene un elevado coeficiente de encefalización (relación entre la masa cerebral real de una especie y su masa cerebral esperada): el tercero (5.3; Figura 4), después del humano (*Homo sapiens*: 7.4-7.8) y el delfín septentrional sin aleta (*Lissodelphis borealis*: 5.6;

Roth & Dicke, 2005; Cairó, 2011). Tiene una gran capacidad cognitiva, un neocórtex complejo (Marino et al., 2007), y el neocórtex y estructuras paleocorticales en su cerebro son consistentes con la noción que los delfines experimentan emociones y son sensibles a las emociones de otros individuos (Kuczaj et al. 2013).

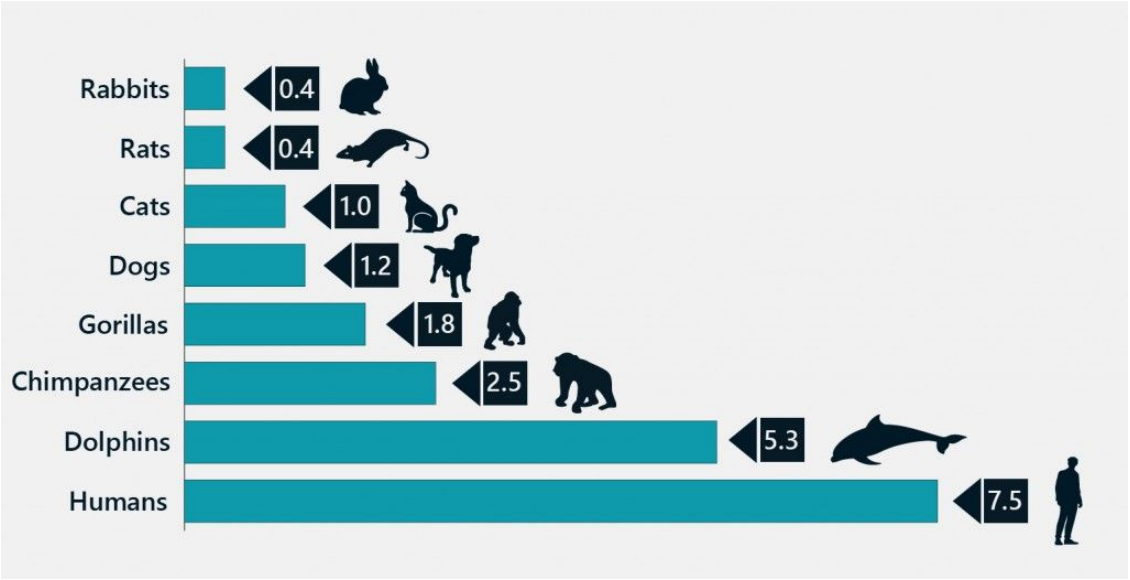

Figura 4. Coeficiente de encefalización de diferentes especies (Cay Leytham-Powell/Sapiens)

1.5.3. Comportamiento

Es una especie altamente social, gregaria, que tiene relaciones sociales consistentes y fluidas, que se manifiestan en tamaño, cohesión y composición de grupo (Shane et al., 1986; Pack & Herman, 2006; Dudzinski & Frohoff, 2008). Viven en grupos sociales dinámicos de fisión-fusión (Kuczaj et al., 2013) que pueden ser permanentes o cambiantes (Connor et al., 2000), y las relaciones pueden ser breves o durar toda la vida. Así pues sus sociedades son complejas, con una variedad de tipos de relaciones, con vinculaciones de parejas a largo plazo, alianzas con jerarquías y asociaciones cooperativas (Highfill & Kuczaj, 2010). El vínculo entra las madres con sus crías es duradero, y se observa el cuidado de crías por otras hembras adultas o subadultas (Shane at al., 1986). Las unidades sociales básicas consisten en grupos de guardería, grupos mixtos de juveniles, y machos adultos solitarios o en parejas fuertemente unidas (Wells et al., 1987). Pueden viajar solos, en parejas o en manadas de hasta 15 individuos, que se pueden juntar con otras manadas y llegar a formar grupos de hasta 1000 individuos (Wells & Scott, 2018). Son nadadores

rápidos, con velocidades promedio de 22 Km/h (Noren et al., 2011). Están activos tanto durante el día como la noche, intercalando episodios de socialización, desplazamiento, descanso y alimentación, con picos de alimentación en la mañana temprano y en la tarde (Shane at al., 1986).

El comportamiento social es un componente importante de las actividades diarias mostrando variedad de interacciones tanto en el cuidado entre individuos, la cooperación en la caza, la protección frente a los depredadores, entre otros (Kuczaj et al., 2013). Los delfines mulares se comunican con contacto, lenguaje corporal, señales visuales, acústica (clics, chasquidos, silbidos y pulsaciones explosivas), y diferentes tipos de comportamiento (Mann & Smuts, 1999; Dudzinski, 1998). El nado sincronizado se considera una pauta afiliativa pues los sujetos permanecen en contacto o muy próximos mientras se desplazan, descansan o se socializan (Connor et al., 2006; Dudzinski, 2010). Las crías aprenden por imitación los patrones de forrajeo de sus madres, manifestando transmisión cultural de determinados comportamientos a través de generaciones (Wells, 2003). Las estrategias de caza son variadas en las que se detecta una planificación deliberada, coordinación, sincronización y cooperación. Se han observado cooperando con otras especies, por ejemplo, cercando grupos de peces y dirigiéndolos hacia las redes de los pescadores (Holmes & Neil, 2012). También se ha observado el uso de herramientas en esta especie, utilizan esponjas para cubrir y proteger sus rostros al explorar entre corales afilados (Patterson & Mann, 2011).

OBJETIVOS

2. OBJETIVOS

El objetivo general de esta tesis ha sido estudiar el comportamiento solitario y social de un grupo de ocho delfines mulares (*Tursiops truncatus*) en cautividad (Zoo de Barcelona), durante dos periodos reproductivos, con el fin de identificar las estructuras de comportamiento y de personalidad, y explorar cómo este conocimiento se puede aplicar para la mejora del bienestar y el éxito de programas de conservación *ex situ.*

Los objetivos específicos de la tesis han sido los siguientes:

- Explorar la relación entre los patrones de comportamiento y los perfiles de personalidad con el bienestar de los individuos para identificar qué características pueden favorecer una mejor adaptación a la cautividad y ayudar a mejorar su manejo.
- Comparar los patrones de actividad en diferentes contextos sociales y ambientales, con el fin de determinar la respuesta comportamental en diferentes contextos a lo largo del tiempo, e identificar aquellos patrones que favorecen el bienestar en condiciones de cautividad.
- Investigar y comparar dos metodologías para detectar rasgos de personalidad a partir de observaciones directas de las interacciones sociales: 1) un análisis de patrones temporales multivariado, y 2) un análisis de reducción de dimensiones, con el fin de identificar rasgos de personalidad de la especie y evaluar la efectividad de cada metodología para conseguir este propósito.
- Identificar la relación directa entre comportamientos observados y adjetivos que describen rasgos de personalidad, comparando dos diferentes metodologías de evaluación de personalidad, a través de: 1) observaciones directas (“codings”), y 2) calificaciones indirectas de adjetivos (“ratings”), con el fin de identificar la estructura de personalidad y validar para ella la metodología de “codings”.

ESTRUCTURA DE LA TESIS

3. ESTRUCTURA DE LA TESIS

Esta tesis está compuesta por tres capítulos que abarcan tres temas principales relacionados con el comportamiento animal, que son: 1) patrones de comportamiento, 2) estructuras de comportamiento, y 3) estructuras de personalidad, y su relación con el bienestar animal y la conservación de especies.

En el primer capítulo se identifican los patrones de comportamiento para un grupo de ocho delfines mulares que estuvieron estabulados en el Zoo de Barcelona. El primer capítulo se titula: "Solitary and social behavioral patterns of bottlenose dolphin (*Tursiops truncatus*) in captivity: a tool for managing welfare".

En el segundo capítulo se identifica la personalidad de dos hembras preñadas, pertenecientes al mismo grupo de delfines mulares, utilizando dos métodos diferentes: un análisis de patrones temporales multivariado y un análisis de reducción de dimensiones. El segundo capítulo se titula: "Effects of pregnancy and maternal care on the stability of personality traits of two female bottlenose dolphins (*Tursiops truncatus*)".

En el tercer capítulo se hace una evaluación de la personalidad de siete individuos pertenecientes al grupo de delfines mulares, utilizando dos metodologías de evaluación que consisten en observaciones directas e indirectas. El tercer capítulo se titula: "Bottlenose dolphin (*Tursiops truncatus*) personality structure assessment: Comparing behavior measures and adjective ratings".

CAPÍTULO 1

Patrones de comportamiento social y solitario del delfín mular (*Tursiops truncatus*) en cautividad: una herramienta para la gestión del bienestar

4. CAPÍTULO 1: Solitary and social behavioral patterns of bottlenose dolphin (*Tursiops truncatus*) in captivity: a tool for managing welfare

4.1. Abstract

The study of solitary and social behavioral patterns of non-human animals under human care is very useful for management practices, as the impacts of all the experiences perceived and expressed by individuals represent their welfare states. Despite there is a great number of studies on activity budgets in odontocetes, few have established the range and threshold of appropriate behavioral patterns in facilities. This study investigated the proportion of behaviors in a group of eight bottlenose dolphins (*Tursiops truncatus*) engaged in solitary and inter-individual interactions during their free time, in nine different environmental and social contexts, using all-occurrence continuous follow sampling bouts and instantaneous scans. Findings suggest that the most common behaviors out of the total visible activity budget were solitary swimming (18% - 28%), close swimming (20%) and maternal close swimming (20% - 42%). Different contexts significantly modulated mean frequencies of solitary and social behaviors. This study contributes to the knowledge of behavioral responses of bottlenose dolphins to different living conditions, and its application can be extended to decision-making for management and welfare improvements of small and medium-sized odontocetes under human care.

Keywords: marine mammal; cetacean; captivity; activity budget; activity patterns.

4.2. Introduction

Non-human animal welfare refers to the state of the individual animal and how it is coping with its living conditions. Caretakers continuously seek to improve the understanding of animal welfare in order to promote positive states of the species under their care. To achieve this, evidence is needed to carry out effective welfare monitoring and assessment processes, using indices that align specifically with the species' physical/functional states. Under the 'Five Domains' model to understand and assess the animal welfare status, behavior is one of the four physical/functional domains, and mental state is the fifth domain that completes the model (Mellor et al., 2015). In the behavioral domain, a good welfare state is indicated when the animal's behavioral needs are met, the animal is comfortable, able to express innate behavior and it is not suffering from fear, pain or distress (Mellor et al., 2015). Because animals undertake essential behaviors for their survival, motivated by their feelings and sensations, behavioral patterns are fundamental indicators of how subjects perceive their surroundings, express their experiences and adapt to their environment, thus representing welfare states of individuals (Broom, 1991; Mellor et al., 2015). In this way, welfare is good when positive experiences predominate, neutral when negative and positive experiences are in balance overall, and poor when negative experiences predominate.

The understanding of species-specific needs and behavioral patterns is crucial to promote positive welfare states while reducing negative experiences. Understanding behavioral traits in groups and individuals is an ongoing priority to improve management aspects of welfare and endorse appropriate species-specific care of wild animals. For this reason, studies have developed evidence to interpret cautiously the link of subjective experiences to particular behaviors, and therefore behavioral observations have been used effectively as indicators of animal welfare states (Mellor et al., 2015). In order to avoid or replace negative experiences related to specific situations, activities such as environmental and social enrichment generate positive experiences such as interest, curiosity, companionship, playfulness, among others, and provide opportunities for the animals to engage in behaviors they will find rewarding (Mellor et al., 2015). On the other hand, unsuitable social structures of groups are often related to negative experiences for social animals. Fortunately, such unsuitable structures can be modified in a controlled environment, in order to improve experiences and welfare states of the individuals (Mellor et al., 2015).

Odontocetes are social aquatic mammals that can travel long distances (a mean of 28 km/day; Klatsky et al., 2007), sometimes at very high speeds (up to 54 km/h; Iosilevskii & Weihs, 2008) and that is why during the past few decades there has been a great concern about the welfare of these animals in captivity enclosures. Despite the existence of a great number of studies on activity budgets in medium and small odontocetes, few of them have established the range and threshold of appropriate and common behavioral patterns in facilities, and therefore more information is needed to guarantee good welfare for this group of animals. The Bottlenose dolphin (*Tursiops truncatus*) is the most common cetacean species found in captivity, it has a gregarious nature, a wide behavioral repertoire and it is easily observable under controlled conditions, which makes it a good model to study behavioral patterns (Clegg et al., 2017). There are a great number of studies on bottlenose dolphin behavioral patterns and activity budgets, both in wild and captive environments (see Table 1 for examples). Such studies consider solitary behaviors and social interactions, including specific behavioral categories such as affiliative, agonistic, sexual, play, stereotypic, maternal and resting.

Previous studies have found that bottlenose dolphins kept for public display spend most of their time engaged in swimming, mother-calf swimming, resting, synchronous swimming and surfacing events with humans. However, even though this is a well-studied species, there are no fixed thresholds or range of occurrences considered to be common, suboptimal and acceptable under human care, together with their welfare designations (Clegg et al., 2015). Common behaviors are those that individually comprise ≥ 15% of the activity budget, while rare behaviors individually comprise < 15% (Margulis & Westhus, 2008). Despite there being sufficient evidence of specific behaviors as indicators of dolphin affective states, welfare scientists stress the need of further research to clearly define the direct link between dolphin behavior and welfare (Clegg et al., 2017).

The aim of this study was to investigate the frequencies of common behaviors of bottlenose dolphins in captivity during their free time, and to assess whether or not, and to what extent, such behaviors can be indicators of either positive or negative emotions of the animals; this information could be useful in future welfare assessments of the species and in management decisions. To make a quantitative approach to the range of frequent behaviors displayed by bottlenose dolphins in captivity, we investigated free-time activity budgets in a group of eight subjects housed in one facility, and we

Table 1. Activity budget studies of captive and free-ranging bottlenose dolphins.

Behavior	Percentage[1]	First Author (Year)
CAPTIVITY		
• Swimming:	72	Shorter et al. (2017)
Fluking	23	
Gliding	17	
Surfacing	6	
Other/unidentified	26	
• Surfacing event (with humans)	28	Shorter et al. (2017)
• Synchronous swimming:	35.2	Clegg et al. (2017)
Slow-close	22	
Slow-distant	14	
Fast-distant	6	
Fast-close	1	
• Anticipatory	6	Clegg et al. (2017)
• Sexually motivated	2	Clegg et al. (2017)
• Overt aggressive	1	Clegg et al. (2017)
• Play	6	Clegg et al. (2017)
• Mother-calf swim	41.5	Hill et al. (2007)
• Object play	22.8	Hill et al. (2007)
• Solitary activities	18.2	Hill et al. (2007)
• Resting (during high activity time)	38.5	Sekiguchi and Kohshima (2003)
WILD		
• Travelling	53	Durden et al. (2019)
	27	Vermeulen et al. (2015)
• Resting	28	Vermeulen et al. (2015)
• Milling	27	Durden et al. (2019)
	5	Vermeulen et al. (2015)
• Foraging	17	Durden et al. (2019)
• Surface feeding	15	Vermeulen et al. (2015)
• Diving	12	Vermeulen et al. (2015)
• Socializing	6	Vermeulen et al. (2015)
	2.3	Durden et al. (2019)

[1] Percentage of occurrence of the different behavior categories, out of total visible activities per observation.

compared our results with average behaviors engaged by other dolphins in previous studies. Because experiences can be enhanced by social and environmental enrichment, a second aim of our study was to assess the effect of social enrichment and environmental variations in the same group of eight bottlenose dolphins, by tracking repeated behavioral patterns or changes in solitary behaviors and social relationships across time, under a variety of contexts. Results could provide insights to determine which social context and environmental conditions promote optimal welfare for these animals as well as to identify behavioral indicators of welfare for further informed care decisions.

4.3. Methods

Study Subjects

The study group consisted of eight bottlenose dolphins, of different sexes and ages, from neonate to 44 years old (Table 2). Distinct physical characteristics such as body size, marks, pigmentation, scars and fin shape were used to identify the study subjects (Lehner, 1998).

Table 2. Characteristics of the study subjects.

Abbreviated name	Name	Sex[1]	Birth type	Birth date	Parentage	Rearing	Arrival date to zoo
Ni	Nika	F1	Wild	~1964	–	Unknown	27/10/1970
Ne	Nereida	F2	Wild	~1980	No's Dam	Unknown	13/10/1982
An	Anak	F3	Wild	~1986	Le's Dam	Unknown	01/10/1990
In	Inuk	M1	Captive	20/09/1983	Bl, Tu, Le and No's Sire	Dam	20/09/1983
Bl	Blau	M2	Captive	01/07/1999	In's offspring	Dam	01/07/1999
Tu	Tumay	M3	Captive	13/04/2002	In's offspring	Dam and Nika	13/04/2002
No	Neo	M4	Captive	24/08/2003	In and Ne's offspring	Dam	24/08/2003
Le	Leia	F4	Captive	25/08/2003	In and An's offspring	Dam	25/08/2003

[1] F: Female, M: Male

Housing and Husbandry

Study subjects were housed in the marine mammal main facility of the Barcelona Zoo (Barcelona, Spain), a cylindrical enclosure with a diameter of 22 m, a depth of 6.4 m (Figure 1), and 2432 m^3 of sea water capacity, which was extracted and filtered from the Mediterranean Sea using a pump system. Water had a pH 8, a salinity of 26-28g/liter and

a temperature that oscillated between 10ºC and 30°C, depending on the season of the year. Observations were made by underwater vision, from one of the five windows measuring 1.4 m by 1.7 m, and 4 cm thick, and that had a railing that prevented the observers from being less than one meter away from the viewing windows.

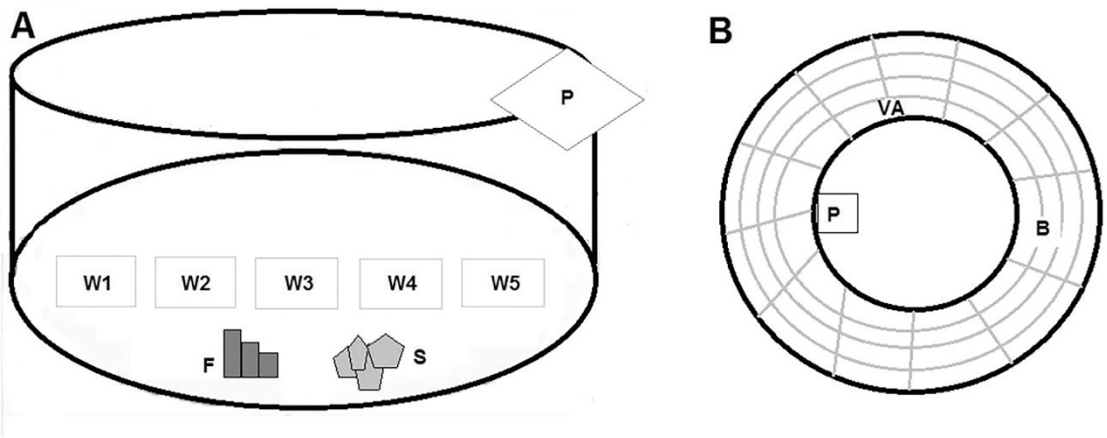

Figure 1. Scheme of the facility where the group of bottlenose dolphins was housed. **A.** Front view: W1 to W5 = Windows 1 to 5, S = Stones, F = Filters, P = Platform. **B.** Apical view: B = Bleachers (for visitors), VA = Visitors' access and P = Platform (Soriano et al., 2015).

Subjects ate an average of 11 kg of frozen fish (30% mackerel, 50% sardine and 20% capelin combined with sprat), distributed five times throughout the day: during the half-hour shows (scheduled at 11:00 and 13:30), and mixed with vitamins at 14:00, 16:00 and 20:00 (Soriano et al., 2015).

Study Phases

The focal sampling method was used for data collection using simultaneously instantaneous scans made at 1-min intervals and all-occurrence continuous follow sampling bouts in sessions of 10, 15 and 30 minutes (Altmann, 1974). A total of 513 hours of observations of spontaneous behaviors were recorded and divided into nine different study phases that varied in social context (size and composition) and season (Table 3).

Observations were made during 694 (10-minute) sessions from January to March 2003 (phase 1: baseline), 636 (15-minute) sessions from June to August 2003 (phase 2: pre-partum), 306 (15-minute) sessions from August to September 2003 (phase 3:

parturition and post-partum), 256 (15-minute) sessions from October 2003 to March 2004 (phase 4: development of calves), 26 (15-minute) sessions from March to April 2004 (phase 5: five dolphins in spring), 29 (15-minute) sessions from November to December 2004 (phase 6: five dolphins in fall), 141 (15-minute) sessions from December 2004 to January 2005 (phase 7: four dolphins), 158 (15-minute) sessions from October 2005 to April 2006 (phase 8: three pregnant females) and 18 (30-minute) sessions in May 2008 (phase 9: three dolphins). Frequencies of solitary and social behaviors were obtained from a total of 3851 bouts for the eight focal subjects, distributed among 419 hours during five phases (one to five), and 15603 one-minute scans of six focal subjects, distributed among 260 hours during eight phases (two to nine).

Table 3. Study phases that varied in social context and season.

Study phase	Group Composition	Period (date)	Season	Observation time (h)	Water temperature (mean ± SD)
1. Baseline	6 (3.3)	27/01/03 – 03/03/03	Winter	116	12 (± 0)
2. Pre-partum	2 (0.2)	18/06/03 – 23/08/03	Summer	159	30 (± 1)
3. Parturition and post-partum	4 (1.3)	24/08/03 – 30/09/03	Summer – Fall	77	27 (± 2)
4. Development of calves	4 (1.3)	02/10/03 – 24/03/04	Fall – Spring	64	14 (± 5)
5. Five dolphins (spring)	5 (1.4)	25/03/04 – 27/04/04	Spring	7	15 (± 0.4)
6. Five dolphins (fall)	5 (1.4)	25/11/04 – 11/12/04	Fall – Winter	7	13 (± 1.7)
7. Four dolphins	4 (1.3)	24/12/04 – 19/01/05	Winter	35	12 (± 0)
8. Three pregnant females	3 (0.3)	17/10/05 – 07/04/06	Fall – Spring	40	14 (± 5)
9. Three dolphins	3 (1.2)	02/05/08 – 09/05/08	Spring	9	15 (± 0.4)

Data Collection

The variables studied during both instantaneous and continuous recordings were:

(1) Study phase.

