Social relationships and death-related behaviour in aquatic mammals: a systematic review

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Abstract

Some aquatic mammals appear to care for their dead whereas others abandon their live offsprings,when conditions are unfavourable. This incredible variety in behaviours suggests the importance of comparing and contrasting mechanisms driving death-related behaviours among these species. We reviewed 106 cases of aquatic mammals (81 cetaceans, 25 non-cetaceans) reacting to a death event, and extrapolated 'participant' (*age class, sex, relationship, decomposition*) and 'social' characteristics (*escorting, calf dependence, alloparental care, herding, dispersal patterns*) from published and unpublished literature. A Multiple Correspondence Analysis (MCA) was performed to explore the relationships between these characteristics and death-related behaviours, with species clustered based on MCA scores. Results showed that both cetaceans and non-cetaceans react to death but in different ways. Non-cetaceans, characterized by a short maternal investment, were observed to protect the dead (defending it from external attacks), while cetaceans spent much longer with their offspring and display carrying (hauling, spinning, mouthing with the carcass, diving with it) and breathing-related (lifting and sinking the carcass) activities with the dead generally in association with other conspecifics. Our work emphasises the need of increased documentation of death-related cases around the world to improve our understanding of aquatic mammals and their responses to death.

Keywords

Death, behaviour, sociality, aquatic mammals, multiple correspondence analyses

1.Background

'Death-related behaviour' [1], including grieving and other complex responses to dying or to distressed conspecifics, were long considered an exclusive prerogative of our species [2]. Darwin was one of the earliest to suggest that animal species, like humans are capable of pleasure, pain, happiness and misery [3]. Death-related behaviour is described as a subcategory of epimeletic or nurturant behaviours (i.e. -a healthy individual which gives attention to an injured or dead one, as summarized in [4]) and usually seen as a consequence of the cooperative, succouring and protective nature of social mammals [4-8]. Considering that the individual receiving this attention is often a young, some authors suggested that this behaviour could be a consequence of the strong mother-offspring bond [9-12], or a revival attempt through violent manipulation of the bodies [13,14]. In certain cases where the dead or dying individuals were adults, a sexual component and/or a dominance display is involved as observers recorded erections, mounting attempts and other dominance display behaviours [15, 16]. Generally, social structure features, anatomic constraints and ecological conditions could influence death related behaviours, while an evolutionary or direct benefit is still far from being inferred [8].

According to the available literature, epimeletic death responses among land and marine mammals include stereotyped behaviours such as the carrying of dead offspring (primates using hands, cetaceans against their dorsal fin or similarly to *Canis* in their mouth) and having the mother-dead infant pair (or simply the dead infant) protected or escorted by other members of their groups, as observed in elephants, cetaceans and primates [4,7]. In cases where individuals were unable to carry the dead (e.g.- lemurs, giraffes and elephants), these species are known to stay near a dead conspecific for extended periods and move back and forth between their groups and their distressed or dead offsprings [6, 7, 8]. Many aquatic mammal species react to the death of a conspecific, most often a calf, and adults can be observed staying close to, maintaining physical contact, lifting, keeping at the surface or carrying the dead one, even in an advanced state of decomposition. While carrying the carcass adults may stop eating focusing all their attention on it.

79 They can also display defensive and aggressive behaviours if predators, conspecifics (e.g.
80 pinnipeds) cross their paths, and have escorts accompany and defend them from intruders (e.g.
81 cetaceans, [4,7]). There are also records of species (e.g. sea otters [17,18, 19], Antarctic fur seals
82 [20], which have been observed to routinely abandon their live pups, due to environmental changes,
83 illness or nutritional stress.

84 While death-related behaviours of dolphins are known to be highly variable [4,7], there has
85 not been a comprehensive review of the available information on this topic including all cetaceans.
86 The only exception is a recent encyclopaedia chapter focusing on epimeletic behaviour among
87 cetaceans [4]. Regarding pinnipeds, sea otters and manatees, the current available information is
88 lacking, and the few studies are often descriptive and include sporadic observations. However, in
89 the majority of reported cases a change in behaviour occurred after the death of a conspecific
90 suggesting that that event may have caused disruption/distress in the species displaying death-
91 related behaviours. In this study, the association between aquatic mammal species' social
92 characteristics and death-related behaviours was explored by using a multiple correspondence
93 analysis (MCA) of the literature and available unpublished material. The aim was to answer the
94 following questions: 1) Can behaviours displayed during death events be linked to certain species
95 social characteristics? 2) If so, which social characteristics can be used to categorize the type of
96 behaviour displayed? 3) How do these behaviours differ among cetaceans and non-cetacean
97 species? Sightings published in the literature and in the field were collected and were critically
98 assessed highlighting inconsistencies and identifying key areas for further work and future analysis.
99