(2) Water temperature (ºC).

(3) Season (winter: December, January, February; spring: March, April, May; summer: June, July, August; fall: September, October, November).

(4) Period of the day (morning: 07:00 – 11:59, midday: 12:00 – 14:59, afternoon: 15:00 – 22:00; the recording schedule was from 9:00 to 20:00 in spring, from 7:00 to 22:00 in summer, from 8:00 to 19:00 in fall, and from 9:00 to 18:00 in winter).

(5) Sex.
(6) Age class (calf: <4 years, juvenile: 4 – 7/8 years, sub-adult: 8/9 – 11/13 years, adult: >12/14 years; Mann et al., 2000).
(7) Birth type (wild, captivity).
(8) Number of visitors (number of people that were watching the dolphins while the registries were taken: one to five, six to ten, 11 to 15, more than 15).
(9) Visitor behavior (no interactions: visitors only observed the animals through the viewing windows; photos with flash: visitors took photos with flash lights; call attention: visitors hit the windows, made gestures and shouted to attract the animals' attention; touch window: visitors placed their hands over the viewing windows).
(10) Proximity (when two or more individuals were less than 2 m apart).
(11) Contact (when the animal gently placed its pectoral fin or belly on another subject's body).
(12) Use of space.
(13) Behaviors (see Table 4).

The variables that were additionally studied during continuous recordings were:

(1) Initiator.
(2) Receiver.
(3) Subject that joins.
(4) Subject that terminates.
(5) Duration of the interaction (short: ≤ 300 s, medium: 301 – 600 s, long: > 600 s).

Even though data were not collected while trainers undertook daily medical checks, routine trainings or show performances, trainers occasionally interacted with the subjects during the behavior registries, while trained observers remained passive during the data collection. To ensure reliability between the eleven observers that collected the data, we calculated Kappa coefficients, which resulted in concordance levels higher than 0.95 for the identification of subjects, 0.89 for the identification of behaviors and 0.87 for proximity reliability. The selection of focal subjects was chosen from a randomized list.

Table 4. Definitions of behaviors analyzed in this study.

Behavior	Description
SOLITARY	The animal is more than 2 m away from another dolphin, and it is not engaged in any social interaction with conspecifics.
• Locomotion:	The animal moves from one place of the facility to another.
Fast swimming	The animal moves by propelling its tail fluke, with strong and intense hits, at a frequency greater than 3 or 4 drives per minute, and rapid body movements.
Slow swimming	The animal moves by making little thrust with its tail fluke, with short and low intensity strokes, at a rate of less than 3 or 4 drives per minute, and slow body movements.
• Stationary	The animal floats or rests with its muscles relaxed.
• Maintenance:	The animal engages in activities that contribute to its physiological well-being.
Respiration	The animal places its spiracle on the water surface, opening it to catch oxygen from the air.
• Solitary Play	The animal carries out exaggerated, well-known movements with its body, jumping, playing with bubbles and/or with objects.
SOCIAL	The animal engages in whatever social interaction.
• Affiliation[1]:	The animal shows affection towards another dolphin.
Approaching	The animal reduces its distance to less than 50 cm from another dolphin.
Close swimming	The animal swims less than 20 cm away from another dolphin.
Swimming with contact	The animal swims alongside another dolphin, gently placing its pectoral fin or belly on its conspecific's back or pectoral fin.
• Maternal	Behaviors that occur between mother and calf pairs, with no other dolphin involved.
• Social Play[1]	The animal shows a playful attitude towards another dolphin, jumping, hiding, stationary, chasing and/or with objects.
• Agonistic	The animal shows an aggressive attitude towards another dolphin, biting, jaw-popping, hitting with fins, swim interrupting, aggressive chasing and touching with melon or rostrum.
• Sexual	The animal makes contact with its pelvis, (the male exposing its penis) rubbing it against the ventral part of another dolphin.
• With humans:	The animal gazes out, plays and/or interacts with visitors and/or trainers/keepers.
Interaction with visitors	The animal stops in front of the window, gazes at the visitors, and tries to attract their attention through body movements and/or bubbles.
OTHER	
• No interactions	No social interactions are observed.

[1] Mother-calf dyads must be joined by another dolphin to be qualified for these behaviors, otherwise they are considered to be maternal behaviors.

Data Analysis

Frequencies of the different behaviors were converted to percentages per total visible scans (96%) and bouts (100%), and proportions of behaviors from the different subjects were averaged to obtain overall mean occurrences of each behavior, for every phase. Only behaviors that were observed at frequencies higher than 5% of the activity budget were analysed. All statistical analyses were done using R 3.4.0 (R Development Core Team, 2017) and at a significance level of $P < 0.05$.

We performed a Pearson's chi-squared significance test of independence and a Goodman Kruskal's tau to measure the association between behavior and study phase, water temperature, season, period of day, sex, age class, birth type, number of visitors, visitor behavior, proximity, contact, space use, initiator, receiver, subject that joins and terminates and duration of the interaction.

To take into account repeated measures from the different subjects over time, we performed generalized linear mixed-models (GLMM) for binomial distribution, using the glmer() function of the *lme4* package, with individual as a random effect, proportions per visible scans and bouts of the main overall behaviors as dependent variables, phase (factor with eight levels for scans and five levels for bouts) as a fixed effect, and duration (factor with three levels), age class (factor with three levels for scans and two levels for bouts) and birth type (factor with two levels) as covariates. Owing to multicollinearity between age class and birth type, these factors were not included in the same models. *P*-values were calculated using likelihood ratio tests and post-hoc comparisons were conducted to compare the mean proportions of behaviors that were significant.

Ethical statement

This research project was designed in accordance with best practices and highest ethical standards, and meets national and international legislation requirements. Moreover, all methods comply with the EAZA Code of Ethics (www.eaza.net) and the WAZA Code of Ethics and Animal Welfare, namely the Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquaria (www.waza.org).

4.4. Results

Association Between Behavior and Socio-environmental Factors

Behavioral variables showed a strong association with the following eight variables: phase (behavior: $\tau(x,y) = 0.3$), age class (behavior: $\tau(x,y) = 0.34$, classification: $\tau(x,y) = 0.26$), birth type (behavior: $\tau(x,y) = 0.33$, classification: $\tau(x,y) = 0.25$), contact (behavior: $\tau(x,y) = 0.71$, classification: $\tau(x,y) = 0.5$), proximity (behavior: $\tau(x,y) = 0.29$, classification: $\tau(x,y) = 0.26$), initiator (behavior: $\tau(x,y) = 0.26$), receiver (behavior: $\tau(x,y) = 0.29$) and duration of interactions (behavior: $\tau(x,y) = 0.3$). The reverse association was also strong between behavior classification and two variables: initiator ($\tau(y,x) = 0.33$) and receiver ($\tau(y,x) = 0.38$).

Activity Budget

Overall mean frequencies of observed behaviors differed significantly (scans: $\chi^2(59) = 545.01$, $P < 0.001$; bouts: $\chi^2(43) = 308.93$, $P < 0.001$). The most frequent behavioral categories observed through visible scans were locomotion (27%), followed by maternal (26%), maintenance (10%), affiliative (9%) and solitary play (6%). Other behaviors such as interactions with humans, inactivity, exploration, vigilance and social play were observed at very low frequencies (≤ 5%). Solitary slow swim and maternal close swim were the most frequent behaviors, followed by close swim, solitary fast swim, respiration and stationary (Figure 2). Other behaviors such as interactions with humans, play (solitary and social), locomotion, maintenance, vigilance, exploration and maternal behaviors were observed at frequencies lower than 5% of the activity budget.

The most frequent interactions observed through bouts were classified as affiliative (36%), followed by maternal (20%), no interactions (16%), with humans (12%), agonistic (7%), social play (6%) and sexual (3%). Close swim was significantly the most frequent behavior, followed by no interactions, interaction with visitors and approaching, and swim with contact and maternal close swim (Figure 3). Other interactions with humans, affiliative, social play, agonistic, sexual and maternal behaviors were observed at frequencies lower than 5%.

Factors Affecting Behaviors

All common solitary and social behaviors differed significantly with respect to the different phases ($P < 0.001$ for all; see Table 5). Only solitary behaviors differed significantly with respect to age class ($P < 0.001$ for all, except for solitary fast swimming, where $P = 0.002$), as subadults engaged more in solitary fast swimming and stationary, while calves engaged less in these behaviors, and adults engaged more in respiration and solitary slow swimming. Respiration ($P = 0.005$) and solitary slow swimming ($P < 0.001$) also differed significantly with respect to birth type, as animals born in the wild engaged in these two behaviors at higher frequencies. All social behaviors differed significantly with respect to the duration of interactions ($P < 0.001$ for all, except for maternal close swim, where: $P = 0.004$).

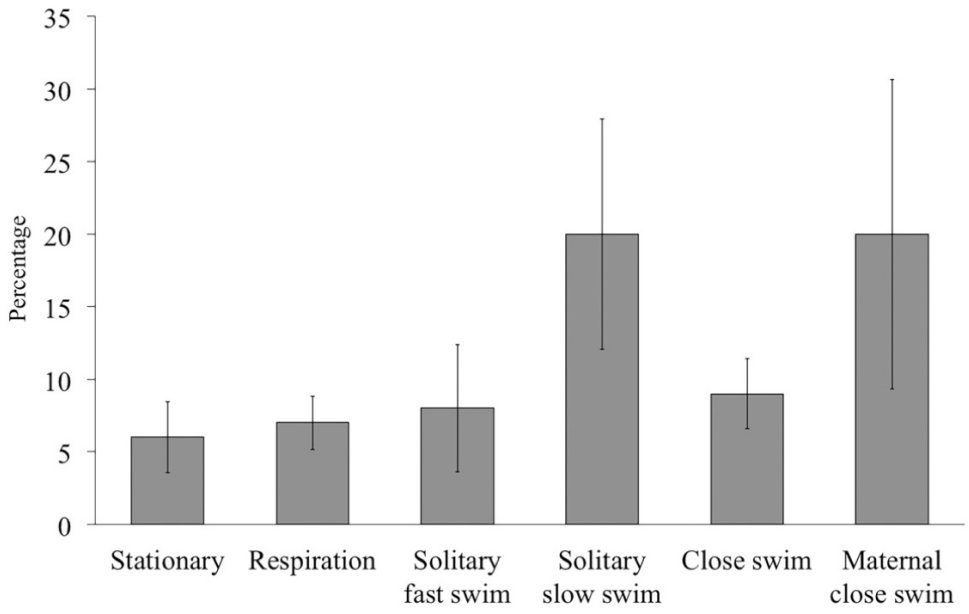

Figure 2. Occurrence of solitary (stationary, respiration, solitary fast swimming, solitary slow swimming) and social (close swimming and maternal close swimming) behaviors, obtained through visible scans for bottlenose dolphins (N = 6) housed in the Barcelona Zoo, during 260 hours. Behaviors at frequencies < 5% are not considered. Means ± SEM are shown.

Table 5. Effects of phase, age class, birth type and duration on behaviors engaged by eight bottlenose dolphins. Significant differences are highlighted in bold.

Response variable	Predictor variable	χ^2	*df*	*P*
Stationary	Phase	638.49	7	**<0.001**
	Age class	25.92	2	**<0.001**
	Birth type	1.66	1	0.198
Respiration	Phase	750.59	7	**<0.001**
	Age class	21.25	2	**<0.001**
	Birth type	7.75	1	**0.005**
Solitary fast swimming	Phase	728.85	7	**<0.001**
	Age class	12.14	2	**0.002**
	Birth type	0.68	1	0.411
Solitary slow swimming	Phase	1080.10	7	**<0.001**
	Age class	16.56	2	**<0.001**
	Birth type	16.44	1	**<0.001**
Close swimming	Phase	141.73	4	**<0.001**
	Age class	0.32	1	0.570
	Birth type	0.46	1	0.500
	Duration	229.70	2	**<0.001**
Maternal close swimming	Phase	375.21	4	**<0.001**
	Age class	0.13	1	0.720
	Birth type	0.16	1	0.685
	Duration	11.09	2	**0.004**
Swimming with contact	Phase	82.66	4	**<0.001**
	Age class	2.96	1	0.085
	Birth type	2.60	1	0.107
	Duration	41.07	2	**<0.001**
Approaching	Phase	182.84	4	**<0.001**
	Age class	2.31	1	0.128
	Birth type	1.28	1	0.258
	Duration	213.25	2	**<0.001**
Interaction with visitors	Phase	141.73	4	**<0.001**
	Age class	0.32	1	0.570
	Birth type	0.46	1	0.500
	Duration	229.70	2	**<0.001**
No interactions	Phase	420.11	4	**<0.001**
	Age class	3.55	1	0.059
	Birth type	1.06	1	0.303
	Duration	1092.10	2	**<0.001**

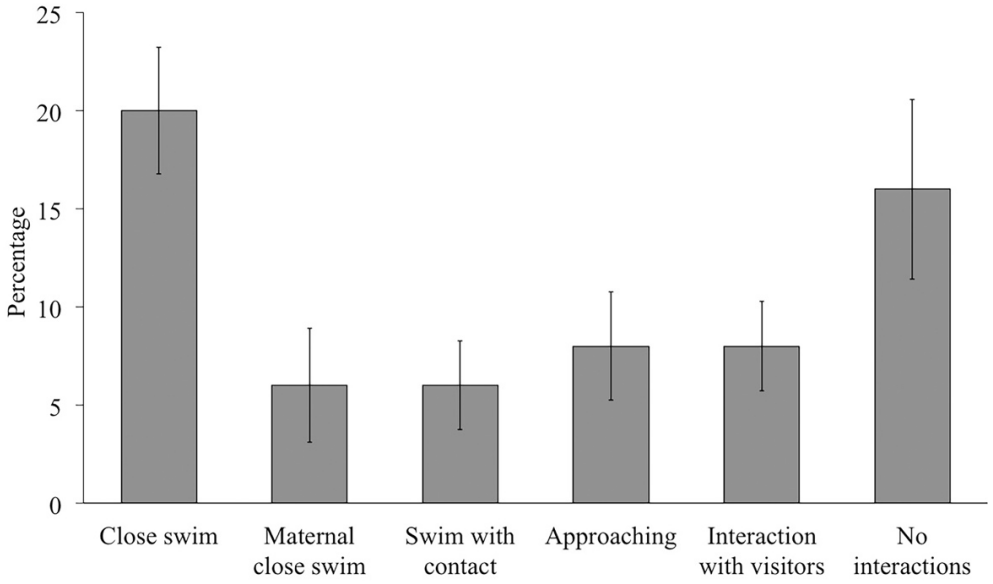

Figure 3. Occurrence of social behaviors (close swimming, maternal close swimming, swimming with contact, approaching, interaction with visitors and no interactions), obtained through bouts for bottlenose dolphins (N = 8) housed in the Barcelona Zoo, during 419 hours. Behaviors at frequencies < 5% are not considered. Means ± SEM are shown.

Behaviors Across Different Contexts

Solitary fast swim and stationary behaviors were observed at significantly higher frequencies during the pre-partum and the three dolphins phases, being common during the latter, while respiration was observed at significantly lower frequencies during the three dolphins and development of calves phases (Figure 4). On the other hand, respiration was frequent during the three pregnant females and the four dolphins phases, as was solitary slow swim, which was also common during the pre-partum and the five dolphins in fall phases, being significantly more frequent during the pre-partum and the three pregnant females phases.

Close swim was common during the baseline, pre-partum, parturition and post-partum, development of calves and five dolphins phases in spring, being significantly more frequent when there were five dolphins in spring, while being less frequent when there were six dolphins (Figure 5). Maternal close swim was also common during the five dolphins in spring and development of calves phases, being significantly most frequent during the development of calves.

Swim with contact and approaching, on the other hand, were rare in all phases, and decreased significantly across the different contexts, from the baseline to five dolphins in spring. Interaction with visitors was also rare in all phases and significantly less frequent during the parturition and post-partum phase, while being more frequent during the previous (pre-partum) and following (development of calves) phases. The behavior No interactions also showed a significant decrease across the first five phases of the study, but was common during the baseline and pre-partum phases, being the most frequent behavior during the former. Episodes of close swim were significantly longer, while episodes of interaction with visitors were significantly shorter and episodes of no interactions were significantly medium in length.

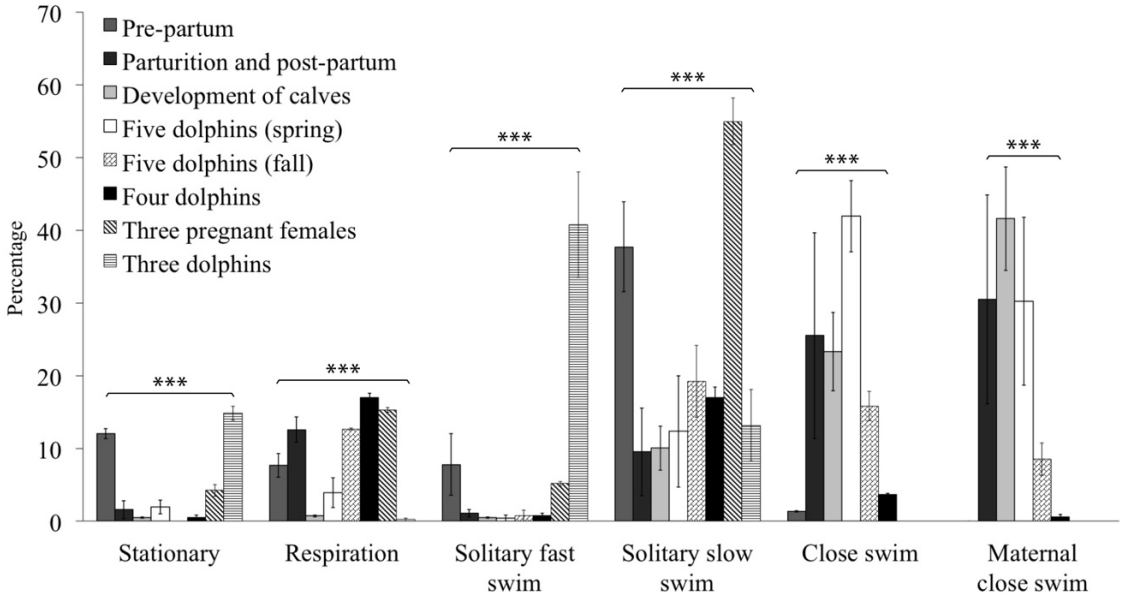

Figure 4. Occurrence of solitary (stationary, respiration, solitary fast swimming, solitary slow swimming) and social (close swimming and maternal close swimming) behaviors, obtained through visible scans for bottlenose dolphins (N = 6) housed in the Barcelona Zoo, during eight different study phases. Behaviors at frequencies < 5% are not considered. Means ± SEM are shown. Asterisks represent significant differences of behaviors throughout the study phases (three asterisks represent significance at $\alpha < 0.001$).

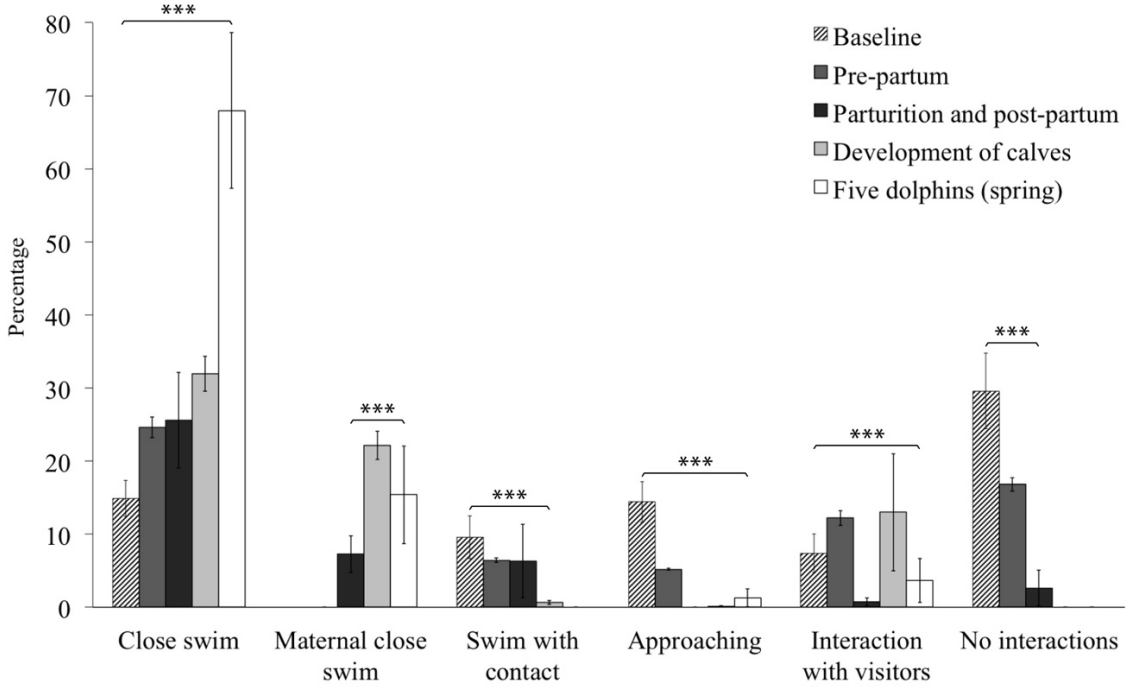

Figure 5. Occurrence of social behaviors (close swimming, maternal close swimming, swimming with contact, approaching, interaction with visitors and no interactions), obtained through bouts for bottlenose dolphins (N = 8) housed in the Barcelona Zoo, during five different study phases. Behaviors at frequencies < 5% are not considered. Means ± SEM are shown. Asterisks represent significant differences of behaviors throughout the study phases (three asterisks represent significance at $\alpha < 0.001$).

4.5. Discussion

The study of daily activity patterns of a group of eight dolphins, using a combination of two recording systems, namely scans and bouts, allowed identifying and quantifying solitary behaviors and types of interactions, as well as their durations, under different contexts. Findings suggest that the most common behavior using scan recordings was solitary swimming, followed by maternal close swimming, while the most common interaction found using bout recordings was long episodes of close swimming, followed by medium-size episodes of no interactions. No interactions decreased across the different phases, being the most frequent behavior during the baseline of the study, when the maximum number of individuals was in the facility at the same time. Subjects that were born in the wild engaged in higher frequencies of respiration and solitary slow swimming,

and subadults engaged more in solitary fast swimming and stationary, while calves engaged less in these two behaviors.

Factors that Predict Behavior

Results showed a strong significant association between both behavior and behavior classification with age class, birth type, contact and proximity, as well as between behavior with initiator, receiver, duration and phase, which suggests that if we know the behavior of an episode, then we can predict those social factors. The reverse association between behavioral classification and the initiator and receiver of an episode was also strong, which suggests that if we know which animal initiated or received an interaction, then we can predict the behavioral category of the episode. Such associations could exist due to individual differences between subjects, as the social network and interactions are structured by personality in bottlenose dolphins (Díaz-López, 2020). In this way, animal managers can predict whether an individual is prone to initiate an episode (it is bold) or it is not keen on initiating or receiving interactions (it is shy), or whether the animal is prone to initiate and participate in agonistic (it has high levels of *Neuroticism*) or affiliative (it has high levels of *Agreeableness*) episodes (Highfill & Kuczaj, 2007). Understanding the link between observed behavior and social organization, as well as the factors that contribute to bonding and affiliation, are a key to maintain optimum welfare of animals. Identifying such behaviors may help define personality traits, and provide information of individuals that play important roles in group cohesion (Díaz-López, 2020).

Frequent Behaviors of Bottlenose Dolphins in Their Free Time

Results showed that, in average, the most frequent solitary behavior engaged by the subjects was slow swimming and the most frequent social behaviors were maternal close swimming and close swimming. Findings concur with the results obtained in a previous study by Clegg et al. (2017), who found that synchronous swimming was the most frequent behavior. The frequency of close swimming found in our study was exactly the same as that of distant synchronous swimming found in the cited previous study. On the other hand, maternal close swimming was found at lower frequencies in our study as compared to a previous study by Hill et al. (2007), while solitary swimming was found at higher frequencies than solitary activities found in the same study.

Activity Budget in Different Contexts

We found that the different contexts significantly modulated the occurrence of solitary and social behaviors, possibly because a range of environmental and social conditions give rise to a range of experiences (Mellor et al., 2015), and thus a variety of behaviors to express such experiences. The predominant relationships between the study subjects were affiliative, which is linked to positive emotions and a sign of good welfare in dolphin species (Connor et al., 2006; Clegg et al., 2017). Social species living in facilities where they can explore, bond, play, care for young and be sexually active, will be more likely to go through positive experiences, feel more engaged, be affectionately social and parentally rewarded (Mellor et al., 2015). As synchronous close swim helps maintain close bonds between individuals (Connor et al., 2006; Dudzinski & Frohoff, 2008), and good social bonds are measured by the time spent swimming in synchrony together (Clegg, 2018), long episodes of close swimming in our study indicate close social bonds between the individuals. However, while close swimming increased significantly across the different contexts, swim with contact decreased significantly across the phases, and was found at lower frequencies than in a previous study by Clegg et al. (2017).

The no interactions category also decreased significantly across the first five study phases and was common in the overall activity budget, mostly found at medium-length durations. Despite close swimming being common during the baseline (the phase with most individuals in the facility at the same time), no interactions was also common during this phase, and was found at significantly higher frequencies than close swimming. Complex social compositions allow the performance of a variety of natural behavioral patterns, but high social stress may arise if there is not enough space in the facility (Galhardo et al., 1996). The high occurrence of no interactions in the baseline, may indicate that the artificial social structure during this phase was not appropriate to the animals' welfare, whether it was due to the large number of animals in the enclosure, or because of the mixed structure of sex and age classes (one adult male, three adult females and two male calves not related to the females) not being convenient for the environment or nor being similar to natural group compositions, which commonly consist of nursery groups of mothers with their calves, mixed-sex juvenile groups, and sub-adult and adult bachelor male groups (Dudzinski & Frohoff, 2008).

Solitary slow swimming was common and significantly more frequent during the phases where two and three females were pregnant. Such results concur with a previous study by Noren et al. (2011), who found that mean and maximum swimming speeds,

stroke amplitude and distance per stroke, diminish in pregnant bottlenose dolphins. Pregnant females save energy in their movements to maintain levels of cardiac and respiratory rhythms similar to the levels found during resting (Williams et al., 1992), in preparation for delivery (Tizzi et al., 2010). Such reduced mobility also causes a decrease in participation in social activities and a withdrawal from social contact (Tizzi et al., 2010), making female dolphins more solitary during gestation (Tavolga & Essapian, 1957). No interactions and close swimming were also common in the pre-partum phases, but were found at lower frequencies than solitary slow swimming, which allows us to suggest that pregnant dolphins were more solitary during the last phase of gestation as compared to the other pregnancy stages. Distancing from the group may be a way to avoid problems like theft of the newborn, which has been previously observed when the calf is born in front of the group (Amundin, 1999). Moreover, as the same two individuals were pregnant in both pre-partum phases, it can be suggested that their pre-natal behavior was consistent across time and contexts, thus possessing stable personalities. This concurs with previous studies that have found that bottlenose dolphins possess distinct individual characteristics that are stable over time, both in captive (Highfill & Kuczaj, 2007) and wild (Díaz-López, 2020) environments.

Apart from the baseline and pre-partum phases, close swimming was also common during parturition and post-partum, development of calves and significantly more frequent when there were five dolphins during spring. This allows us to suggest that social bonds improved after the calves were born, as intense activity of young animals may have provided stimuli and prevented symptoms of boredom (Galhardo et al., 1996). The highest occurrence of close swimming was observed during the phase in spring when there were five dolphins, reflecting that a composition of three adult females and two calves resulted in an adequate social structure for the group. This concurs with group compositions found naturally in the wild, where nursery groups of adult females with their calves are common (Dudzinski & Frohoff, 2008). As close swimming is a behavioral indicator of good welfare, the high occurrences of this behavior indicate that such group composition is also optimal in captive conditions; this is a structure to consider when transferring individuals between groups or facilities of the same or different institutions. Because our study was carried out during nine of the first 17 months of two calves' lives, maternal behaviors were also observed at overall high frequencies. Maternal close swimming was common during the development of calves and five dolphins in spring phases, being significantly most frequent during the development of calves. The high

occurrence of this behavior concurs with the average frequency found in previous studies by Hill et al. (2007) and Von Streit et al. (2013), who found that during the first year of calves' lives, the most frequent mother-calf interaction corresponds to close swimming.

Each type of synchronous swimming at different rates of occurrence may express different roles in dolphin interactions (Clegg et al., 2017). Although in the wild, synchronous swimming is faster in aggressive settings (Herzing, 1996), in captive bottlenose dolphins, fast swimming shows positive high arousal (Clegg, 2018). Study subjects engaged in solitary fast swimming in an overall low mean percentage. However, solitary fast swimming and stationary behaviors were observed at higher frequencies during the pre-partum and the three dolphins phases, resulting in drastic changes in locomotion rates in these two phases. In this study, stationary behaviors were found at lower frequencies than resting (in high activity time) found in a previous study by Sekiguchi and Kohshima (2003). Respiration, on the other hand, was observed at lower frequencies during the three dolphins phase, as well as during the development of calves. As results showed a low overall mean frequency of respiration, it is therefore considered a rare behavior in the overall activity budget of this study. Breathing is considered a survival-critical behavior, driven by the negative experience of breathlessness, as it is essential to motivate animals to acquire life-sustaining oxygen (Mellor et al., 2015).

In this study, interaction with visitors was found at lower frequencies than surfacing events with humans found in a previous study by Shorter et al. (2017). Although short and rare in all phases, interaction with visitors was more frequent during the pre-partum and development of calves phases, and less frequent during the parturition and post-partum phase. In the wild, an excessive interaction with humans of a solitary dolphin is considered an abnormal behavior, as it is a cause and effect of solitary living (Müller & Bossley, 2002). For most animals under human care, the appearance of caretakers indicates an opportunity for food acquisition (Mellor et al., 2015), which may indicate why dolphins are likely to interact with their trainers, but the interaction with visitors through a viewing glass may have another motivation. In captivity, if a dolphin does not hold a good relationship with its conspecifics, it will swim less with them and will become closer to humans (caretakers and/or visitors) in order to interact and play, which suggests a poor animal welfare (Clegg, 2018). Because episodes of interaction with visitors were short and rare in our study, we can suggest that subjects did not reflect a poor welfare, according to this indicator.

Both social and solitary play was observed at low frequencies, consistent with results found in a previous study by Clegg et al. (2017), which allows us to suggest that play is not a common behavior engaged by captive bottlenose dolphins in their free time, without environmental enrichment. Play induces positive affect in animals and is considered an indicator of positive emotions, as it mostly occurs when no other needs have to be fulfilled (Boissy et al., 2007). Environmental or social stressors may decrease frequencies of this behavior, and low frequencies and durations of it suggest negative welfare in cetaceans (Clegg, 2018). Agonistic and sexual behaviors were also observed at low frequencies, again consistent with results found in the study by Clegg et al. (2017). A lack of negative experiences, such as agonistic behaviors, also gives hints of good welfare states of animals under human care.

4.6. Conclusion

Our study contributes to the knowledge of behavioral responses of bottlenose dolphins to different living conditions, and suggests ranges and thresholds of common and rare behaviors in the activity budget of these animals during their free time under human care. This information can be useful when carrying out welfare assessments and management endeavors, for example by suggesting appropriate group compositions to attain an optimum welfare of this species in captive environments.

The variation of common behaviors in every phase of this study suggests that different social factors modulated the overall social and solitary behavior occurrences, which is why context should be taken into account when measuring behaviors for assessments. In the activity budget found in this study, solitary slow swimming was predominant during the phases where two and three females were pregnant, while close swimming was less frequent, which suggests that females tended to be more solitary and less social during their late pregnancy stage. Furthermore, during the first pre-partum phase, interaction with visitors was also found at higher frequencies, which suggests that solitary females at this stage were more eager to engage in inter-specific, rather than intra-specific, interactions. Another interesting finding was that solitary fast swimming and stationary were also predominant behaviors during the pre-partum phase, as well as during the phase with three dolphins, showing that there were drastic changes in locomotion rates in those two contexts.

Apart from social factors, individual differences between subjects may have also modulated behavioral differences in the study phases. Likewise, behavioral patterns found in every phase may provide insights on the personality profiles of individuals, an aspect that could also be useful for welfare assessments and management decisions, and that could indicate individuals' needs, preferences and activities. However, the direct link between behavioral patterns and personality profiles of bottlenose dolphins is a topic that needs to be further explored, in order to be properly applied in welfare and management of small and medium odontocetes under human care.

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CAPÍTULO 2

Efectos del embarazo y el cuidado materno en la estabilidad de los rasgos de personalidad de dos hembras del delfín mular (*Tursiops truncatus*)

5. CAPÍTULO 2: Effects of pregnancy and maternal care on the stability of personality traits of two female bottlenose dolphins (*Tursiops truncatus*)

5.1. Abstract

Animal personality is defined as the behavioural differences between individuals of the same species, which are consistent over time and across contexts. As animal welfare depends on how an individual copes with its living conditions and challenges, the identification of personality profiles contributes to a better understanding of individual needs and can be used to guarantee optimum welfare. Ethological observations were made during a reproductive stage of a group of captive bottlenose dolphins (*Tursiops truncatus*), to study behavioural patterns in different contexts and detect personality structures. This research aimed to identify the personality traits of two female bottlenose dolphins during different reproductive status, using a multivariate T-pattern analysis (implemented using the software Theme) and a dimension reduction analysis, to investigate how to improve welfare conditions according to individual needs. Both methods used for this purpose were then compared to test their effectiveness in identifying personality traits in social mammals. We identified four personality profiles (*Extraversion, Agreeableness, Neuroticism* and *Carefulness*), being Extraversion the most common for both females. Behavioural structures varied according to context, as structures were more complex during the pre-natal phase, suggesting that endocrine and physiological changes during the advanced pregnancy stage may modulate behavioural patterns of mothers. Expectant females seemed uncomfortable during the pregnancy stage, possibly due to an inappropriate birthing environment, but their relationship improved when their calves were born. We also found that a better approach to assess personality profiles is achieved by inferring dimensions, rather than studying temporal behavioural structures. Despite this, more research is needed to benefit from the potential advantages of using temporal behavioural structure analysis in ethology and its application in improving welfare and conservation strategies, specific for every individual under human professional care.

Keywords: behavioural structure, captivity, marine mammals, reproductive behaviour, T-patterns, Theme.

5.2. Introduction

In non-human animals, personality (also known as temperament or coping styles), refers to behavioural differences among individuals of the same species, which are consistent over time and across different situations or contexts (Pervin and John, 1997). The study of personality of animals under human care is important because individuals may show different vulnerability to housing conditions and stress, which may affect their welfare state (Carere and Maestripieri, 2013). As animal welfare depends on how an individual copes with its living conditions (Mellor et al., 2015) and challenges in its environment, defining personality profiles and understanding individual needs may contribute to achieve optimum welfare conditions and solve welfare problems (Manteca and Deag, 1993).

Personality has been studied across a wide range of taxa, from invertebrates, such as arthropods and cephalopods, to vertebrates, such as non-human primates (see Gosling, 2001, for a review). Most studies intended to determine personality in animals have been made using subjective ratings or a combination of subjective ratings and behavioural measures, while few studies (around 20) have assessed personality using only observed behavioural measures.

Behavioural traits that represent personality are often inter-correlated and grouped into different clusters. In the 1980s, researchers proposed to group inter-related human personality traits into five common domains, the so-called The Five-Factor Model (FFM) by Digman (1990), which included the following factors: *Openness to experience, Conscientiousness, Extraversion, Agreeableness* and *Neuroticism*. The FFM was later modified to allow its application on species different from humans. The first empirical evidence that revealed that non-human animals could express personality traits that fit into the FFM was collected for chimpanzees (*Pan troglodytes*) by King and Figueredo (1997), who grouped traits into five personality factors similar to those of the FFM, plus an additional one identified as Dominance.

Animals with high scores of *Openness to experience* are creative, clever, exploratory, curious, inquisitive and not simple. *Conscientiousness* consists of traits that show planned behaviour or self-discipline, such as careful, cautious, alert, vigilant, attentive and not lazy. *Extraversion* can be represented by traits that show a tendency to seek stimulation, such as excitable, playful, active, energetic and not timid. *Agreeableness* is characterized by friendliness, and a tendency to be cooperative, while *Neuroticism*

consists of a tendency to experience uncomfortable emotions, such as aggression, anxiety, not relaxed and not calmed (Highfill and Kuczaj, 2007).

Animal behaviour is complex and multi-dimensional, thus a description of the behaviour of an individual based on isolated components, separated from the behavioural architecture, is not enough to reconstruct the meaning of the behaviour engaged by every individual (Asher et al., 2009). Behavioural structure can be studied by detecting hidden repetitive events that are organized in non-random sequences within a time interval, known as temporal patterns (T-patterns), and their derived types, like T-associates (behaviours that have a significant positive or negative tendency to occur near to, or during, occurrences of a T-pattern) and T-packets (T-patterns with their T-associates during a particular time zone; Magnusson, 2000, 2004).

T-pattern analysis (TPA) has been previously used to study behavioural structures in humans (see Casarrubea et al., 2015, for a review) and animals (eg. Hocking et al., 2007; Dalton et al., 2018), as well as human-animal interactions (eg. Kerepesi et al., 2006). TPA allows the description and detection of intra-individual and inter-individual patterns during interactions (Magnusson, 2020) and thus can help determine personality traits. For example, through T-pattern detection, Brilot et al. (2009) found individual differences in starlings' use of space, and several studies have demonstrated that personality influences the organization of behaviour (Jonsson, 2006).

Bottlenose dolphins (*Tursiops truncatus*) are highly social and possess a diverse behavioural repertoire, which make it possible to distinguish consistent individual differences concerning their preferred behaviours (Highfill and Kuczaj, 2010). Moreover, they are easily observable under controlled conditions, which make them good models to study behavioural patterns of cetaceans under human care (Clegg et al., 2017). Previous studies have found that bottlenose dolphins possess distinct individual personalities that are stable over time, both in captivity (Highfill and Kuczaj, 2007) and in the wild (Díaz-López, 2020). However, the stability of dolphin personalities may differ due to a myriad of factors like social rank, context and reproductive activity (Kuczaj et al., 2012).

The objective of this research was to detect the underlying personality structures of two female bottlenose dolphins, by studying the stability of their personality traits during a reproductive cycle (from pregnancy to the first six months of calf rearing). Two methods were used to investigate this: 1) a T-Pattern analysis (TPA) that detect hidden recurring sequences of interactions across time, and 2) a multiple correspondence analysis (MCA) that group interactions into a low-dimensional space. Both methods were then

compared to identify which (TPA or MCA) was better to describe personality structures in social mammals. The model used in this study was the FFM because it is commonly used for social animals, and it is regarded as one of the best ways to map personality (Gosling and John, 1999). This study aimed to provide knowledge of individual needs and preferences during a vital stage, which is fundamental for *ex situ* conservation welfare.

5.3. Methods

Subjects and husbandry

The study subjects were two wild-born female bottlenose dolphins, aged 17 (Anak, taxon report: 2803) and 23 years old (Nereida, taxon report: 424), that were housed in the marine mammal main facility of the Barcelona Zoo (Barcelona, Spain), an outdoor cylindrical facility measuring 22 m in diameter and 6.4 m in depth, and that has the capacity to hold 2430 m^3 of saltwater, which is extracted and filtered from the Mediterranean Sea. The water had a pH 8, a salinity of 26-28g/l and a temperature that oscillated between 10°C and 30°C, depending on the season of the year. Observations were made by underwater vision, from one of the five 4 cm thick windows measuring 1.4 m by 1.7 m, which were located behind a railing that prevented the observers to be placed at less than one meter away from the dolphins.

Subjects ate an average of 11 daily kg of frozen fish (30% mackerel, 50% sardine and 20% capelin combined with sprat), distributed along five meals throughout the day as follows: during two half-hour shows, scheduled at 11:00 h and 13:30 h and, mixed with vitamins and three times at 14:00 h, 16:00 h and 20:00 h (Soriano et al. 2015). Distinct physical characteristics such as body size, marks, pigmentation, scars and fin shape were used to identify the study subjects (Lehner, 1998).

Study phases

Subjects were housed with four other conspecifics of different ages and sexes, in a variable social group, which ranged from two to six individuals. A total of 280 hours (Anak: 136 hours, Nereida: 144 hours) of observations were recorded and divided into four study phases (Table 1), that varied in environmental (season and water temperature) and social (group size and composition) contexts. Phases represented different stages of the reproductive cycle: 1) baseline (early pregnancy) 2) pre-natal (advanced pregnancy)

3) parturition and neo-natal (delivery and the first month immediately after delivery) and 4) development of calves (first six months of calf rearing). The number of hours of observation per subject was similar between both females, in every phase.

Table 1. Group size and composition (number of males and females in the facility), period of data recording (date), season, water temperature (ºC) and hours of observation for the four study phases, used for the comparison of intra-individual behavioural structure among the two dolphins.

Study Phase	Group Composition	Period (date)	Season	Water Temperature (mean ± SD), ºC	Hours of Observation
1. Baseline	6 (3.3)	27/01/03 – 03/03/03	Winter	12 (± 0)	47
2. Pre-natal	2 (0.2)	18/06/03 – 23/08/03	Summer	29 (± 2)	159
3. Parturition and Neo-natal	4 (1.3)	24/08/03 – 30/09/03	Summer	28.2 (± 2.4)	41
4. Development of Calves	4 (1.3)	02/10/03 – 25/03/04	Autumn -winter	13.4 (± 4.3)	33

Behavioural recording

Behavioural data were collected using 10 and 15-minute all-occurrence continuous focal follow bout sampling (Altmann, 1974). The occurrence of interactions between the subjects was registered using an extensive ethogram that contained a repertoire of 43 predefined behaviours, within seven categories (Table 2). Apart from the behavioural events, other environmental and social variables were recorded: 1) study phase 2) season 3) water temperature (ºC) 4) initiator 5) receiver and 6) duration of the interaction (short: ≤ 300 s, medium: 301 – 600 s, long: > 600 s).

Six trained observers collected data during 11 months within a 14-month study period, from 9:00 to 19:00 h from March to July, from 7:00 to 22:00 h from August to October, and from 9:00 – 18:00 h from November to February, before and after the half-hour shows, that were scheduled at 11:00 h, 13:30 h and 16:00 h. A total of 281 (10-minute) observing sessions were conducted from January to March (baseline), 655 (15-minute) sessions were conducted from June to August (pre-natal), 197 (15-minute) sessions were conducted from August to September (parturition and neo-natal) and 586 (15-minute) sessions were conducted from October to March (development of calves).

Table 2. Ethogram with description of the social behaviours used in this study.

Category	Behaviour	Description
Agonistic	Bite	The animal places its teeth in contact with any body part of another subject, with strength and intensity.
	Jaw-pop	The animal opens and closes its mouth rapidly several times towards another dolphin.
	Fin-hit	The animal touches and pushes forward or backward with its fins an object, the surface of the water or any part of the body of another dolphin.
	Swim interruption	The animal interrupts the swim of another dolphin/s interposing itself ahead of it in the case of a single dolphin and between the individuals in the case of more than one dolphin, thus separating them.
	Aggressive chase	The animal swims energetically after another animal in an attempt to reduce the separation between them. The dolphin opens its mouth and emits vocalizations, behind another dolphin/s, less than a meter and a half away, following its same orientation and speed for a period of time.
	Aggressive approach	The animal reduces its distance to less than 50 centimetres away from another dolphin/s in an aggressive manner.
	Touch with melon	The animal puts its melon in contact with another dolphin in an aggressive manner.
Affiliative[1]	Close swim	The animal swims less than 20 cm away from another dolphin/s.
	Swim with contact	The animal swims alongside another dolphin, gently placing its pectoral fin or its belly on the back or on the pectoral fin of the other subject.
	Stationary contact	The animal swims without making hardly any movement, touching any part of the body of another dolphin/s.
	Approach	The animal reduces its distance to less than 50 centimetres away from another dolphin/s.
Play[1]	Hide	The animal swims swiftly ahead of another dolphin, and stays at a place in the enclosure until the other dolphin/s pass by.
	Stationary play	The animal is located in a fixed area of the enclosure and gently touches any part of the body of another dolphin, receiving the same response from the other subject.
	Social play with objects	The animal picks up an object (ball, leaf, etc.) with its snout or mouth, and pushes or passes it to another dolphin, which returns it back in the same way.
	Play chase	The animal follows another dolphin, swimming very fast without contact. When the dolphin being followed changes direction and speed, so does the chasing dolphin. This is repeated several times. Sometimes, during the same episode, the individual being followed may become the chasing dolphin (role inversion).
	Leap	The animal moves all or part of its body outside the water along with another dolphin/s, propelling itself, and falling into the water on the ventral region and/or rostrum and melon.
Maternal (M.)	Suckle	The calf nuzzles its rostrum into its mother's slit, feels for the nipple with its tongue and suckles the milk from the female dolphin's mammary glands.
	Suckling attitude	The calf approaches its mouth to its mother's nipple but cannot suckle milk.
	M. approach	The mother/calf reduces its distance to less than 50-60 centimetres away from its calf/mother.
	M. close swim	Mothers and their calf swim close to each other, with no other dolphin involved.
	M. swim with contact	Mothers and their calf swim in touch, with no other dolphin involved.