100 **2. Systematic and analytic literature review**

101 We used the Committee on Taxonomy [21] to create an updated list of aquatic mammals,
102 distinguishing cetacean (odontocetes and mysticetes) from non-cetaceans (pinnipeds, sea otters and
103 manatees) for this study. To find published cases we utilized a combination of search words (See
104 Table S1-A for how these words are combined) including *calf*, *pup*, *adult*, *mortality*, *died*, *dead*,

105 *death*, *mother*, *behaviour*, with the Latin name of each species, through the search engine Google
106 Scholar. We also searched the reference section of online published papers to find additional
107 articles not located in the online searches. Lastly, we contacted authors who had published several
108 papers focusing on sociality, death and mother-calf bond among non-cetacean species. We added
109 new field sightings from other researches to the literature review, and a complete list of all the cases
110 including reference, species and participants characteristics is reported in Table S1-B (see electronic
111 supplementary material). Video and photographs available on the web and collected by a non-
112 scientific audience were excluded due to potential bias caused by cinematographic editing in videos
113 (such as the loss of the correct temporal sequence of events due to efforts to increase the dramatic
114 nature of the images) and to the lack of detailed information about death events for photographs. A
115 total of nine 'characteristics' (adapted from [22]) were gathered and were categorised as follows.
116 Four of these were used to describe the 'participant characteristics': *age class* (adult, juvenile,
117 subadult, calf), *sex* (male, female), *relationship* (between the alive 'giver' and the dead 'receiver':
118 mother, inferred mother, unrelated) and *decomposition* (fresh, moderate, advanced; following [23]).
119 Five provided information about the sociality, hereafter 'social characteristics' (see electronic
120 supplementary material, table S2): *alloparental care* (presence, absence), *calf dependence* (defined
121 when a calf relies on its mother for food, protection, spending the majority of its time with her; 6-11
122 months, 1-1.5 years, 2-5 yrs, 4 yrs, 5.5 yrs, 6 yrs, 6 -10 yrs), *herding* (mother-calf pair living in
123 female groups, living in mixed-sex groups, living in mother-calf pair groups only, solitary),
124 *dispersal patterns* (intended as the choice of offspring to stay, leave their natal group once they
125 reached sexual maturity, or to return after a period of separation), and *escorting* (defined by the
126 presence or absence of other conspecifics involved; helper, group, none). We chose these social
127 characteristics because the death of a conspecific can affect group composition and survivability,
128 with group composition potentially influenced by age class, sex, reproductive condition and kinship
129 [24-26], and the social characteristics by group cohesion, parental care, social structure, and
130 reproductive success [27].*Dependence, alloparental care, herding,* and *dispersal patterns*

categories were inferred and generalized from population studies found in literature (see supplementary material, table S2). The category *Unknown* was used when the information was not certain, *Not Applicable* when the receiver was an object, another species or the receiver was severely wounded and close to death (Alive-then-Dead), and *Not Reported* when a parameter was not described in the literature.

An ethogram of death-related behaviours for cetacean and non-cetacean species was created consisting of a total of 23 behavioural types using terms which were found in the literature review we conducted. Potential sources of bias in our dataset are linked to 1) low frequencies of some behavioural components, and 2) the species-specificity of some behaviours. In order to prevent the low frequency of some behaviours from biasing our results, we created behavioural categories and grouped multiple behaviours within them. To avoid creating categories that include behaviours displayed solely by one species, we included behavioural components displayed by both cetaceans and non-cetaceans. The only exception is the category 'protection', (see electronic supplementary material, table S5) which is only displayed by non-cetaceans. In some species of pinnipeds females display a protecting behaviour towards their young ones in response to aggressive juvenile male competitors wanting to separate them from their calves during the mating season. Given the uniqueness and importance of this category we decided to retain it. We therefore classified all behavioural types into the following six behavioural categories: 1) Carriage: carrying, hauling, spinning, mouthing, diving 2) Breathing: lifting, sinking 3) Contacts: striking, licking, body contact, nosing, arousing, suckling, grooming 4) Protection: protecting 5) Other: vocalizing, kidnapping, searching, unknown, sniffing, sexual 6) Resting: laying beside it, stationing. See table S5 listed in the supplementary material for the full list of typesand categories.