	M. stationary contact	Mothers and their calf make body or fin contact, with no other dolphin involved.
	Slow swim calf	The calf moves by making little thrust with its caudal fin (short and low intensity strokes), with a rate of less than 3 or 4 drives per minute and slow body movements.
	Fast swim calf	The calf moves by propelling strongly its caudal fin (with strong and intense hits), with a frequency greater than 3 or 4 drives per minute and rapid body movements.
	Push downwards	The mother carries her calf towards the bottom of the enclosure, by pushing it from its back, rostrum or tail, for about a minute.
	Push upwards	The mother places her rostrum somewhere in her calf's body, preferably its ventral zone, and pushes it upwards.
	Swim away/Escape	The calf separates from its mother by swimming away for a few seconds, and then returns to its mother's side or she slowly approaches her calf.
	Escape attempt	The calf attempts to separate from its mother.
	M. chase	The mother chases her calf by swimming in the same direction, speed and at a distance of less than a meter and a half away.
	M. play	Mother and calf put their snouts on the side, up, down, front, repeatedly, while their snouts gently touch different parts of their bodies. The mother/calf picks up an object (ball, leaf, etc.) with its snout or mouth, and pushes or passes it to the calf/mother, which returns it in the same way.
	M. intervention	The mother interrupts her calf's activity, by means of contact or no contact, by placing herself by her calf's side, or between it and other dolphins, thus separating them.
	Changes of position	The calf swims next to its mother's dorsal fin, from side to side, and from her melon to her dorsal fin.
	Rub	The calf rubs itself against both sides of its mother, from the pectoral fin towards the flow and against the dorsal, for repeated times.
	Nuzzle	The mother/calf touches, rubs or presses gently and affectionately against any part of the body of its calf/mother with its rostrum or melon.
Sexual	Male request	The male dolphin makes contact with its pelvis, exposing its penis, rubbing it against the ventral part of the other dolphin.
	Female request	The female dolphin makes contact with its pelvis, rubbing it against the ventral part of the other dolphin.
With humans	Interaction with visitors	The animal stops in front of the window for a moment, gazes at the visitors, and follows the movements they make.
	Play with visitors	The animal looks at the window intermittently, sometimes picks up an object with its snout or mouth and takes it to the window, throws it towards the trainer or the public, or throws water to the nearest person with its snout.
	Hit window	The animal pushes its caudal fin, snout or blowhole against the window, sometimes opening and closing the mouth.
	Glance through window	The animal approaches and looks to the window where visitors are.
	Trainer with bucket	The animal stops in front of the window and stares at the keeper who carries the bucket. When the keeper passes by, the dolphin sticks its head out of the water and looks at the platform.
Other	No interactions	No social interactions are observed.
	Unidentified	The subject or behaviour cannot be identified.

[1]Mother-calf dyads must be joined by an/other dolphin/s to be qualified for these behaviours, otherwise they are considered maternal behaviours.

Even though data was not collected during routine behaviour trainings, show performances or medical checks, trainers interacted with the subjects during the behaviour recordings, while observers did not interact and remained passive during the observations.

Quality of data

To ensure consistency between observers, reliability tests were performed for the identification of individuals, ethogram's behaviours and proximity, by asking pairs of observers to engage in simultaneous focal samplings following the same subject at the same time, during a preliminary training period of 15 to 20 hours. Simultaneous follow-ups were repeated until a 0.9 value of concordance was achieved, and after this, data collection started. Concordance and Kappa coefficients were always calculated prior and during the study, when a new observer was incorporated (Martin and Bateson, 2007), resulting in concordance levels higher than 0.95 for dolphin identification, 0.89 for behavioural identification and 0.87 for proximity reliability.

Statistical analysis

T-pattern detection

Significant T-patterns were detected using Theme 6 EDU [http://patternvision.com/products/theme/] (PatternVision Ltd., 2017), a free software that detects behavioural sequences of co-occurring events (Magnusson, 1996). The analyzed variables were behaviour, initiator and receiver of interactions. We compared real and randomized data, by using five runs of shuffling and rotation randomizations, and we chose the search parameters that detected more patterns in the real data than in the randomized data (PatternVision Ltd. and Nodus Information Technology bv., 2004), which was a minimum occurrence of three and a significance level of $P < 0.01$. T-pattern variables used for subsequent analysis were: 1) total event types in T-patterns 2) mean event types in T-patterns 3) most frequent event types in T-patterns 4) events in T-patterns 5) total number of different T-patterns 6) total T-pattern occurrences 7) mean occurrences of T-patterns 8) T-pattern mean lengths (number of event types in a T-pattern) 9) mean T-pattern durations and 10) mean levels of hierarchy in T-patterns. We also explored how

behaviours related to T-patterns by detecting: 1) number of T-packets 2) T-packet occurrences 3) positive T-associates and 4) negative T-associates.

Frequencies and durations of interactions were analyzed through non-parametric statistics using R V.3.4.0 (R Development Core Team, 2017) and a significance level of $P < 0.05$. In order to test trait consistency between subjects (inter-individual) and across the different phases for every subject (intra-individual), we compared the total number of different T-patterns per observation time and the total number of T-pattern occurrences per observation time, using the non-parametric R function *prop.test*, corrected to calculate chi-square tests based on Yates' continuity, due to the low value of *N*. We also compared T-pattern mean occurrences, lengths, levels and durations between and within subjects, using the Kruskal-Wallis test and the post-hoc pairwise comparisons were made by using the Mann-Whitney-Wilcoxon test, when there were significant differences.

Dimension reduction

Personality dimensions were inferred using multiple correspondence analysis (MCA), in order to identify systematic relationships between interaction variables (behaviour, initiator and receiver) in a low dimensional space, and to see how they grouped together in domains, in every phase and all phases, for each subject. MCA was done using the *MCA* function of the *FactoMineR* package and the *mjca* function of the *ca* package. To test trait consistency between and within subjects, resulting dimension scores were compared using Spearman's rho correlations and interpreted according to Hinkle et al. (2003).

Ethical statement

This research project was designed in accordance with best practices and highest ethical standards, and meets national and international legislation requirements. Moreover, all methods comply with the EAZA Code of Ethics (www.eaza.net) and the WAZA Code of Ethics and Animal Welfare, namely the Ethical Guidelines for the Conduct of Research on Animals by Zoos and Aquaria (www.waza.org).

5.4. Results

A total of 2245 bouts (focal subject Anak: 1126, focal subject Nereida: 1119) were obtained, 85% of which were interactions and 15% were no interactions. From the

interactions, 47% of the bouts were classified as affiliative (30% initiated by Anak, 41% initiated by Nereida, 43% received by Anak and 29% received by Nereida), 18% were classified as maternal (14% initiated by Anak, 39% initiated by Nereida, 13% received by Anak and 15% received by Nereida), 11% were classified as agonistic (85% initiated by Anak, 14% initiated by Nereida, 10% received by Anak and 78% received by Nereida), 5% were classified as play (41% initiated by Anak, 55% initiated by Nereida, 53% received by Anak and 37% received by Nereida) and 19% were interactions with humans (66% initiated by Anak, 33% initiated by Nereida, 5% received by Anak and 5% received by Nereida). Mean durations were longer for affiliative interactions (mean = 342, SD = 291), while shorter were for play (mean = 191, SD = 201), maternal (mean = 185, SD = 252), agonistic (mean = 151, SD = 178) and interactions with humans (mean = 115, SD = 163).

Multivariate T-pattern analysis

Table 3 shows the total number of occurrences and percentages of the most frequent (≥ 9%) event types in T-patterns detected in every phase for both subjects. *No interactions* and *initiate/receive close swim* were the most frequent event types found in T-patterns in the baseline phase for both females. Similarly, *no interactions, initiate/receive close swim* and *initiate interactions with visitors* were the most frequent event types found in T-patterns in the pre-natal phase for both females. During the parturition and neo-natal phase, *Initiate swim with contact*, *initiate/receive close swim*, and *no interactions* were the most frequent event types found in T-patterns for Anak, while *initiate/receive maternal swim with contact*, *initiate maternal close swim* and *initiate/receive close swim* were the most frequent event types found in T-patterns for Nereida. During the development of calves, *Initiate interactions with visitors* and *initiate/receive maternal close swim* were the most frequent event types found in T-patterns for Anak, while *initiate maternal play* and *initiate/receive maternal close swim* were the most frequent event types found in T-patterns for Nereida.

Two and three T-packets were detected in all phases for Anak, except in the pre-natal phase, while 15 T-packets were detected only in the parturition and neo-natal phase for Nereida (Table 4). Moreover, negative T-associates were detected only during the baseline phase for Anak and during the development of calves for Nereida, which made it difficult to find relationships between positive and negative T-associates of T-patterns, and thus to identify personality profiles. Table 4 also shows rates of different T-patterns

and total T-pattern occurrences per hours of observation, total event types in T-patterns, total events in observations, mean values (± SD) of event types and mean values (± SEM) of levels of hierarchy, durations, lengths and occurrences of significant T-patterns, for the two subjects in every study phase. There were significant differences ($P < 0.001$ for all T-pattern parameters) between the rates of different T-patterns and total T-pattern occurrences per hours of observation, and between the mean values of levels of hierarchy, durations, lengths and occurrences of significant T-patterns, both within each subject, suggesting there was no intra-individual stability of behavioural structures across contexts, as well as between both subjects, suggesting inter-individual differences of behavioural structures.

Table 3. Total occurrences and percentages of the most frequent (≥ 9%) event types in T-patterns detected in every phase for the two subjects.

Dolphin	Phase	Event type		Event type Occurrences	Percentage of Event types
Anak	Baseline	–	No Interactions	54	31%
		Initiate	Close Swim	17	10%
	Pre-natal	Receive	Close Swim	81	16%
		–	No Interactions	78	16%
		Initiate	Interactions with Visitors	45	9%
	Parturition and Neo-natal	Initiate	Swim with Contact	21	16%
		Initiate/Receive	Close Swim	15	11%
		–	No Interactions	13	10%
	Development of Calves	Initiate	Interactions with Visitors	121	37%
		Initiate/Receive	Maternal Close Swim	40	12%
Nereida	Baseline	–	No Interactions	98	47%
		Receive	Close Swim	20	10%
	Pre-natal	–	No Interactions	87	18%
		Initiate	Close Swim	80	16%
		Initiate	Interactions with Visitors	49	10%
		Receive	Close Swim	44	9%
	Parturition and Neo-natal	Initiate	Maternal Swim with Contact	33	23%
		Initiate/Receive	Close swim	14	10%
		Initiate	Close swim	14	10%
		Initiate	Maternal Close Swim	14	10%
		Receive	Maternal Swim with Contact	13	9%
	Development of Calves	Initiate	Maternal Play	28	10%
		Initiate/Receive	Maternal Close Swim	26	9%

Table 4. Number of T-packets (and T-packet occurrences), positive and negative (+/-) T-associates, observation time (s), rates of different T-patterns and of total T-pattern occurrences per hours of observation, number of total event types in T-patterns and of total events, mean (± SD) of event types and mean values (± SEM) of T-pattern levels of hierarchy, durations, lengths and occurrences, for the two subjects during the four study phases.

Dolphin	T-pattern Variables	Baseline	Pre-natal	Parturition and Neo-natal	Development of Calves
Anak	T-packets (Occurrences)	2 (14)	0	2 (19)	3 (25)
	T-associates (+/-)	5/1	0/0	3/0	2/0
	Observation Time (s)	51823	184944	61272	43120
	Rate of Different T-patterns per Hour	5.6^{a}	355.1^{b}	6^{c}	7.4^{d}
	Rate of total T-pattern Occurrences per Hour	27.6^{a}	1113.3^{b}	23.8^{c}	38.1^{d}
	Total Event types in T-patterns	14	27	14	15
	Total Events	174	491	131	330
	Event types (mean ± SD)	5 ± 9.3	12 ± 18.2	5.7 ± 5.2	9.7 ± 21.1
	Levels of Hierarchy (mean ± SEM)	2.4 ± 0.1^{be}	6 ± 0^{a}	2.3 ± 0.1^{b}	3.3 ± 0.2^{abf}
	T-pattern Durations (mean ± SEM), s	1412.1 ± 61.4^{be}	21694.2 ± 51.6^{a}	2313.2 ± 81.6^{ab}	2582.7 ± 158.9^{bf}
	T-pattern Lengths (mean ± SEM)	4 ± 0.2^{b}	13.1 ± 0^{a}	3.6 ± 0.1^{b}	6.2 ± 0.4^{ab}
	T-pattern Occurrences (mean ± SEM)	4.9 ± 0.7^{b}	3.14 ± 0^{a}	4 ± 0.2^{b}	5.1 ± 1.2^{b}
Nereida	T-packets (Occurrences)	0	0	15 (93)	0
	T-associates (+/-)	0/0	0/0	4/0	11/3
	Observation Time (s)	79298	191798	61294	40209
	Rate of Different T-patterns per Hour	2.1^{a}	56^{b}	2.9^{c}	6.6^{d}
	Rate of total T-pattern Occurrences per Hour	14.5^{a}	186.4^{b}	15.5^{c}	28.9^{d}
	Total Event types in T-patterns	13	24	11	20
	Total Events	208	492	142	277
	Event types (mean ± SD)	8.7 ± 19.6	11.4 ± 19.3	5.7 ± 7.3	6.9 ± 7.5
	Levels of Hierarchy (mean ± SEM)	1.8 ± 0.1^{b}	4.7 ± 0^{a}	1.9 ± 0.1^{b}	1.8 ± 0.1^{b}
	T-pattern Durations (mean ± SEM), s	934.6 ± 57.2^{ab}	14052.2 ± 104^{a}	3032.9 ± 166.5^{b}	506.9 ± 38.6^{ab}
	T-pattern Lengths (mean ± SEM)	3.1 ± 0.2^{b}	9 ± 0.1^{a}	3.2 ± 0.2^{b}	2.8 ± 0.1^{b}
	T-pattern Occurrences (mean ± SEM)	6.9 ± 2^{bg}	3.3 ± 0^{a}	5.3 ± 0.7^{b}	4.4 ± 0.3^{bh}

Within a row, mean values with superscripts differ: a±b±c±d, $P < 0.001$; e±f, $P < 0.005$; g±h, $P < 0.05$; indicating intra-individual significant differences between phases.

Post-hoc comparisons showed that T-pattern levels of hierarchy and lengths were significantly different between the pre-natal phase and the baseline phase, the pre-natal phase and the parturition and neo-natal phases, the pre-natal phase and the development of calves phase for both females ($P < 0.001$ for all parameters), and between the development of calves phase and the baseline ($P = 0.002$). On the other hand, there were significant differences between the development of calves phase and the parturition and neo-natal phase ($P < 0.001$), only for Anak.

There were also significant differences between T-pattern occurrences in the pre-natal phase and the baseline phase, the pre-natal phase and the parturition and neo-natal phases, and the pre-natal phase and the development of calves phase for both females ($P < 0.001$ for all parameters), as well as between the baseline and the development of calves phase for Nereida only ($P = 0.04$). There were also inter-individual significant differences of all T-pattern variables between both subjects in every study phase ($P < 0.05$ for all parameters), except between T-pattern lengths during the parturition and neo-natal phase ($W = 3019$, $P = 0.058$), as well as T-pattern occurrences ($W = 2807.5$, $P = 0.083$) and rates of different T-patterns per observation time ($\chi_1^2 = 0.5$, $P = 0.462$), during the development of calves phase.

The pre-natal phase had significantly higher rates of different T-patterns per hour, higher rates of total T-pattern occurrences per hour, higher mean levels of hierarchy in T-patterns, longer T-pattern mean durations and longer T-pattern lengths, but fewer mean T-pattern occurrences, suggesting that the significant T-patterns detected in the pre-natal phase were more complex than in the other three study phases, for both females. Figure 1 shows examples of the first and longest T-patterns detected in the pre-natal phase of each subject. The sequence of events of this T-pattern for Anak (Figure 1A), read from the top was: *initiate touch with melon, no interactions, receive approach, receive close swim, no interactions, receive approach, receive play chase, no interactions, initiate aggressive chase, initiate fin-hit, initiate swim interruption, initiate fin-hit, initiate swim interruption, initiate fin-hit, no interactions, receive stationary contact, no interactions, initiate aggressive chase, receive close swim, no interactions, receive close swim, initiate swim interruption, initiate fin-hit, no interactions, initiate swim interruption* and *initiate touch with melon*. These events are classified as: *initiate agonistic* behaviours, *receive affiliative* and *play* behaviours and *no interactions*, which are traits that represent high *Neuroticism* and low *Extraversion*.

In contrast, the sequence of events of this T-pattern for Nereida (Figure 1B),

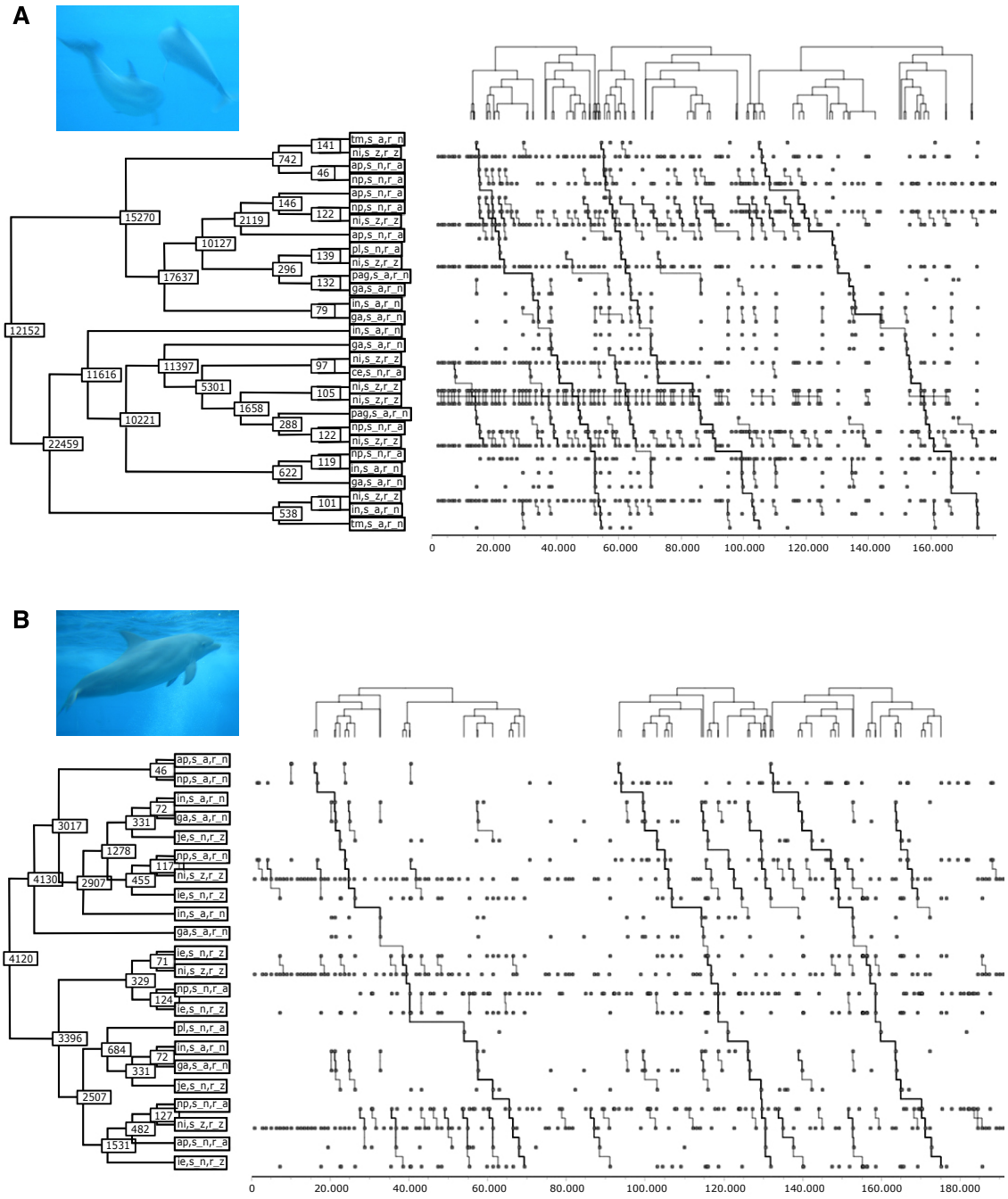

Figure 1. First and longest T-patterns detected in the pre-natal phase for **A.** Anak (*m* = 29), and **B.** Nereida (*m* = 22). The binary detection tree on the left represents the hierarchical sequence of events of the time points on the right, which represent occurrences of events and their connection to form the complete pattern. Occurrences of the complete T-pattern over time are indicated on the three trees above. The horizontal axis shows time in seconds, the vertical axis shows the pattern terminal event type, with codes of behaviour, initiator and receiver of interactions. Frame shots above represent the most frequent events detected in the pre-natal phase for each dolphin, which was *receive close swim* for Anak (A), and *no interactions* for Nereida (B). Description of codes; ap: approach, ce: stationary contact, ga: fin-hit, ie: interaction with visitors, in: swim interruption, je: play with visitors, ni: no interactions, np: close swim, pag: aggressive chase, pl: play chase, r_a: receive Anak, r_n: receive Nereida, r_z: receive none, s_a: initiate Anak, s_n: initiate Nereida, s_z: initiate none, tm: touch with melon.

from the top was: *receive approach, receive close swim, receive swim interruption, receive fin-hit, initiate play with visitors, receive close swim, no interactions, initiate interaction with visitors, receive swim interruption, receive fin-hit, initiate interaction with visitors, no interactions, initiate close swim, initiate interaction with visitors, initiate play chase, receive swim interruption, receive fin-hit, initiate play with visitors, initiate close swim, no interactions, initiate approach* and *initiate interaction with visitors.* These events are classified as: *initiate interactions with humans, affiliative* and *play* behaviours, receive *agonistic* behaviours and *no interactions*, which are traits that represent high *Agreeableness* and high/low *Extraversion*.

Personality profiles

Three to five dimensions, with a cumulative variance ranging from 55% to 90%, were inferred in every phase and all phases for both subjects. Table 5 shows the behavioural events, from the 43 predefined behaviours contained in the ethogram, that were grouped along the first two and three inferred dimensions for both subjects.

There were weak positive and negative correlations between the behavioural dimensions inferred across the study phases for each subject (Anak: $-0.26 \leq r_s \leq 0.33$, $P < 0.005$; Nereida: $-0.31 \leq r_s \leq 0.42$, $P < 0.001$), which suggests that there was intra-individual stability of personality profiles across time and contexts. There were also positive and negative significant correlations between four behavioural dimensions for Anak and three behavioural dimensions for Nereida. However, as Spearman's rho values were negligible ($-0.07 \leq r_s \leq 0.15$, $P < 0.05$), behavioural dimensions between both subjects were not considered similar, suggesting there were individual differences between the behavioural profiles inferred for both study subjects.

5.5. Discussion

In this study we identified personality traits of two female bottlenose dolphins, during a reproductive cycle, using a dimension reduction analysis and TPA, in order to better understand the animals' individual needs during reproductive activity, and to accordingly promote optimum welfare for animals under human care. Results showed there were inter-individual differences between the behavioural profiles and structures of both females, suggesting they had different personality traits. Moreover, weak significant correlations between behavioural dimensions across phases for each female

Table 5. Number of behavioural dimensions, percentage of cumulative variance and interactions grouped in the first three dimensions for every study phase and overall, for both subjects. I: initiate, R: receive, I/R: initiate/receive, NS: one variable was not significant.

Dolphin	Phase	No. dimensions	Cumulative variance	Estimate	Dimension 1		Dimension 2		Dimension 3	
Anak	Baseline	4	85%	Positive	R	Affiliative	I	Agonistic	R	Agonistic, sexual
				Negative	–	No interactions	R	Sexual, affiliative	I	Affiliative
	Pre-natal	4	89%	Positive	R	Affiliative, play	I	Agonistic	I/R	NS
				Negative	I	No interactions, interactions with visitors	R	Affiliative, no interactions	R	
	Parturition and Neo-natal	5	90%	Positive	–	No interactions, interactions with visitors	R	Maternal	I/R	Affiliative
				Negative	R	Affiliative	I	Maternal, play	I/R	Maternal
	Development of calves	5	67%	Positive	R	Maternal, affiliative	R	Affiliative	R	Maternal, play
				Negative	I	Interactions with visitors	I/R	Maternal	I	Affiliative
	All phases	5	60%	Positive	R	Maternal	R	Affiliative	I	Agonistic
				Negative	I	No interactions, interactions with visitors	I/R	Maternal	R	No interactions, maternal
Nereida	Baseline	3	89%	Positive	R	Affiliative	I	Agonistic	NS	NS
				Negative	–	No interactions	R	Agonistic		
	Pre-natal	4	87%	Positive	R	Agonistic	R	Agonistic	I/R	NS
				Negative	–	No interactions, interactions with visitors	I/R	Play, affiliative	I	
	Parturition and Neo-natal	4	83%	Positive	I/R	Affiliative	R	Maternal	–	NS
				Negative	R	Maternal	I	Maternal	I/R	
	Development of calves	5	55%	Positive	R	Affiliative	I	Affiliative	R	Play
				Negative	I	Trainers with buckets, interactions with visitors	R	Maternal, affiliative	I/R	Maternal
	All phases	5	58%	Positive	R	Agonistic	I/R	Maternal	I/R	Affiliative
				Negative	I	No interactions, interactions with visitors	R	Agonistic	I	Maternal

evidenced intra-individual stability of personality profiles. On the contrary, significant differences between the rates and mean values of all T-pattern parameters (different T-patterns per hour, total T-pattern occurrences per hour, levels of hierarchy, durations, lengths and occurrences of significant T-patterns) tested across phases for each subject, suggest there was no intra-individual stability of behavioural structures across contexts.

Recent additions to TPA, such as T-associates and T-packets, detect behaviours that occur significantly more or less often around or during a T-pattern or an event type (Magnusson, 2000), which could help determine personality factors, but such additions have been used in few studies (Magnusson et al., 2016). The lack of detected T-packets and negative T-associates in this study did not allow us to find clear evidence of personality factors through TPA. However, this analysis showed that there were higher rates of T-pattern occurrences per hour, of different T-patterns per hour, higher T-pattern levels of hierarchy, longer durations and lengths, but fewer T-pattern occurrences, in the pre-natal phase for both females, suggesting dolphins had a more complex structure during the pre-natal phase, possibly due to the physiological, hormonal, morphological, and behavioural fluctuations that expectant females face during pregnancy (Tizzi et al., 2010; Noren et al., 2011).

Levels of reproductive and stress hormones (progesterone, androgens and cortisol), and frequencies of side arches and body flexions increase during gestation in dolphins (Tizzi et al., 2010; Legacki et al., 2020), while mean and maximum swim speeds, stroke amplitude and distance per stroke, diminish (Noren et al., 2011). Before parturition, there is also an increase in the duration of apnoeas together with a low respiratory rate, related to the tiredness faced by mothers, due to the increase in body size and weight, as well as to metabolic changes during gestation (Tizzi et al., 2010).

In preparation for delivery, progesterone values decrease and pregnant females save energy in their movements in order to maintain levels of respiratory and cardiac rhythms similar to those found during resting (Williams et al., 1992; Tizzi et al., 2010). Such reduced mobility also causes a decrease in their participation in social activities and a withdrawal from social contact (Tizzi et al., 2010), which makes mothers more solitary during gestation (Tavolga and Essapian, 1957). Despite this, detected T-patterns in the pre-natal phase indicated there were complex structures of interactions during the advanced pregnancy stage which were not extended over time, possibly due to the endocrinal and physiological fluctuations mothers face before parturition.

Personality profiles obtained through MCA are consistent with previous studies that support the hypothesis that bottlenose dolphins possess distinct individual personalities, which are stable over time and across contexts (Highfill and Kuczaj, 2007; Díaz-López, 2020), whereas results obtained through TPA do not support this hypothesis, as personality traits detected in behavioural structures were not consistent across contexts. However, the variation in personality traits found in this study is also consistent with previous studies that suggest that the stability of bottlenose dolphin's personality may vary according to different contexts (Kuczaj et al., 2012).

Synergic evaluation between findings inferred with dimension reduction and TPA suggest that interactions between dolphins could be grouped into four personality profiles, in levels that varied throughout the different contexts. We identified the first dimension as *Extraversion* (Figure 2A and 2B), which was comprised positively by *receive play, affiliative, maternal* and *agonistic* behaviours, and negatively by *initiate interactions with humans, trainers with buckets* and *no interactions*. *Extraversion* was the most common dimension found in this study, as it was identified in all phases for both females, except in the parturition and neo-natal phase for Nereida.

We identified the second dimension as *Agreeableness*, which was composed positively by *initiate/receive affiliative, maternal* and *play* behaviours, and negatively by *receive agonistic* and *sexual* behaviours. We identified the third dimension as *Neuroticism*, which was composed positively by *initiate agonistic* behaviours, and negatively by *receive affiliative, maternal*, *sexual* and *agonistic* behaviours, and *no interactions*. We identified the fourth dimension as *Carefulness* (Figure 2B), which was related to calf care and was comprised positively by *initiate*/*receive maternal* behaviours, and negatively by *receive play* behaviours. There was a fifth dimension that was not easy to identify, as it was composed positively by *initiate/receive affiliative* behaviours and *initiate maternal* and *play* behaviours, and negatively by *initiate/receive maternal* behaviours and *receive affiliative* and *play* behaviours. We noticed that the four personality dimensions identified in this study could be organized along two continuums: 1) the *Extraversion-Carefulness* continuum (which is similar to the Boldness-Shyness continuum used by behavioural ecologists), and 2) the *Neuroticism-Agreeableness* continuum.

Even though our findings were consistent with previous studies done by Morton et al. (2021), who also found four personality domains in captive bottlenose dolphins using an adjective rating assessment, there were variations in the identification

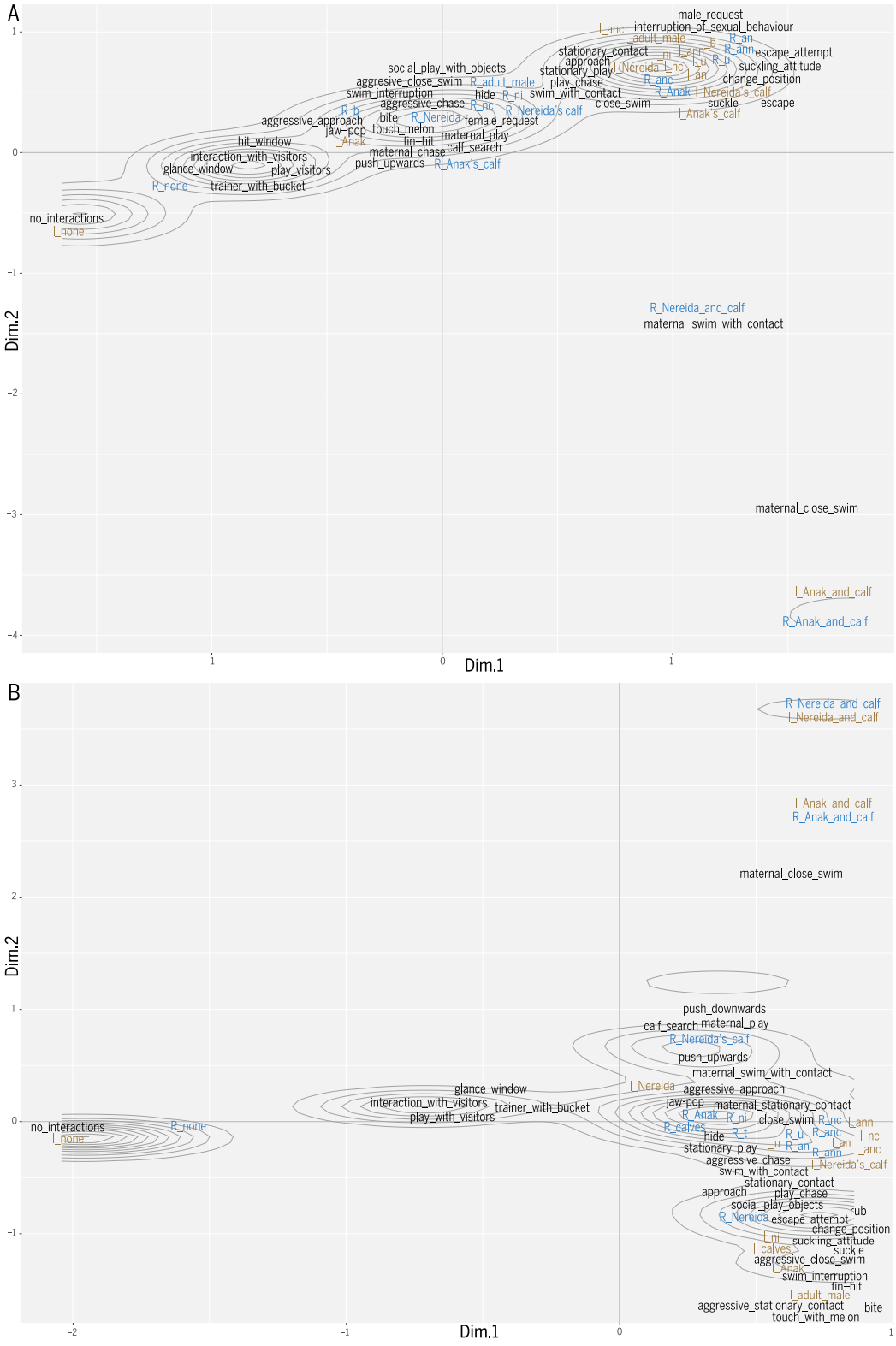

Figure 2. Multiple correspondence analysis plots with behaviours (black), initiator (brown) and receiver (blue) of interactions in all study phases for **A.** Anak, and **B.** Nereida. The horizontal axis represents Dimension 1: Extraversion (low < 0 < high), and the vertical axis represents Dimension 2 (B): Carefulness (low < 0 < high). Description of codes; I: initiate, R: receive, an: Anak and Nereida, anc: Anak, Nereida and calves, ann: Anak, Nereida and Nereida's calf, b: young male one, nc: Nereida and calves, ni: adult female, t: young male two, u: unidentified.

of factors. Morton et al. (2021) identified a factor as *Openness*, characterized by a tendency to be active and investigate the environment, which could not be related to any of the factors found in our study, possibly because such traits were not registered among the observed interactions analysed. Morton et al. (2021) identified a factor as *Directedness*, which was a blend of low *Neuroticism* and high *Conscientiousness*, and could be related to the factor we identified as *Carefulness*.

Despite previous studies have found the FFM fifth personality factor, *Openness to experience*, in bottlenose dolphin personality structure (Morton et al., 2021), as well as in personality structures of other species that live in social groups, like chimpanzees (King and Figueredo, 1997), bonobos (Weiss et al., 2015) and horses (Lloyd et al., 2008), it could not be clearly identified with the observational methodology used in this study. The absence of the *Openness to experience* factor in our study may have been due to the lack of exploratory behaviours engaged in social interactions, or to the negative relationship between progesterone (a hormone that increases its levels during gestation) and exploratory behaviours (Tizzi et al., 2010). This factor could be tested by studying behavioural patterns under conditions which include enrichment programs, where subjects can show interest in new objects, be curious, inquisitive and find creative ways to play with objects; or by undertaking cognitive experiments, where subjects have the possibility to show their cleverness, address tasks in novel and resourceful ways, show interest in new situations and learn easily and understand quickly the tasks they are asked for during the tests (Highfill and Kuczaj, 2007).

Even though Morton et al. (2021) did not find a strong *Neuroticism* factor, their domain identified as *Disagreeableness*, characterized by agonistic behaviours, was similar to the domain we identified as *Neuroticism*. Similarly, they did not identify *Extraversion* and *Agreeableness* as independent domains, but the factor they identified as *Sociability* was similar to the factors *Extraversion* and *Agreeableness* found in our study. Discrepancies between the identification of domains between Morton et al.'s (2021) and our study may have been caused by the use of different methodologies to assess personality structure, or to the variations in environmental and social contexts between both studies, such as housing conditions, group compositions and reproductive activity; parameters that are worth examining in future research.

The two analytical methods used in this study revealed similar personality traits, but they were mostly found at opposite levels. Results attained with the dimension reduction analysis suggest that, overall, both females had high levels of *Extraversion* and

Anak had also high levels of *Neuroticism*, while Nereida had also high levels of *Agreeableness*. On the other hand, the most frequent event types in T-patterns detected overall for the two subjects were: *no interactions* and *initiate interactions with visitors* (traits of low *Extraversion*), *initiate*/*receive affiliative* behaviours (traits of high *Agreeableness*) and *initiate*/*receive maternal* behaviours (traits of high *Carefulness*). This evidences that most T-patterns detected had latencies of no interactions between affiliative, maternal and interactions with humans.

Both females showed similar personality profiles (high *Extraversion*, high *Neuroticism* and low *Agreeableness*) during the baseline and the pre-natal phases, which did not vary with the season changes, water temperature, group composition or number of dolphins in the facility, and this suggests that subjects were uncomfortable or were not compatible. This may be related to the increase of cortisol levels that dolphins and other mammals experience during pregnancy (Tizzi et al., 2010). A recommendation to improve welfare during gestation is to group pregnant dolphins with other compatible females but no males, so that the group resembles matrilineal pods found in the wild, which consist of females with their calves and other females that assist during the birth and act as calf-sitters that help rear offspring (Wells et al., 1987).

On the contrary, during the parturition and neo-natal phase, Anak showed low *Extraversion*; whereas during the development of calves, both females showed high *Extraversion* and Nereida also showed low *Carefulness*, suggesting females exhibited different maternal styles: Nereida seemed to be more permissive, while Anak seemed to be more vigilant with her calf. This concurs with previous studies that have found that dolphin mothers may vary in the style of disciplining their calves and may modify it as the social context changes and their calves grow (Hill et al. 2007; Von Streit et al., 2013). Moreover, the lack of traits that represent *Neuroticism* during this post-partum stage, suggests that the relationship between mothers improved with the presence of their calves.

5.6. Conclusions

In this study we found there were individual differences of personality profiles between both study subjects. Pregnancy and maternal care affected the stability of dynamic behavioural structures across time and contexts, detected with T-pattern analysis, while it did not affect the stability of personality traits across contexts, discovered with dimension reduction of interactions. This allows us to suggest that a better approach to

determine personality traits is done by inferring dimensions (MCA), as it shows how interactions that have positive and negative correlations are grouped, even though profiles sometimes cannot be clearly identified. Despite this, TPA complements traditional quantitative behavioural methodology, as it reveals repeated sequential ordering of interactions across time and behavioural structure complexity. This study helps to establish a starting point for future work intended to relate personality profiles and behavioural structures in gregarious animals, but more research is needed to benefit from the potential advantages of using TPA in ethology, as well as its application in improving welfare and conservation strategies, specific for every individual under human professional care.

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CAPÍTULO 3

Evaluación de la estructura de la personalidad en el delfín mular (*Tursiops truncatus*): comparación entre medidas de comportamiento y calificaciones con adjetivos

6. CAPÍTULO 3: Bottlenose dolphin (*Tursiops truncatus*) personality structure assessment: Comparing behavior measures and adjective ratings

6.1. Abstract

Animal personality is defined as behavioral differences of individuals of the same species, which are consistent across time and contexts. Few studies on odontocetes have established the correspondence between behavioral measures and questionnaire-based evaluations aiming at determining personality. In this study we assessed the personality structure of a group of bottlenose dolphins, using observed interactions and ratings of adjective items. Three to five factors were found: *Extraversion, Neuroticism* and *Conscientiousness* were identified using both assessments, while *Agreeableness* was identified only with behavioral measures, and *Openness to experience* was only slightly represented with adjective items that were grouped within *Extraversion* factor, which was inferred with the adjective ratings assessment. The factors inferred with both assessments correlated statistically and traits grouped similarly. The study of personality can be used to identify individual needs, being useful in management and welfare endeavors.

Keywords: Behavioral profiles, behavioral syndromes, temperament, marine mammals, ratings *vs.* codings, zoos, Five Factor Model

6.2. Introduction

Personality in non-human animals is defined as behavioral differences between individuals from the same species, that are consistent over time and across contexts (Pervin & John, 1997), which is why personality dimensions should describe maximum inter-individual variability while maintaining minimum intra-individual variability (Forkosh et al., 2019). Knowledge of animal personality can be useful in animal care and management, especially related to welfare and conservation, like planning group composition of social species, enrichment programs and husbandry schedules according to the subjects' individual needs (Highfill & Kuczaj, 2010). For example, male gorillas (*Gorilla gorilla*) with high scores for the personality factor *Understanding*, display higher rates of affiliative behaviors and less contact aggression, and thus are more suitable to be housed in social groups (Kuhar et al., 2006). In conservation welfare, personality research can help identifying profiles that are more likely to reach reproduction success in breeding programs. For example, the personality factor *Fearfulness* in cheetahs (*Acinonyx jubatus;* Wielebnowski, 1999) and *Dominance* in male black rhinoceros (*Diceros bicornis*; Carlstead et al., 1999), are correlated with reduced reproduction success, while *Dominance* in female black rhinoceros is correlated with increased breeding success (Carlstead et al., 1999). With this information in hand, conservationists and zoo managers are able to predict which individuals will be successful in reproduction and rearing of offspring: in these examples, black rhinoceros breeding pairs were constituted by a submissive male and a dominant female (Carlstead, 1999), and cheetahs were housed in facilities adapted to provide hiding places and isolated areas which reduce tense and fearful behaviors (Wielebnowski, 1999). Another example of the utility of personality research in conservation efforts is to identify individuals that are likely to be successful in release and reintroduction programs.

Personality profiles can be classified using the Five Factor Model (FFM) which is commonly used in human personality research (Goldberg, 1990) and has been proven to be a useful tool to identify personality structure in animals (Kuczaj et al., 2012). The five personality factors that constitute this model are: *Openness to experience, Conscientiousness, Extraversion, Agreeableness* and *Neuroticism.*

Personality structures in animals can be assessed using spontaneous behavioral measures, based on direct observations and recordings of animal behavior during naturally occurring activities ("codings"), or using adjective "ratings", based on long-

term indirect observations of experts familiar with the study subjects (Gosling, 2001). Currently there is much debate on which assessment is better for comparative research (Tkaczynski et al., 2019) and, over the last two decades, there has been a growing interest in investigating the correspondence of the different animal personality assessments as well as a need to determine a direct link between behaviors and personality traits (Barnard et al., 2016). Even though there is a fair amount of agreement between the personality factors identified with adjective ratings and behavioral measures (Barnard et al., 2016), some studies have shown a limited correlation between the personality structures found using both types of assessments (Tkaczynski et al., 2019). However, studies in primate behavior have found that consistency over time is high when using adjective ratings and observed behaviors, while coherence across responses and stability across situations are moderate to low (Uher & Asendorpf, 2008). Thus, ethologists recommend further comparative studies to continue using validated assessments for the identification and comparison of personality structures of species (Tkaczynski et al., 2019).

To date, few studies have assessed personality profiles of odontocetes. In the wild, Díaz (2020) and Evans et al. (2021) have assessed personality profiles using codings (behavioral measures), whereas in captivity, other authors have studied personality using ratings (Highfill & Kuczaj, 2007; Kuczaj et al., 2012; Úbeda et al., 2019; Morton et al., 2021), or a combination of both assessment methods (Moreno et al., 2017; Lilley et al., 2018; Hill et al., 2019; Bagley et al., 2020). However, studies that determine the direct link between personality traits of odontocetes from observed interactions in daily activity patterns, which are consistent across time and contexts, are rare. Among odontocetes, the bottlenose dolphin (*Tursiops truncatus*) is the most common species under human professional care, it has a broad behavioral repertoire and it is easily observable under water and in various contexts, which makes it a good model to conduct behavioral studies (Clegg et al., 2017).