An exploratory analysis of the potential relationships between aquatic mammal species and their death-related behaviours and social characteristics was performed using a Multiple Correspondence Analysis (MCA) [28,29]. MCA allows for the analysis of multivariate categorical

156 data and to visualise the results in a graphical manner. For each species each behavioural and social
157 parameter was marked as a '1' if present and '0'if absent (see Table S4).

158 The matrix data, comprising 23 behavioural types for 28 aquatic species (see details below
159 in 'participant characteristics' and death-related behaviour'), was then converted into dimensions
160 which are structured from the most explicative to the least. To permit visualisation, the scores from
161 the two dimensions that account for the most variance are projected to create a factor plane. The
162 scores on the factor plane can be used to explore the relationship between species where the
163 distances between points reflect the similarities in type of social and behavioural characteristics,
164 with the shorter the distance, the greater the similarity.We clustered species into groups by using the
165 scores of the first *n* axes where *n* is defined by finding the cut-off where an increase in the axes does
166 not provide significant discriminative properties (inertial gain). A hierarchical clustering is
167 performed with the scores from these *n* axes using the Euclidian distance and Ward's clustering
168 method. All analyses were performed using the R programming environment (R Core Team 2017)
169 using the *FactoMineR* [30] and associated packages for the MAC and clustering analysis.
170

171 **3. Participant characteristics and death-related behaviour**

172 A total of 106 cases were found (81 of cetacean and 25 of non-cetacean species), with 28 species
173 involved (20 were cetaceans and 8 non-cetaceans; see electronic supplementary material, table S1).
174 For cetaceans, *Tursiops sp*., *Globicephala macrorynchus* and *Sousa chinensis* were the most
175 recorded species displaying death-related behaviours (see electronic supplementary material,
176 histogram S3*a*), and *Otaria flavescens* and *Phoca vitulina* for non-cetacean species (see electronic
177 supplementary material, histogram S3*b*). However, it must be acknowledged that results presented
178 in this study refer to the number of death cases found through search engines and do not indicate the
179 total number of existing cases. The results in this study could also be biased downwards due to a
180 possible omission of pertinent papers, although care was taken by the authors to provide the most
181 comprehensive systematic review of death-related cases across all aquatic mammals. For both

cetaceans and non-cetaceans, ‘givers’ were adults, females and usually inferred mothers, while ‘receivers’ were most often dead calves in a fresh state of decomposition. ‘Receivers’ were calves in 84 cases, adults in 11, subadults in 1, juveniles in 7, while an amniotic sac was targeted in 1 case (see electronic supplementary material S3 *f, g*).

4. Social characteristics and death-related behaviour

Both cetaceans and non-cetaceans react to death but display different behaviours. MCA (Fig. 1) results highlight that parameterssuch as *calf dependence* and the presence of *alloparental care* are related to the behavioural type which is displayed and to the participation of other individuals during death events (i.e. *escorting*). Cetaceans with more dynamic moving patterns and with a longer time spent with their offsprings are found to display carrying- (hauling, spinning, mouthing the carcass, diving with it) and breathing-related (lifting and sinking the carcass) activities, generally in association with other conspecifics. More than one individual commonly interacted with the mother-calf pair in cetaceans, either approaching the couple or contributing (see electronic supplementary material, histogram S3*h,i*). Conversely, non-cetacean species, with a shorter maternal investment react to the death of a conspecific displaying ‘protecting’ as a behavioural type. Both cetaceans and seals live in fission-fusion societies [31], so the different shades of gregariousness typical of these groups could explain the frequent involvement of other members of the same species during death events.

5. Cetacean versus non-cetacean species

For non-cetaceans, the dendrogram shows that Phocidae (*Phoca groenlandica*, *P. vitulina*, and *P. vitulina concolor*), Trichechidae (*Trichechus manatus*) and the majority of Otariidae (*Otaria flavescens*, *Zalophus californianus*) are clustered separately from cetaceans (Fig. 2, Table 1). The grouping between cetacean and non-cetacean species mirror the behavioural and social differences existing between these two animal groups (see paragraph ‘Social characteristics and death-related

behaviour'). Our data also show that females of *P. vitulina, P. vitulina concolor* and *O. flavescens* display protective behaviors towards their dead young. This could relate to the protective behaviour mothers display towards their offspring after birth to defend them against danger. For example, females in *O. flavescens* protect their calves from juvenile male competitors who want to reproduce with them separating mothers from their calves [32,33]. The remaining Otariidae *Arctocephalus gazella* clusters with *Enhydra lutris* (Mustelidae) as these species both display grooming during death events and although abandonment was not considered in the analysis both species are also reported to abandon their alive pups due to changes in environmental or body conditions [19,20]).