Highfill and Kuczaj (2007) carried out the first systematic study of personality in bottlenose dolphins under human care, using adjective ratings. The authors modified the FFM described by Goldberg (1990) by listing adjectives that cohered with dolphin behaviors within the five factors so that dolphins with high scores of *Openness to experience* are creative, curious, clever, exploratory, inquisitive and not simple; those with high scores of *Conscientiousness* are careful, cautious, alert, vigilant, attentive and not lazy. *Extroverted* dolphins enjoy being the center of attention, sometimes by swimming frantically or doing spectacular leaps, and are energetic, active, playful,

excitable and not timid. *Agreeable* dolphins are affiliative, obedient, cooperative and friendly with other dolphins and humans, while dolphins with high *Neuroticism* are aggressive, temperamental, jealous, anxious, not relaxed and not calmed. On the other hand, Díaz (2020) carried out the first study of personality in wild bottlenose dolphins, using behavioral observations. Both studies found individual differences in personality that were consistent over time and across situations. However, Kuczaj et al. (2012) later found that dolphin individual differences varied according to different contexts, like interactions with conspecifics, with humans as well as with the physical world.

The aim of this study was to validate two personality assessment methods used in the bottlenose dolphin by identifying the correspondence between personality factors of a group of individuals that were housed at the Barcelona Zoo, inferred with direct observations of multi-variable spontaneous interactions and indirect observations of behavioral adjective items rated by trainers who were acquainted with the study subjects. We expected that there would be stability of personality factors across time and contexts, and that personality factors inferred with both assessments would correlate and show similar trait groupings. Lastly, we wanted to explore which assessment described more accurately personality factors of small and medium cetaceans, by comparing our findings with previous studies done in odontocetes in wild and captive environments.

6.3. Methods

Subjects and facilities

The study subjects were seven bottlenose dolphin individuals of different sexes and ages (Table 1). Subjects were housed in the marine mammal main facility of the Barcelona Zoo (Barcelona, Spain), an outdoor cylindrical enclosure with a diameter of 22 m, a depth of 6.4 m, and 2432 m^3 of sea water capacity, which is extracted and filtered from the Mediterranean Sea using a pump system (Figure 1). Water had a pH 8, a salinity of 26-28g/liter and a temperature that oscillated between 10 and 30°C, depending on the season of the year. Subjects ate an average of 11 kg of frozen fish (30% mackerel, 50% sardine and 20% capelin combined with sprat) daily, distributed five times throughout the day: during the two half-hour shows (scheduled at 11:00h and 13:30h), and mixed with vitamins at 14:00h, 16:00h and 20:00h. Adult females were trained for the show performance for zoo visitors, every day at 13:00 h (Soriano et al. 2015).

Table 1. Characteristics of the study subjects.

Name	Sex[a]	Birth type[b]	Birth date	Parentage	Rearing	Arrival date to Zoo
Nika	F	W	~1964	None	Unknown	27/10/1970
Nereida	F	W	~1980	Neo's dam	Unknown	13/10/1982
Anak	F	W	~1986	Leia's dam	Unknown	01/10/1990
Inuk	M	C	20/09/1983	Blau's, Leia's, Tumay's and Neo's sire	Dam	20/09/1983
Blau	M	C	01/07/1999	Inuk's offspring	Dam	01/07/1999
Tumay	M	C	13/04/2002	Inuk's offspring	Dam and Nika	13/04/2002
Neo[c]	M	C	24/08/2003	Inuk's and Nereida's offspring	Dam	24/08/2003
Leia	F	C	25/08/2003	Inuk's and Anak's offspring	Dam	25/08/2003

Note. [a] F: Female, M: Male; [b] W: Wild, C: captive. [c] Subject was not included in the analyses due to few years of acquaintance with the trainers to carry out the ratings assessment.

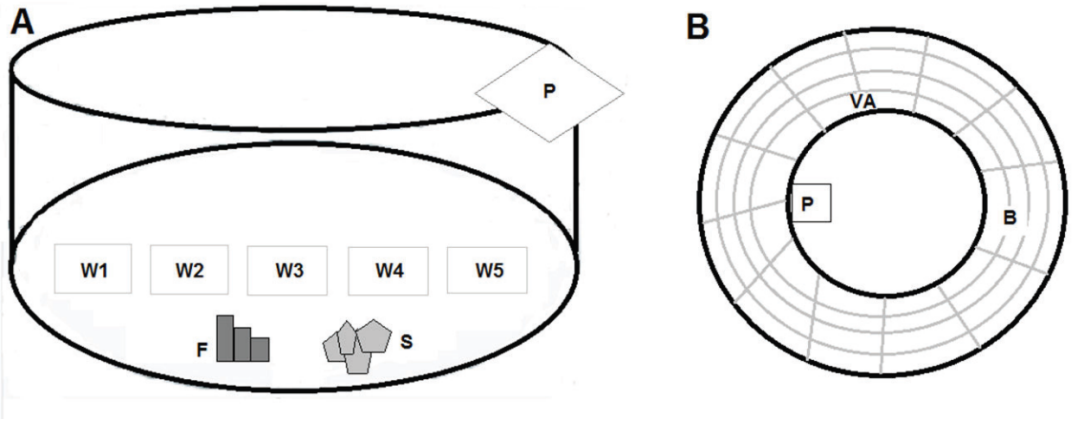

Figure 1. Scheme of the facility where the group of bottlenose dolphins was housed during the study. (A) Front view of the facility: F = Filters, P = Platform for exhibitions, S = Stones, W1 to W5 = Visitors and researchers viewing windows. (B) Apical view of the facility: B = Bleachers for visitors, P = Platform for exhibitions, VA = Visitors' access (Soriano et al., 2015).

Behavioral observations

Direct behavioral observations were made by underwater vision, from one of the five, 4-cm thick windows measuring 1.4 m by 1.7 m, which had a railing that prevented the observers from being less than one meter away from it. Data were collected using 10 and 15-minute all-occurrence continuous focal follow bout samplings (Altmann, 1974). The occurrence of social interactions between the subjects was registered using an extensive

ethogram that contained a repertoire of 43 predefined behaviors, within seven categories (Table 2). In addition, it was recorded which individual initiated the interaction and who received it.

A total of 384 hours of observations (2583 bouts) were recorded by six trained observers, before and after the half-hour shows that were scheduled at 11:00 h, 13:30 h and 16:00 h. The observation sessions were divided into five different study phases that varied in social contexts (Table 3). Variables registered were: 1) study phase, 2) behavior (within the repertoire of the 43 predefined behaviors), 3) initiator 4) receiver, and 5) duration of the interaction (s). The 2583 bouts were registered in 1766 sessions, distributed along the five study phases in the following way: 694 (10-minute) sessions in the "baseline", 636 (15-minute) sessions in the "pre-partum), 221 (15-minute) sessions in the "parturition and post-partum", 193 (15-minute) sessions in the "development of calves" and 22 (15-minute) sessions in the "five dolphins" phase.

Even though data was not collected during daily medical checks, routine trainings or show performances, trainers occasionally interacted with the subjects during the behavior recordings, while observers remained passive. Distinct physical characteristics such as body size, marks, pigmentation, scars and fin shape, were used to identify the study subjects following Lehner (1998). The order in which focal subjects were observed was chosen randomly and the same subject was never observed continuously for more than 30 minutes.

To ensure consistency between the observers that collected the data, reliability tests were performed for the identification of individuals, ethogram's behaviors and proximity, by asking pairs of observers to engage in simultaneous focal samplings following the same subject, during a preliminary training period of 15 to 20 hours. Simultaneous follow-ups were repeated until a .90 value of concordance was achieved, and after this, data collection started. Inter-observer agreement was evaluated using Cohen's Kappa Coefficients, always calculated prior and during the study, when a new observer was incorporated (Martin & Bateson, 2007), and resulted in concordance levels higher than .95 for the identification of subjects, .89 for the identification of behaviors and .87 for proximity reliability.

Table 2. Ethogram with the description of the social behaviors used in this study.

Category	Behavior	Description
Agonistic	Biting	The animal places its teeth in contact with any body part of another subject, with strength and intensity.
	Jaw-popping	The animal opens and closes its mouth rapidly several times towards another dolphin.
	Fin-hitting	The animal touches and pushes forward or backward with its fins an object, the surface of the water or any part of the body of another dolphin.
	Swim interruption	The animal interrupts the swim of another dolphin interposing itself ahead of it in the case of a single dolphin and between the individuals in the case of more than one dolphin, thus separating them.
	Aggressive chasing	The animal swims energetically after another animal in an attempt to reduce the separation between them. The dolphin opens its mouth and emits vocalizations, behind another dolphin, less than a meter and a half away, following its same orientation and speed for a period of time.
	Aggressive approaching	The animal reduces its distance to less than 50 cm away from another dolphin/s in an aggressive manner.
	Touching with melon	The animal puts its melon in contact with another dolphin in an aggressive manner.
Affiliative[a]	Close swimming	The animal swims less than 20 cm away from another dolphin.
	Swimming with contact	The animal swims alongside another dolphin, gently placing its pectoral fin or belly on the back or pectoral fin of another subject.
	Stationary contact	The animal swims without making hardly any movement, touching any part of the body of another dolphin/s.
	Approaching	The animal reduces its distance to less than 50 cm from another dolphin.
Play[a]	Hiding	The animal swims swiftly ahead of another dolphin, and stays at a place in the facility until the other dolphin/s pass by.
	Stationary play	The animal is located in a fixed area of the facility and gently touches any part of the body of another dolphin, receiving the same response from the other subject.
	Social play with objects	The animal picks up an object (ball, leaf, etc.) with its snout or mouth, and pushes or passes it to another dolphin, which returns it back in the same way.
	Play chasing	The animal follows another dolphin, swimming very fast without contact. When the dolphin being followed changes direction and speed, so does the chasing dolphin. This is repeated several times. Sometimes, during the same episode, the individual being followed may become the chasing dolphin (role inversion).
	Leaping	The animal moves all or part of its body outside the water along with another dolphin/s, propelling itself, and falling into the water on the ventral region and/or rostrum and melon.
Maternal (M.)	Suckling	The calf nuzzles its rostrum into its mother's slit, feels for the nipple with its tongue and suckles the milk from the female dolphin's mammary glands.
	Suckling attitude	The calf approaches its mouth to its mother's nipple but cannot suckle milk.
	M. approaching	The mother/calf reduces its distance to less than 50-60 cm away from its calf/mother.
	M. close swimming	Mothers and their calf swim close to each other, with no other dolphin involved.
	M. swimming with contact	Mothers and their calf swim in touch, with no other dolphin involved.

	M. stationary contact	Mothers and their calf make body or fin contact, with no other dolphin involved.
	Slow swimming - calf	The calf moves by making little thrust with its caudal fin (short and low intensity strokes), with a rate less than 3 or 4 drives per minute and slow body movements.
	Fast swimming – calf	The calf moves by propelling strongly its caudal fin (with strong and intense hits), with a frequency greater than 3 or 4 drives per minute and rapid body movements.
	Pushing downwards	The mother carries her calf towards the bottom of the facility, by pushing it from its back, rostrum or tail, for about a minute.
	Pushing upwards	The mother places her rostrum somewhere in her calf's body, preferably its ventral zone, and pushes it upwards.
	Swimming away/Escape	The calf separates from its mother by swimming away for a few seconds, and then returns to its mother's side or she slowly approaches her calf.
	Escape attempt	The calf attempts to separate from its mother.
	M. chasing	The mother chases her calf by swimming in the same direction, speed and at a distance of less than a meter and a half away.
	M. play	Mother and calf put their snouts on the side, up, down, front, repeatedly, while their snouts gently touch different parts of their bodies. The mother/calf picks up an object (ball, leaf, etc.) with its snout or mouth, and pushes or passes it to the calf/mother, which returns it in the same way.
	M. intervention	The mother interrupts her calf's activity, by means of contact or no contact, by placing herself by her calf's side, or between it and other dolphins, thus separating them.
	Changes of position	The calf swims next to its mother's dorsal fin, from side to side, and from her melon to her dorsal fin.
	Rubbing	The calf touches repeated times against both sides of its mother, from the pectoral fin towards the flow and against the dorsal.
	Nuzzling	The mother/calf touches, rubs or presses gently and affectionately against any part of the body of its calf/mother with its rostrum or melon.
Sexual	Male request	The male dolphin makes contact with its pelvis, exposing its penis, rubbing it against the ventral part of the other dolphin.
	Female request	The female dolphin makes contact with its pelvis, rubbing it against the ventral part of the other dolphin.
With humans	Interaction with visitors	The animal stops in front of the window, gazes at the visitors, and follows the movements they make.
	Play with visitors	The animal looks at the window intermittently, sometimes picks up an object with its snout or mouth and takes it to the window, throws it towards the trainer or the public, or throws water to the nearest person with its snout.
	Hitting window	The animal pushes its caudal fin, snout or blowhole against the window, sometimes opening and closing the mouth.
	Glancing through window	The animal approaches and looks out the window where visitors are.
	Trainer with bucket	The animal stops in front of the window and stares at the keeper who carries the bucket. When the keeper passes by, the dolphin sticks its head out of the water and looks at the platform.
Other	No interactions	No social interactions are observed.
	Unidentified	The subject or behavior cannot be identified.

Note: [a] Mother and calf dyads must be joined by another dolphin to be qualified for these behaviors, otherwise they are considered maternal behaviors.

Table 3. Study phases that varied in social context and season.

Study Phase	No. males (M) and females (F)	Period (date)	Season	Water Temperature (mean ± SD, ºC)	Hours of Observation
1. Baseline	6 (3 M, 3 F)	27/01/03 – 03/03/03	Winter	12 ± 0	116
2. Pre-partum	2 (2F)	18/06/03 – 23/08/03	Summer	29 ± 2.01	159
3. Parturition and post-partum	4 (1M, 3F)	24/08/03 – 30/09/03	Fall	28 ± 2.30	55
4. Development of calves	4 (1M, 3F)	02/10/03 – 25/03/04	Winter	14 ± 4.56	48
5. Five dolphins	5 (1M, 4F)	25/03/04 – 27/04/04	Spring	15 ± 0.47	6

All analyses were done using R V.3.4.0 (R Development Core Team, 2017) and SPSS Statistics 1.0.0.1447 (IBM Corp., 2020), and two-tailed tests were considered significant when $p < .05$. The interaction variables (behavior, initiator and receiver) were grouped into reduced dimensions using multiple correspondence analyses (MCA), with the *MCA()* function from the *FactoMineR* package and the *mjca()* function from the *ca* package. To test for the stability of factors across time and contexts, personality factor scores were standardized and then correlated using Pearson's correlation with the *rcorr()* function from the *Hmisc* package.

To infer personality dimensions with the reliable behavioral items for each subject in every rating period, we conducted factor analyses using unweighted least squares as extraction method, due to the small sample size (Jung et al., 2020), with an orthogonal (varimax) rotation and salient factor loadings ≥ |.40| (Jung & Lee, 2011). If the item was ≥ |.40| in more than one component, it was considered to describe the component with the highest loading. The reliability of each inferred factor was then tested using Cronbach's alpha. To test for stabilities of the factors over time and contexts, as well as the correspondence between both assessments used to infer personality dimensions, factor scores were standardized and then correlated using Pearson's correlation.

Ratings

Behavioral ratings were collected using a questionnaire that consisted of 34 adjective-based items (Table 4), previously studied to identify the FFM personality factors in bottlenose dolphins (Highfill & Kuczaj, 2007) and other social mammals living in groups (gorillas, *Gorilla gorilla*: Gold & Maple, 1994). Items were scored on a 10-point Likert scale, from 1 (strongly disagree) to 10 (strongly agree), by eight independent raters who were trainers that had at least four years of acquaintance with the rated

Table 4. Bottlenose dolphin personality questionnaire used for the adjective ratings assessment.

Adjective item	Description	Example
Active	Moves a lot, is energetic.	The animal is in constant motion, swims, leaps, etc.
Apprehensive	Anxious, distressed, nervous.	The animal is timid, uneasy, hesitant to a circumstance and/or avoids any risk.
Curious	Explores novel situations, environments and/or objects without qualms.	The animal easily approaches objects, or is the first to approach them.
Affectionate	Responsive and provides security to others.	Gently interacts with other dolphins. Affectionately touches fellow dolphins.
Opportunistic	Seizes a chance as soon as it arises.	The animal would eat other dolphins' food, attempt to steal a prize or take over possession of an object.
Permissive	Has the opportunity, but does not interfere with the behavior of other dolphins.	Mothers allow their calves to interact without intervening. Adults do not interfere in play episodes of calves or fellow dolphins.
Excitable	Displays dramatic behavior to changes that occur in its environment.	The animal is greatly affected by variations in its facility and displays a low tolerance to change. The animal leaps, exhibit signs of nervousness, decreased appetite and/or erratic swim behavior when confronted with a change.
Fearful	Avoids disturbances and/or objects.	The animal retreats immediately from objects and/or from disturbances that occur outside or in its environment.
Insecure	Hesitates to act alone, seeks reassurance from others.	The animal requires to be trained with other dolphins and/or cannot be left alone in the facility for more than 24 hours.
Irritable	Reacts negatively to little provocation.	Reacts negatively when an interaction is requested, actively avoids or swims away from other dolphins.
Popular	Is constantly sought by other dolphins.	Other dolphins interact with the animal to play and/or swim.
Protective	Prevents harm or potential harm to other dolphins, is alert and watchful.	The animal is attentive and makes a positive surveillance of other dolphins.
(Physically) Slow	Swims very slowly and deliberately, in a relaxed and calmed manner.	The animal does not move or moves passively through the water in a constant style.
Sociable	Actively seeks companionship of other dolphins.	The animal interacts with other dolphins when possible, is actively social with other dolphins.
Solitary	Spends time alone.	Does not approach or interact with other dolphins, when given the opportunity.
Strong	Has sturdiness and muscular strength.	The animal has brute force, displays powerful pectoral and/or fluke slaps, or ability to bite, destroy or sink objects.
Subordinate	Readily gives in to others.	The animal allows other dolphins to play and/or take its objects away.
(Physically) Tense	Shows restraint in its movement and keeps its body rigid.	The animal displays tightness during veterinary checks and/or is not easily persuaded to transfer to the treatment/management facility.

Independent	Does what it wants.	The animal does what it wants, regardless of what it is assigned to do.
Peculiar 1 (abnormal)	Shows peculiar behaviors.	The animal shows specific, characteristic features, or unusual and repetitive habits, like the habit of associating an undesirable behavior to a given cue.
Peculiar 2 (humans)	Interacts very frequently with humans (visitors/trainers).	The animal spends more time with visitors/trainers than with other dolphins or has an excessive interest in interacting with visitors/trainers.
Eccentric	Shows stereotypes or unusual mannerisms.	The animal shows stereotypes or repetitive abnormal behaviors, such as swimming in circles repeatedly, regurgitating, scratching, head bobbing, self-mutilating, chewing facility furniture, biting paint from walls, having comatose episodes, playing with its tongue, etc.
Aggressive	Causes harm or potential harm to other dolphins and/or humans.	The animal exhibits agonistic behaviors, harms, threats, chases, bites or slaps other dolphins and/or humans.
Playful	Participates in play interactions.	The animal usually initiates play interactions with other dolphins and participates when play is solicited.
Adept	Adept at understanding the training exercises.	The animal easily understands the training exercise. The animal displays the correct behavior when requested, adapts its response to the situation.
Slow learner	Its learning ability is gradual.	The animal takes time to learn the exercises or to associate the training reinforcements.
(Mentally) Tense	Has difficulty concentrating and gaining positive reinforcement in timely manner.	The animal has difficulty concentrating during training, is unable to perform behaviors, not due to lack of capacity, but due to lack of concentration and/or takes longer than it should to exhibit the behavior. During the show, the animal misses many rewards.
Methodical	Follows a method.	The animal follows training in a systematic way and performs the exercises methodically.
Extroverted	Active, has many interactions with other dolphins.	The animal moves actively, synchronized and/or gently touching other dolphins, shows positive social behaviors and frequent play interactions.
Friendly (with conspecifics)	Affectionate, non-aggressive with conspecifics.	The animal seeks positive social contact with other dolphins.
Friendly (with humans)	Affectionate, non-aggressive with humans.	The animal seeks positive social contact with humans (visitors/trainers).
Temperamental	Aggressive, moody.	The animal exhibits agonistic behaviors, threatens or harms others, has a predilection for interacting with the object of another dolphin.
Clever	Handles problems in new and creative ways.	The animal is able to solve problems and is a quick learner. Explores, learns and perceives any new changes in its environment.
Careful	Cautious, attentive, alert, watchful, avoids aggressive behaviors.	The animal's actions are done with caution, is interested but hesitant with new situations. The trainer would place the animal between two other dolphins while feeding because he knows that the animal would prevent one dolphin to take the other dolphin's food.

subjects (years of acquaintance: mean ± S.D. = 11.64 ± 5.62). All raters were asked to base their scores on the total length of their relationship with each subject, fill out the questionnaires independently and not discuss their choices or talk about the questionnaire with other raters during the course of the study. In order to calculate test-retest reliabilities, trainers filled out a total of 57 questionnaires in twodifferent rating periods (first: 31 questionnaires in 2013/2014, rated by seven trainers; second: 26 questionnaires in 2015/2017, rated by six trainers). Each trainer rated between four and seven dolphins (mean ± S.D. = 4.75 ± 1.16) and each dolphin was rated by between two and eight trainers (mean ± S.D. = 5.43 ± 2.37). Missing values from questionnaires were replaced with the overall mean rating of the behavioral item across non-missing values (Downey & King, 1998).

Inter-rater reliability between seven trainers for the first period and six trainers for the second period was tested using intraclass correlation coefficients (ICC). ICC (3,1) indicated the reliability for single raters and ICC (3,k) indicated the mean reliability of the ratings per dolphin (Shrout and Fleiss, 1979). Reliability scores were calculated separately for each rating period. Items with ICC (3,k) < .60 and negative values were not included in the subsequent analyses. Internal consistency of the scale was tested using Cronbach's alphas (α) between the adjective items. When the scale was not acceptable (α < .70), unreliable items were removed and α was recalculated. Temporal stabilities were calculated using Cronbach's alpha, ICC (3,1) and ICC (3,k) on the mean rating scores aggregated over the raters within each rating period.

6.4. Results

Dimension reduction

Behavioral measures

The dimension reduction obtained using multiple correspondence analyses (MCA) of the interaction variables (behavior, initiator and receiver), resulted in five factors that accounted for different accumulated variances depending on the study phase: baseline (83%), parturition and post-partum (94%), development of calves (54%) and five dolphins (41%), except for the pre-partum phase in which there were four factors accounting for 91% of the accumulated variance.

The first factor positively grouped affiliative, play and maternal behaviors, and negatively behaviors related to interactions with humans and no interactions. This factor was labeled as *Extraversion*, and was found positively during the baseline and pre-birth phases. The second factor positively grouped affiliative and maternal behaviors, and negatively behaviors related to interactions with humans and no interactions. This factor was labeled as *Agreeableness,* and was found positively during the development of calves and five dolphins phases, and negatively during the pre-birth and the parturition and post-partum phases. The third factor positively grouped sexual and agonistic behaviors, and negatively affiliative and maternal behaviors. This factor was labeled as *Neuroticism* and was found positively during the baseline and the pre-birth phases. The fourth factor positively grouped play behaviors and negatively maternal behaviors, and was found positively during the baseline, parturition and post-partum and the development of calves phases, and negatively during the five dolphins phase. The fifth factor positively grouped maternal behaviors and negatively affiliative behaviors, and was found positively during the parturition and post-partum and the five dolphins phases.

There were weak significant positive and negative correlations between factors inferred for all the study phases ($-.26 \leq r_p \leq .29$; $p < .05$; Table 5), which suggests that there were stabilities of the personality factors across time and contexts. Most correlations were found between the baseline and the development of calves and parturition and post-partum phases, while fewer correlations were found between the pre-partum and the baseline and five dolphins phases.

Adjective ratings

Six items (*methodical*, *insecure*, *affectionate*, *friendly with conspecifics*, *popular* and *permissive;* Table 4) were not included in the factor analyses because they had low inter-rater reliability in both rating periods. Additionally, twelve items (*clever, friendly with humans, peculiar 2, irritable, apprehensive, peculiar 1, physically tense, fearful, sociable, solitary, curious* and *excitable*) were not included in the factor analysis of the second rating period because they also had low inter-rater reliability. After performing the factor analyses, five items (*subordinate, peculiar 1, solitary, opportunistic* and *neurotic*) were not included in the first rating period and two (*physically slow* and *careful*) were not included in the second rating period, because they were not reliable within the inferred factor. Using 23 adjective items, five components were extracted for

Table 5. Pearson correlations between factor scores inferred by multiple correspondence analysis using behavioral measures.

		Baseline					Pre-partum				Parturition and post-partum					Development of calves					Five dolphins				
		F1	F2	F3	F4	F5	F1	F2	F3	F4	F1	F2	F3	F4	F5	F1	F2	F3	F4	F5	F1	F2	F3	F4	F5
Baseline	F1	—	.00	.00	.00	.00	-.03	.04	.02	.03	-.02	-.01	-.10	**.11**	-.08	.03	**.08**	.02	.02	.02	.04	-.15	.10	**-.22**	.07
	F2			.00	.00	.00	.04	-.06	-.02	-.04	**.13**	.05	**.16**	-.09	.08	**.07**	.06	.00	**-.12**	**-.12**	-.03	-.03	.04	.04	-.02
	F3				.00	.00	-.01	.05	.02	-.03	**.15**	.03	-.01	.06	.02	**-.07**	**-.12**	-.03	-.04	.03	.17	-.08	-.09	-.13	-.01
	F4					.00	-.02	.06	.01	.00	-.02	**.15**	.10	-.02	-.05	**-.13**	**-.10**	-.04	**-.07**	-.01	-.13	.15	.11	-.10	.07
	F5						.04	-.05	.05	**.10**	.07	**-.14**	**.14**	.08	-.02	**.15**	**.08**	.01	**-.10**	**-.10**	-.08	**.28**	.11	.09	.02
Pre-partum	F1							.00	.00	.00	**-.14**	.02	-.05	-.05	.04	.02	**.07**	-.02	-.06	-.01	.03	-.01	-.08	.18	.02
	F2								.00	.00	.04	.01	-.06	.03	.06	.02	.01	.01	**.07**	**.10**	-.05	-.10	.10	-.04	-.07
	F3									.00	.01	.03	-.10	.04	.00	.00	.04	-.02	-.05	.02	-.14	-.05	.11	-.16	-.06
	F4										**.10**	**-.10**	**-.16**	.07	-.02	.03	.03	.02	.06	.00	**-.20**	-.01	.15	.05	-.02
Parturition and post-partum	F1											.00	.00	.00	.00	.08	-.04	.00	.00	-.06	**-.26**	.03	.18	.13	.00
	F2												.00	.00	.00	.05	.05	-.01	.03	.02	-.07	**.23**	-.08	.18	.00
	F3													.00	.00	**-.11**	**-.20**	-.07	**-.17**	-.04	-.12	**.22**	-.02	-.10	.00
	F4														.00	**.14**	.07	.06	.05	.00	.00	**.29**	-.09	-.02	.04
	F5															.05	-.10	-.04	-.04	.08	-.01	**-.20**	-.04	-.15	-.01
Development of calves	F1																.00	.00	.00	.00	-.09	.18	.01	.03	.02
	F2																	.00	.00	.00	.03	**-.22**	-.09	.13	-.08
	F3																		.00	.00	-.12	.05	-.05	-.09	-.07
	F4																			.00	-.14	**.23**	.10	-.05	-.12
	F5																				.07	-.14	.00	.10	.07
Five dolphins	F1																					.00	.00	.00	.00
	F2																						.00	.00	.00
	F3																							.00	.00
	F4																								.00
	F5																								—

Note. Significant correlations at the .05 level are in bold. F: factor.

the first rating period, which accounted for 98% of the total accumulated variance, whereas using 14 adjective items, only three factors were inferred for the second rating period, which accounted for 100% of the total accumulated variance (Table 6).

Table 6. Factor loadings obtained using adjective item ratings and using an unweighted least squares factor analyses, for both rating periods.

	Rating period 1					Rating period 2		
Adjective item	F1	F2	F3	F4	F5	F1	F2	F3
Aggressive	**.96**	-.23	.01	.01	.04	**.96**	-.25	.09
Protective	**.88**	-.31	.18	.17	.20	**.72**	.55	-.42
Independent	**.77**	-.03	-.24	.26	-.39	**.86**	-.41	-.31
Strong	**.74**	.55	-.24	.24	-.05	**.95**	-.09	.29
Fearful	**-.90**	.06	-.08	.40	.13	NR	NR	NR
Irritable	**.87**	.28	.12	.34	.16	NR	NR	NR
(Physically) Tense	**.55**	-.15	.11	.48	.47	NR	NR	NR
Subordinate	**-.90**	.05	.40	.17	-.09	**-.89**	-.43	.15
Neurotic	.57	.37	-.10	**.72**	-.02	**.92**	.39	-.08
Opportunistic	.61	.08	-.10	**.76**	-.03	**.77**	.11	-.63
Extroverted	.19	**.96**	.16	.02	.11	-.05	**.99**	-.16
Active	-.07	**.83**	.36	.41	.08	.11	**.91**	-.39
Adept	-.25	**.76**	.26	.40	-.18	-.01	**.75**	-.66
Curious	-.11	**.97**	.12	-.15	-.09	NR	NR	NR
Clever	-.24	**.79**	.18	.39	-.35	NR	NR	NR
Physically (Slow)	-.29	**-.63**	-.56	-.37	-.23	-.11	**-.91**	.39
Playful	.08	.36	**.90**	-.09	-.21	-.56	**.68**	.48
Sociable	-.16	.21	**.84**	.38	-.20	NR	NR	NR
Friendly (with humans)	-.06	.53	**.79**	-.19	.22	NR	NR	NR
Excitable	.47	-.20	**-.76**	-.24	.28	NR	NR	NR
Peculiar 2 (humans)	.41	.58	**.66**	.17	-.17	NR	NR	NR
Eccentric	-.08	-.09	-.31	**-.91**	-.21	-.39	-.16	**.91**
Slow learner	.21	-.64	.04	**-.74**	.03	.15	-.29	**.94**
(Mentally) Tense	.20	-.66	-.16	**-.67**	-.14	.07	-.23	**.97**
Apprehensive	-.07	.01	-.10	.07	**.99**	NR	NR	NR
Careful	.19	-.08	-.24	.60	**.66**	.28	.61	**-.74**

Note. Salient loadings are indicated in bold. Two items (*solitary* and *peculiar 1*) are not shown because they were not reliable within the inferred factor for either rating period. NR: The inter-rater consistency was not reliable and therefore the items were not included in the subsequent analyses, F: factor.

The first factor for both rating periods positively loaded the items: *aggressive*, *protective*, *independent* and *strong*. The first factor for the first period (α = .76) also positively loaded: *irritable*, *physically tense*, and negatively: *fearful* and *subordinate*; however, the latter item was not reliable within the factor. The first factor for the second

period (α = .81) also positively loaded: *neurotic*, *opportunistic* and negatively: *subordinate*. The items loaded in the first factor were related to dominant and agonistic interactions and it was therefore labeled as *Neuroticism*. The second factor for both rating periods positively loaded items: *extroverted*, *active* and *adept*. The second factor for the first period (α = .73) also positively loaded: *curious* and *clever*, and negatively: *physically slow*. The second factor for the second period (α = .89) also positively loaded: *playful* and negatively: *physically slow*; however, the latter item was not reliable within the factor. The items loaded in the second factor were mostly related to sociable behaviors and was therefore labeled as *Extraversion*. The third factor for the first period (α = .67) positively loaded: *playful*, *sociable*, *friendly with humans*, *peculiar 2* (with humans) and negatively: *excitable*. Items loaded in this factor were mainly related to social behaviors and interactions with humans. The third factor for the second period (α = .96) positively loaded: *eccentric*, *slow learner* and *mentally tense* and negatively: *careful*; however, the latter item was not reliable within the factor. The fourth factor for the first period (α = .89) negatively loaded: *eccentric*, *slow learner* and *mentally tense*, and positively: *neurotic* and *opportunistic*; however, the latter two items were not reliable within this factor. The fifth factor for the first period (α = .86) positively loaded items: *apprehensive* and *careful*, and was labeled as *Conscientiousness*.

Correlations showed a strong statistical concordance of factors between both rating periods (Table 7). The second factor showed high significant positive correlations between both periods, as did the third factor of the first rating period with the second factor of the second period, while the fourth factor of the first rating period showed a high significant negative correlation with the third factor of the second period, which suggests that both factors represent opposite personality profiles. Moreover, factor two from the first period showed moderate significant positive correlations with factors three and four from the same period.

Interrater reliabilities

Six adjective items had ICC (3,k) < .60 during the first rating period. The reliabilities for the remaining 28 items ranged from .18 to .75 with a mean reliability of .43 for ICC (3,1), and from .61 to .96 with a mean reliability of .82 for ICC (3,k). During the second rating period, on the other hand, 16 items had ICC (3,k) < .60 and two items had negative ICC values. The reliabilities for the remaining 16 items ranged from .20 to .56,

with a mean reliability of .34 for ICC (3,1) and from .60 to .87 with a mean reliability of .74 for ICC (3,k; Table 8).

Temporal and scale reliabilities

Cronbach's alphas indicated good internal consistency for the overall scale (α = .73) as well as for the second rating period (α = .83) and for the first rating period (α = .71), excluding five adjective items. The temporal stability of the adjective items was high, as the mean stability of the study subjects was α = .67, and ranged from .40 to .60 with a mean reliability of .51 for ICC (3,1), and from .57 to .75 with a mean reliability of .67 for ICC (3,k).

Correspondence between behavioral measures and adjective ratings

There were high significant correlations ($-.62 \leq r_p \leq .66$; $p < .05$) between component scores inferred with both assessments (Table 9). The fifth factor inferred for the first rating period showed positive significant correlations with the first and second factors inferred for the five dolphins phase, while the first factor inferred for the second rating period had a negative correlation with the first factor inferred for the five dolphins phase. Moreover, the three factors inferred for the second rating period had positive and negative correlations with three factors inferred in the pre-partum phase.

Table 7. Pearson correlations (r_p) between factors. The two rating periods of this study were considered.

		Rating period 1					Rating period 2		
		F1	F2	F3	F4	F5	F1	F2	F3
Rating period 1	F1	—	-.21	-.13	.06	.08	.35	-.28	.12
	F2			**.49***	**.45***	-.16	-.05	**.75****	-.54
	F3				.26	-.17	-.40	**.66***	-.18
	F4					.22	.26	.33	**-.86*****
	F5						-.11	.06	-.20
Rating period 2	F1							-.11	-.36
	F2								-.49
	F3								—

Note. Correlations significant at the: * .05, **.01 and *** .001 level, are indicated in bold.

F: factor.

Table 8. Interrater reliabilities of adjective items for both rating periods.

	Rating period 1		Rating period 2	
Adjective Item	ICC (3,1)	ICC (3,k)	ICC (3,1)	ICC (3,k)
Independent	.75	**.96**	.38	**.78**
Active	.71	**.95**	.27	**.69**
Clever	.65	**.93**	.10	.39
Extroverted	.60	**.91**	.37	**.78**
Friendly (with humans)	.58	**.91**	.17	.55
Curious	.58	**.91**	-.04	-.31
Strong	.55	**.90**	.37	**.78**
Subordinate	.56	**.90**	.20	**.60**
Temperamental	.52	**.88**	.46	**.83**
Opportunistic	.50	**.88**	.41	**.81**
(Physically) Slow	.51	**.88**	.27	**.69**
(Mentally) Tense	.48	**.87**	.28	**.66**
Playful	.49	**.87**	.33	**.75**
Eccentric	.49	**.87**	.22	**.63**
Careful	.39	**.82**	.28	**.70**
Peculiar 2 (humans)	.39	**.81**	.06	.27
Protective	.36	**.79**	.26	**.67**
Irritable	.33	**.78**	.11	.42
Aggressive	.33	**.78**	.31	**.73**
Apprehensive	.33	**.78**	.05	.20
Adept	.31	**.76**	.56	**.87**
Peculiar 1 (abnormal)	.31	**.76**	.17	.55
Slow learner	.30	**.75**	.46	**.81**
Excitable	.29	**.74**	-.08	-.80
(Physically) Tense	.25	**.70**	.08	.33
Sociable	.22	**.67**	.08	.35
Fearful	.21	**.64**	.14	.49
Solitary	.18	**.61**	.05	.24
Methodical	.16	.58	.06	.27
Affectionate	.11	.47	.07	.31
Insecure	.10	.45	.10	.41
Friendly (with conspecifics)	.10	.45	.16	.54
Popular	.09	.40	.02	.09
Permissive	.02	.12	.01	.06

Note. Intraclass correlation coefficients for the mean scores of raters: ICC (3,k) ≥ .60, are indicated in bold.

Table 9. Pearson correlations (r_p) between factors inferred with adjective ratings and behavioral measures.

		Rating period 1					Rating period 2		
Study phase		F1	F2	F3	F4	F5	F1	F2	F3
Baseline	F1	.07	-.37	-.20	-.30	-.16	.52	-.50	.18
	F2	.38	-.13	-.23	-.12	-.35	.45	-.44	-.04
	F3	.21	-.17	-.28	-.15	-.31	.52	-.49	-.06
	F4	-.14	-.08	.06	-.21	-.09	.04	-.03	.26
	F5	-.19	-.06	.06	-.06	.21	-.40	.22	.41
Pre-partum	F1	.13	-.34	-.26	-.27	.27	.52	**-.55***	.41
	F2	.20	-.28	-.41	-.15	.11	.48	**-.59***	.41
	F3	.11	-.03	-.18	.10	-.14	.24	.06	-.32
	F4	.21	.10	-.03	.28	-.07	**.66***	.12	**-.62***
Parturition and post-partum	F1	.20	.09	-.01	.01	-.35	.19	-.40	-.05
	F2	.26	-.08	-.15	.12	-.17	.19	-.40	-.05
	F3	-.21	.01	.17	-.18	.09	-.19	.40	.05
	F4	-.26	-.06	.04	-.16	.29	-.19	.40	.05
	F5	.27	.04	-.16	.11	-.23	.19	-.40	-.05
Development of calves	F1	-.01	.03	.26	.11	.36	-.30	.32	-.20
	F2	.10	-.42	-.39	-.24	-.24	.43	-.44	.24
	F3	.20	-.01	.23	.21	-.14	.11	-.18	-.06
	F4	.16	.35	.39	.22	.32	-.40	.22	-.11
	F5	-.02	-.21	-.35	-.26	-.03	.26	-.08	.19
Five dolphins	F1	-.15	-.09	-.19	-.01	**.66****	**-.59***	-.09	-.11
	F2	.01	-.25	-.19	-.04	**.63****	-.18	-.40	-.02
	F3	-.10	.20	.21	.11	.20	.38	.46	.06
	F4	.20	.14	.16	.00	-.23	.43	.40	.11
	F5	-.17	.00	.36	.17	-.15	.30	.48	.12

Note. Correlations significant at the: * .05 and **.01 level, are indicated in bold. F: factor.

6.5. Discussion

The main results that this study provided was that captive bottlenose dolphins presented a structured personality, characterized by *Extraversion*, *Conscientiousness* and *Neuroticism*, using the Five-factor model (FFM) of personality framework. Also, the correspondence between the two methodologies used to assess bottlenose dolphin personality in this study (that is, behavioral measures and adjective rating items), allows us to validate the behavioral measures assessment, for this group of dolphins. However, *Agreeableness* was only found through behavioral measures, while *Openness to experience* was only slightly represented in the adjective ratings assessment, within the *Extraversion* factor. Validating personality assessment methodologies helps identifying animal personality more accurately, which provides information to predict individual

behaviors and identify individual needs, and this is useful for management, welfare and conservation endeavors.

Different personality factors were found in this study, concurring with previous studies done in this species by Highfill and Kuczaj (2007), Díaz (2020) and Morton et al. (2021). Five and three factors were identified using the adjective ratings assessment, while five and four of them were identified using the behavioral measures assessment, which concurs with studies done previously in Delphinidae (Moreno et al., 2017; Úbeda et al., 2019; Morton et al., 2021), who also found four personality factors. Moreover, the factors *Extraversion*, *Neuroticism* and *Agreeableness* were clearly identified using behavioral measures. This concurs with the conclusions drawn by Gosling and John (1999) in their inter-specific review of personality profiles, where they found these three factors across a variety of taxa, and suggested that such homologous traits had a foundation on biological mechanisms.

The factor identified as *Extraversion* in this study had a positive correlation with *play, affiliative* and *maternal* behaviors, and items: *extroverted, active, adept, curious, clever* and *playful*; while having a negative correlation with *interactions with humans, no interactions* (with conspecifics), and the item: *physically slow*, which are behaviors and items that relate to sociable and bold individuals. This factor grouped similar items to the ones Úbeda et al. (2019) found in the factor they also denominated *Extraversion*, which was composed by the items *playful, active, gregarious, social* and *cheerful*. Evans et al. (2021) found that free ranging bottlenose dolphins show four social traits (time spent in large groups, time spent alone, average number of associates and average number of same-sex associates) that were stable individually over three decades, from infancy to late adulthood. Strong intra-individual relationships between such social traits suggest wild dolphins have a complex sociable behavioral syndrome, similar to *Extraversion*. Díaz (2020) also found that bold animals showed stronger associations in the social network when he assessed the personality of free-ranging bottlenose dolphins using behavioral responses to novelty and social organization. The adjectives *curious* and *clever*, which were grouped within this factor, characterize the factor *Openness to experience*, which is why this factor was only represented within the factor *Extraversion.* This concurs with findings by Moreno et al. (2017), who found that *Openness to experience* did not significantly predict dolphin bond formation, suggesting that it is not important in dolphin interactions and social structure, but contrasts with findings by Morton et al. (2021), who

identified a factor as *Openness*, which was characterized by the items: *active* and *investigate the environment*.

The factor identified as *Agreeableness* in this study had positive correlations with *affiliative* and *maternal* behaviors, while having negative correlations with *interactions with humans* and *no interactions* (with conspecifics). This factor was similar to the one Moreno et al. (2017) identified as *Affiliative-Support*, which was also composed by *affiliative, synchronous, tolerant* and *supportive* behaviors. Even though we identified the factors *Extraversion* and *Agreeableness* as mutually independent, they were in fact very similar as they both grouped positively affiliative and maternal behaviors and negatively interactions with humans and no interactions with conspecifics. The latter two behaviors suggest that dolphins with lower levels of *Extraversion* and *Agreeableness* behave more solitarily. Our results are similar to findings by Morton et al. (2021), who grouped traits related to *Extraversion* and *Agreeableness* into one factor identified as *Sociability.*

Another factor found in this study had similar traits to those that characterize *Conscientiousness,* which in this study was related to infant care, as it was comprised positively by *maternal* behaviors and the items: *apprehensive* and *careful,* and negatively by *affiliative* behaviors. This contrasts with findings by Úbeda et al. (2019), who grouped traits related to *Conscientiousness* and *Agreeableness* into one factor they identified as *Conscien-agreeableness*, which was composed by the items: *patient, predictable, gentle, generous* and *peaceable*. Additionally, Úbeda et al. (2019) identified another factor as *Careful,* composed by the items: *prudent, responsible, organized*, *helpful, sympathetic* and *sensitive*, which was not similar to the factor we identified as *Conscientiousness* either. Even though traits related to *Conscientiousness* have been previously described in dolphins (Moreno et al., 2017; Lilley et al., 2018; Úbeda et al., 2019), our results contrast with findings by Morton et al. (2021), who did not find this factor in bottlenose dolphins. Moreover, Gosling and John (1999) found that chimpanzees were the only non-human species to have a separate *Conscientiousness* domain, and suggested that this dimension could have evolved recently in the Homininae subfamily. Further research must be made in order to clarify the evolutionary extent of this factor in dolphins.

The factor identified as *Neuroticism* in this study had a positive association with sexual and agonistic behaviors and the items: *aggressive, protective, independent, strong, irritable, physically tense, neurotic* and *opportunistic;* and a negative association with affiliative and maternal behaviors and the items: *fearful* and *subordinate.* This factor was not similar to the domain Moreno et al. (2017) denominated “Conflict-Play” (composed

by *conflict* and *play* interactions), due to absence of *play* behaviors in the same profile, but was similar to the domain Morton et al. (2021) defined as *Disagreeableness,* which was characterized by the items: *aggressive*, *jealous*, *despotic* and *obstinate*. In this study we identified another factor which grouped both positively and negatively the items: *eccentric*, *slow learner* and *mentally tense*, adjectives which could also be related to the *Neuroticism* factor. We also identified a fifth factor which had positive associations with play behaviors and the items: *playful, sociable, friendly with humans* and *peculiar 2* (with humans), and negative associations with maternal behaviors and the item: *excitable*; items which are mostly associated with interactions with both humans and conspecifics.

Personality factors inferred in our study were significantly stable across time and context, which concurs with findings by Hill et al. (2019), who found stable behavioral differences in beluga whales, but no significant clusters that defined personality factors. Factor scores inferred with both assessments showed high significant correlations and, moreover, grouped items were similar to clustered behavioral measures. Our findings concur with previous studies done in great apes by Uher and Asendorpf (2008), who found correlations between behavioral measures and adjective ratings. Even though the assessment done with adjective ratings covered more aspects of the personality structure than observed behaviors of interactions, both assessments give useful information and complement each other when it comes to identify personality factors.

Future research to understand the significant correspondence between observed behaviors and personality traits of dolphins could be done by using the same assessment tool in different facilities, in order to study how different social, environmental and housing conditions modulate personality profiles.

Limitations of this study

This study explored a suitable design to validate personality structure assessments in animals, but further research, with larger samples, is needed in order to clarify the direct link between behavioral traits and personality adjective items. There are limitations or difficulties in assessing personality profiles using either assessment. First of all, they are both time consuming and require expert observers and trainers to collect data and not all experts and trainers are available to fill out ethograms or rating surveys. For this reason, we suggest to restructure the instrument used in this study, with fewer adjectives, such as the ones that were reliable within the factors together with the addition of new items that characterize the factors Openness to experience, Agreeableness and Conscientiousness,

in order to examine if they provide a better representation of these factors. Moreover, behavioral studies to further explore *Conscientiousness* and *Openness to experience* could be done including solitary behaviors, such as *exploratory* (that characterizes *Openness to experience*) and *alert, attentive, vigilant* (that characterize *Conscientiousness*), which can be observed using instantaneous scan samplings.

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DISCUSIÓN GENERAL

7. DISCUSIÓN GENERAL

El conocimiento del comportamiento y la personalidad es relevante para garantizar el éxito reproductivo y la cría en programas de conservación *ex situ* de diferentes especies de la familia Delphinidae catalogadas en peligro de extinción, como el tucuxi (*Sotalia fluviatilis*), el delfín giboso índico (*Sousa plumbea*) y el delfín de Héctor (*Cephalorhynchus hectori*), o en peligro crítico, como el delfín giboso atlántico (*Sousa teuszii*), el delfín del río Irawadi (*Orcaella brevirostris*), así como otras especies de odontocetos, como la vaquita (*Phocoena sinus*; IUCN-CSG, 2023). Ante la baja efectividad de los programa de conservación *in situ*, investigadores y conservacionistas han sugerido que los programas de reproducción *ex situ* son las únicas soluciones potenciales para conservar estas especies amenazadas (Jaramillo-Legorreta et al., 2007).

No obstante es difícil mantener en cautividad a determinadas especies de odontocetos en buen estado de salud durante largos periodos de tiempo, como las marsopas marinas de la familia Phocoenidae (Jaramillo-Legorreta et al., 2007). Las vaquitas, por ejemplo, mueren al ser capturadas porque sufren lo que se conoce como "miopatía de captura", un estrés mortal si no son liberadas, pues los individuos capturados tienen niveles de cortisol en la sangre 10 veces más altos que los de delfines mulares que han sido capturados y liberados para hacer evaluaciones de salud (Rojas-Bracho et al., 2019). Las vaquitas en cautividad tienen una tasa de mortalidad inicial alta y dificultad para que se reproduzcan en estas condiciones. Además, algunos individuos nacidos en cautividad no tendrían los comportamientos necesarios para sobrevivir en libertad y tendrían una tasa de supervivencia baja al ser liberados a la naturaleza (Jaramillo-Legorreta et al., 2007). Es por esto que se promueven estudios de comportamiento y personalidad en odontocetos cautivos, para incrementar el conocimiento sobre los requerimientos de bienestar que permiten aumentar las tasas de éxito de reproducción, cría y supervivencia en cautividad (Rojas-Bracho et al., 2019).

En esta tesis investigamos el comportamiento solitario y social, junto con los rasgos de personalidad, de un grupo de delfines mulares cautivos en el Zoo de Barcelona, con el objeto de entender mejor en qué modo afectan, a nivel individual, los cambios sociales y ambientales que se producen en sus instalaciones (ya sea como consecuencia del propio manejo o a causa de eventos biológicos como la cría). Esta información es necesaria para un adecuado manejo y cuidado de los individuos que están bajo el cuidado

profesional de humanos, con el fin de favorecer los esfuerzos de conservación *ex situ* que deben garantizar el bienestar de los mamíferos marinos cautivos.

El patrón de actividad diaria de los delfines en diferentes fases de estudio estuvo influenciado por factores como el grupo de edad (cría, juvenil, subadulto y adulto), origen del sujeto (cautividad o libertad), grado de proximidad con otros individuos, y las interacciones sociales. Esto coincide con los resultados obtenidos por Huettner et al. (2021), que también encontraron que el patrón de actividad diaria de un grupo de delfines mulares estuvo influenciado por factores individuales, como la edad, y factores externos, como la composición de grupo. También encontramos que los comportamientos solitarios difirieron con respecto al grupo de edad y el origen; así los individuos nacidos en libertad mostraron una mayor frecuencia (porcentaje de ocurrencia) en respiración y nado lento solitario. No obstante, los tres sujetos que mostraron esta pauta fueron hembras adultas nacidas en libertad que estuvieron embarazadas durante parte del estudio. Dicha pauta, una –elevada frecuencia de respiración y nado lento solitario– es, común en delfines gestantes porque necesitan tranquilidad y descanso (Tavolga & Essapian, 1957; Tizzi et al., 2010; Williams et al., 1992).

Puesto que algunos comportamientos se mantuvieron constantes a lo largo de los diferentes contextos, se procedió a investigar los rasgos de personalidad que caracterizaban a los individuos, lo cual se realizó a partir de la tipología de las interacciones sociales. En este apartado de la tesis se hizo una exploración de los comportamientos de manera dinámica, ya que se detectaron patrones de secuencias de interacciones a lo largo del tiempo. El estudio de personalidad se centró en el comportamiento social de dos hembras del grupo, en cuatro fases comprendidas desde el quinto mes de gestación hasta el séptimo mes de crianza, un periodo vital de gran importancia para los programas de conservación *ex situ*. Los registros de conducta se analizaron utilizando dos metodologías: 1) “multivariate T-pattern analysis” (análisis de patrones temporales multivariado), y 2) “multiple correspondence analysis” (análisis de reducción de dimensiones), para determinar cuál de las dos detectaba mejor los rasgos de personalidad de los individuos. Se encontraron diferencias individuales de las estructuras comportamentales entre los sujetos de estudio al comparar ambas metodologías. En cambio, no se encontró una estabilidad de las estructuras de comportamiento a lo largo del tiempo con los patrones temporales, mientras que sí se encontró una estabilidad intraindividual de los perfiles de personalidad a través de diferentes contextos con la reducción de dimensión. Es por esta razón por lo que se propone que la metodología más

efectiva para detectar rasgos de personalidad es la reducción de dimensiones, porque agrupa las interacciones que definen los perfiles de personalidad.

A partir de aquí, se procedió a averiguar con qué tipo de datos se detectaban mejor los factores de personalidad del grupo de delfines. Para esto, se analizaron dos tipos de datos: 1) observaciones directas objetivas de interacciones sociales ("codings" o codificaciones), y 2) calificaciones indirectas subjetivas por parte de entrenadores y cuidadores que conocían muy bien a los sujetos de estudio ("ratings" o calificaciones). Una vez identificados los rasgos de personalidad, se compararon las dos metodologías ("codings" y "ratings") para saber cuál de ellas podía ser más efectiva. Se encontró que las dos metodologías utilizadas son válidas para describir los rasgos de personalidad y que además se correlacionaron entre sí, lo cual sugiere que se complementan adecuadamente. Esto coincide con trabajos que se han realizado en una variedad de animales, sobretodo en perros (Barnard et al., 2016), primates (Carter et al., 2012; Eckardt et al., 2014; Padrell et al., 2020), felinos (Gartner & Powell, 2012), elefantes (Horback et al., 2013), entre otras especies. Sin embargo, a día de hoy, ningún trabajo ha investigado la relación entre medidas de comportamiento y calificaciones de adjetivos de rasgos de personalidad en odontocetos. Cada metodología tiene sus ventajas y desventajas, y se pueden utilizar dependiendo de las condiciones de trabajo. Por ejemplo, una desventaja que tiene la metodología de calificaciones es que la personalidad del calificador puede influir en la relación con el sujeto de estudio y su perspectiva personal, y esto puede afectar la evaluación de la personalidad del animal (Phillips & Peck, 2007). Es por esto que la evaluación por medio de registros sistemáticos del comportamiento observado ("codings") es un buen complemento para la evaluación general de la personalidad en los animales.

En esta tesis se identificaron cuatro de los cinco factores de personalidad propuestos por el Modelo de los Cinco Factores (FFM): *Agradable, Extroversión*, *Neuroticismo* y *Cuidadoso*. El factor *Agradable* está compuesto positivamente por iniciar/recibir comportamientos afiliativos, maternales y lúdicos; y negativamente por interacciones con humanos, no interacciones y recibir comportamientos agonísticos y sexuales. *Extroversión* se caracteriza por comportamientos sociables, ya que está compuesto positivamente por recibir comportamientos lúdicos, afiliativos, maternales y agonísticos, y los adjetivos: *extrovertido, activo, hábil, curioso, listo* y *juguetón*. Mientras que está compuesto negativamente por iniciar interacciones con humanos, no interacciones y el adjetivo: *físicamente lento*. *Neuroticismo* se caracteriza por

interacciones agonísticas y de dominancia ya que está compuesto positivamente por iniciar comportamientos agonísticos y sexuales, y por los adjetivos: *agresivo, protector, independiente, fuerte, irritable, físicamente tenso, neurótico* y *oportunista*. Mientras que está compuesto negativamente por recibir comportamientos afiliativos, maternales, sexuales y agonísticos, y no interacciones, y los adjetivos: *miedoso* y *subordinado*. El factor *Cuidadoso* (o *Concienzudo*) está compuesto positivamente por iniciar/recibir comportamientos maternales y los adjetivos: *cuidadoso* y *aprensivo*; y negativamente por recibir comportamientos lúdicos. El factor *Cuidadoso* se asocia positivamente con *Agradable*, mientras que *Agradable* se asocia negativamente con *Neuroticismo*.

Se observó que Nereida iniciaba más episodios afiliativos y lúdicos sociales, e iniciaba y recibía episodios maternos, mientras recibía más episodios agonísticos, lo cual sugiere que esta hembra era maternal y por lo tanto tenía un nivel alto de *Cuidadosa*, *Agradable* y de *Extroversión*. Anak por el contrario, recibía más episodios afiliativos y lúdicos sociales, e iniciaba más interacciones con humanos e interacciones agonísticas, lo cual sugiere que esta hembra era más agresiva y solitaria y tenía un perfil alto de *Neuroticismo* y bajo de *Extroversión*. El factor común en ambas hembras, en todas la fases de estudio, fue el de *Extroversión*.

Los perfiles de personalidad de las hembras estudiadas fueron diferentes durante la fase pre-natal, porque se obtuvieron menos correlaciones con los perfiles de personalidad de las otras fases de estudio. En la fase pre-natal, las hembras presentaron eventos de no interacción y de interacción con humanos, que sugiere que eran solitarias y tenían un nivel bajo de *Extroversión*. A pesar que en esta fase las hembras eran solitarias, los patrones temporales significativos detectados fueron más complejos en ambas hembras, caracterizándose con patrones de interacciones más largos y variados que en las otras fases. Esto puede deberse a los cambios fisiológicos, hormonales y metabólicos, que pueden afectar los requerimientos energéticos, el comportamiento, la habilidad de moverse libremente, la reducción de la velocidad y la agilidad debido al aumento de peso de la hembra embarazada (Tizzi et al., 2010; Noren et al., 2011).

Por otro lado, las relaciones entre las dos hembras mejoraron con la presencia de las crías, porque en la fase de parto y post-parto el nado próximo fue común y la interacción con visitantes disminuyó, lo cual indica que ambas madres estaban pendientes de sus crías. Así mismo, durante la fase de desarrollo de crías se registraron frecuencias bajas de respiración, sugiriendo un bajo nivel de estrés, y aumento de frecuencias de interacciones afiliativas, maternales e incremento de las interacciones con el público.

Ambas hembras presentaron un nivel bajo de *Cuidadosa* durante esta fase de desarrollo de crías, aunque Nereida siguió siendo maternal y juguetona con las crías, mientras Anak volvió a ser solitaria. En la fase siguiente, cuando entró otra hembra adulta al grupo, Anak presentó un nivel bajo de *Cuidadosa*, y se volvió menos vigilante y más permisiva, mientras que no hay evidencia para decir que Nereida se volvió menos vigilante cuando entró otra hembra adulta al grupo.

A partir de los resultados de esta tesis, y teniendo en cuenta los rasgos de personalidad de los individuos estudiados desde diferentes perspectivas, se pueden proponer diferentes estrategias para mejorar su bienestar bajo el cuidado profesional de humanos. Por ejemplo, Anak tiene un nivel alto de *Extroversión* y *Neuroticismo*, sin embargo, su nivel de *Neuroticismo* disminuye cuando entra otra hembra adulta al grupo. Por otro lado, los perfiles de personalidad de Nereida no variaron cuando otra hembra fue añadida al grupo, ya que tuvo un nivel alto de *Agradable* y *Extroversión*, con y sin la presencia de una tercera hembra adulta en el grupo. Según esto, se podrá saber a qué individuo le afectará más los cambios en la composición del grupo, ya que a una hembra adulta con un perfil de *Neuroticismo* le afecta más los cambios que a una hembra adulta con un perfil de *Agradable*. También se encontró que tener a una hembra embarazada con un perfil de *Neuroticismo* compartiendo la instalación con otra hembra embarazada con un perfil de *Agradable* no garantiza su bienestar. En cambio, conviene que una hembra embarazada con un perfil de *Neuroticismo* esté agrupada con otras dos hembras y a ser posible, que haya presencia de sus crías. En consecuencia, mantener en cautividad composiciones grupales similares a las que se encuentran en la naturaleza (por ejemplo, grupos de hembras con sus crías), es garantía de bienestar para los individuos.

Apertura a la experiencia fue el único, de los cinco perfiles propuestos por el FFM, que no fue claramente detectado en este estudio, posiblemente porque los datos de comportamiento social registrados no describen los rasgos que componen este factor de personalidad, como la curiosidad o la invención. Los muestreos que incluyen elementos de enriquecimiento ambiental y manipulación de objetos podrían servir para estudiar aspectos como la curiosidad, un rasgo que caracteriza la *Apertura a la experiencia*. La curiosidad y la exploración también podrían medirse colocando alimentos u objetos novedosos, y estudiando cómo el animal interactúa con la novedad, por ejemplo, midiendo las latencias para tocar alimentos u objetos novedosos versus no novedosos, las duraciones con la pieza novedosa o número de piezas que son rechazadas (Uher & Asendorpf, 2008). Este factor de personalidad también se podría estudiar con

experimentos cognitivos o de resolución de problemas, que permiten averiguar si los animales son curiosos, creativos, imaginativos o listos (rasgos que caracterizan *Apertura a la experiencia*). Por ejemplo, Bagley et al. (2020) encontraron que los delfines que participaban en interacciones solitarias con un objeto de un experimento cooperativo de resolución de problemas, eran curiosos y juguetones, mientras que los delfines que participaban en interacciones sociales con el objeto experimental mostraban comportamientos afiliativos. Lilley et al. (2018) también encontraron un factor de personalidad relacionado con la Apertura a la experiencia, en un experimento donde probaban la respuesta a estímulos. Dicho factor estaba compuesto positivamente por curiosidad, observador, inteligente, creativo, excitable y exploratorio; y negativamente por simple. Para detectar el factor Apertura a la experiencia utilizando el método de calificaciones, se pueden agregar adjetivos que describan el factor en la herramienta utilizada para realizar los cuestionarios, como por ejemplo: creativo, imaginativo, observador, exploratorio y simple.

Para que los resultados de esta tesis se puedan aplicar en futuros estudios de personalidad en mamíferos marinos, se propone acortar el cuestionario y que sea rellenado por más calificadores, dejando los adjetivos que son representativos de los factores de personalidad y agregando otros que representen el quinto perfil. Con esta herramienta de evaluación validada se pueden inferir perfiles de personalidad de una manera rápida, fiable y sistemática, generando un conocimiento que ayude a la toma de decisiones que tienen implicaciones en el bienestar de los animales cautivos al tener en cuenta sus rasgos de personalidad. Con esta información, los técnicos de centros zoológicos pueden saber qué individuos son más adecuados para ser trasladados a otras instalaciones, para participar en sesiones de entrenamiento o para participar en actividades de interacción con humanos. Por ejemplo, los delfines juguetones se adaptarían mejor a grupos grandes, porque son extrovertidos y amigables con sus congéneres, mientras que son menos solitarios y tienen tendencia interaccionar menos con el público. Estos individuos también son activos, listos y curiosos, por lo que es más probable que participen en sesiones de entrenamiento, experimentos cognitivos y programas de enriquecimiento.

Se propone extender la investigación de comportamiento y personalidad de delfines mulares a diferentes centros zoológicos del mundo para obtener un conocimiento más amplio y poder hacer comparaciones de las estructuras de comportamiento y personalidad en diferentes condiciones de estabulación, ambientales y sociales. Aunque

obtener la colaboración de diferentes centros zoológicos es un reto mayor que trabajar solo con un centro zoológico, puede llegar a tomar mucho tiempo y ser frustrante (Hosey et al. 2009). En esta tesis, por ejemplo, tuvimos dificultades a la hora de recolectar los datos de las encuestas enviadas a diferentes centros zoológicos, debido a que algunas instituciones se negaron a colaborar con el estudio o no contestaron a la petición de colaboración, ya sea porque no tenían tiempo para rellenar las encuestas o porque consideraban que los datos a rellenar era información confidencial del centro.

Una vez determinada la personalidad de los animales, se puede hacer una diversidad de estudios para buscar la relación directa entre personalidad y otros parámetros de importancia para garantizar el bienestar animal. Por ejemplo, se puede comparar la estructura de personalidad con índices de evaluación de bienestar y cuestionarios subjetivos de bienestar (Clegg et al., 2015; Robinson et al., 2017, 2021; Schaefer & Steklis, 2014; Úbeda et al., 2019; Gartner, 2014), para encontrar la relación entre personalidad y bienestar. También se pueden estudiar otras variables fisiológicas o endocrinológicas, como por ejemplo relacionar personalidades con niveles de cortisol, para ver qué perfiles de personalidad son más propensos a presentar cuadros de estrés. Así mismo, se pueden hacer estudios para relacionar personalidad con salud (Robinson et al., 2018), genética y heredabilidad (Weiss et al., 2006; Latzman et al., 2015), cognición (Padrell et al., 2020; Barrett & Benson-Amram, 2021) y comunicación (Sørensen et al., 2023), entre otros indicadores de bienestar. Un conocimiento más completo de la personalidad y su relación con otros parámetros podría ser una herramienta útil para mejorar las condiciones de estabulación, la gestión y el bienestar de los animales en cautividad, y como consecuencia, garantizar el éxito de programas de conservación *ex situ* que tienen un impacto en la supervivencia de las especies.

CONCLUSIONES

8. CONCLUSIONES

1. En el estudio de patrones de actividad (Capítulo 1), se encontró que las diferencias en las frecuencias de los comportamientos solitarios y sociales en las distintas fases de estudio planteadas en esta tesis, demuestran que el comportamiento de los delfines mulares en cautividad es mayormente influenciado por factores sociales, que no ambientales. Encontrar que los delfines mulares se comportan diferente según la composición grupal a la cual pertenecen, destaca la importancia de tener en cuenta las condiciones sociales para garantizar el bienestar de estos animales en cautividad. En conclusión, las composiciones grupales que garantizan el bienestar de los individuos de delfines mulares en cautividad, son aquellas similares a las que se encuentran en la naturaleza.

2. En el estudio de patrones temporales (T-patterns; Capitulo 2), se encontró que los rasgos de personalidad detectados por medio de T-patterns no fueron estables entre contextos, mientras que los rasgos de personalidad detectados con la reducción de dimensiones si fueron estables y, además, agrupados para crear factores de personalidad, por lo cual se puede concluir que esta última es una metodología más efectiva para evaluar perfiles de personalidad.

3. A través del estudio de evaluación de la personalidad utilizando dos metodologías de evaluación (“codings” y “ratings”; Capítulo 3), se identificaron los mismos cuatro perfiles de personalidad de los delfines mulares. Además, la comparativa de ambas metodologías permitió relacionar los adjetivos que describen rasgos de personalidad (“ratings”) con comportamientos observados (“codings”), por lo que se concluye que se puede evaluar la personalidad de delfines cautivos con certeza y rapidez mediante encuestas (“ratings”), lo cual es conveniente a la hora de tomar decisiones de manejo y bienestar, basadas en la personalidad de los individuos.

4. En los dos estudios de personalidad (Capítulos 2 y 3), se encontraron diferencias individuales en los rasgos de personalidad entre los sujetos de estudio y estabilidad intra-individual a lo largo de los diferentes contextos, lo cual permite concluir que los sujetos de estudio tenían diferentes personalidades individuales que se mantenían a través del tiempo.

5. En el estudio de patrones de actividad y los dos estudios de personalidad (Capítulos 1-3), se encontró que los delfines mulares exhiben comportamientos distintos, teniendo las mismas características de sexo, grupo de edad, origen (cautividad o libertad), estado reproductor, y viviendo bajo las mismas condiciones ambientales y agrupaciones sociales. Esto demuestra que los individuos responden de maneras diferentes a las mismas experiencias, por lo cual es útil tener conocimiento de la personalidad de los individuos, para predecir sus comportamientos y conocer las características que ayudan a su adaptación a los cambios y las condiciones particulares de la cautividad. Con esto se concluye que la personalidad es una herramienta útil para mejorar el manejo de delfines mulares bajo el cuidado humano profesional, y para determinar las condiciones sociales que garanticen el bienestar y el éxito de cría, que son relevantes a la hora de realizar programas de conservación *ex situ* de especies en peligro de extinción.

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9. BIBLIOGRAFÍA GENERAL

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