For cetaceans, the dendrogram shows *Sousa chinensis* and *S. sahulensis* clustering together, which is likely due to their display of carrying, lifting and stationing behaviours, and having a long period of calf dependence (5-10 years). In the death-events cases analysed for these two species, mothers initially stayed alone with the dead but were later assisted by escorts in the carrying of the carcass. Another cluster was consisted of *Delphinus capensis, Sotalia guianensis* and *Lagenorhynchus obliquidens* which share a short calf dependence (less than 1 year), the tendency of mother-calf pairs to live in groups with other conspecifics [34,35,36], and the presence of escorts intervening and carrying the dead. Another group was made by *Orcinus orca* and *Pontoporia blainvillei* which were clustered together due to the fact that juveniles remain with the maternal groups for the duration of their lives [37,38], they both show *alloparental care*, and during death events they always had at least one escort present with the mother. The largest cluster consisted of *Cephalorhynchus hectori, Delphinapterus leucas, Grampus griseus, Physeter macrocephalus, Sotalia fluviatilis, Stenella attenuata, S. frontalis, S.longirostris, Steno bredanensis, Tursiops truncatus*, which all displayed carrying, diving, mouthing and lifting as death-related behaviours. Lastly, *Globicephala macrorhynchus* and *Megaptera novaeangliae* were clustered together sharing lifting and sexual behaviours directed toward dead adults (erections and intromission of a male toward dead female for *G. macrorhynchus;* erection and genital slit opened for *M. novaeangliae*). They also tended to display their death related behaviours in the presence of other individuals, a calf

dependence period lasting 1 to 5 years, and the tendency of mothers and calves to group together [39, 40].

6. Conclusion and future recommendations

An important step when summarizing the findings of this work is to address the three aims we outlined at the beginning of this study that relate to the investigation of the association between aquatic mammals species' social characteristics and death-related behaviours. 1) *Can behaviours displayed during death events be linked to certain species social characteristics*? A high number of species show death-related behaviours that can occur due to a mix of ecological, taxonomical, cultural and abiotic factors. Here, we have shown that the behaviours displayed during death events in marine mammals can be linked to certain social characteristics.

2) *Which social characteristics can categorise the type of behaviour displayed*? Death events represent for highly social species the definitive breaking of a strong social bond. Outcomes of this work highlight that for marine mammals, some social characteristics, such as calf dependence and the presence of alloparental care can categorise death-related behavioural patterns.

Lastly, 3) *How do these behaviours differ among cetaceans and non-cetacean species*? Social characteristics, like alloparental care and calf dependence, differ among cetacean and non-cetacean species and consequently their behavioural patterns are influenced by this variation. Our results highlight that the differences in social characteristics shown by these two groups exert a strong influence on the variation of the observed death related behaviours.

In the context of the new interdisciplinary area of comparative thanatology[41], which incorporates animal cognition, social behaviour, inter-individual relatedness and emotion, this study provides scientific advances in understanding how aquatic mammals face death through a systematic and analytical approach to link behavior and social characteristics. However, fully understanding how aquatic mammals perceive and react to death will require more time. As a future consideration, a larger number of death-related events is needed to improve our understanding of grieving,

abandonment and neglect towards the dead. We therefore hope to encourage an increasing number of researchers to report sightings of similar events collecting acoustic recordings, alongside photographs and videos with scientific rigor and strictly accompanied by an accurate description of all behaviours displayed in chronological order. Future analysis could also include the use of mortality rate and predation risk as parameters investigated, as they are known to affect group cohesion and composition, which might ultimately influence how mammals relate to death.

Authors' contributions

M.A.L.R. and C.G.B. conceived the work, performed the systematic literature review, participated in data analysis and drafted the manuscript; L.E. contributed with most of the cetacean literature review. E.P. contributed with a field case, participated in data analysis, and drafted the manuscript; G.A.D.L. contributed with E.P to a case described in the paper; N.McG. analysed the data, prepared all figures present in the paper, drafted the manuscript, and helped revise the use of English. All authors gave final approval for publication.

Competing interests

We have no competing interests.

Funding

No funding were used to produce this paper work

Acknowledgements

We are grateful to James Anderson and the editors of this issue for the invitation to contribute. We are also thankful to Giovanni Bearzi for his constructive suggestions and his help on designing this study. Thanks also go to Claudio Campagna, Fritz Trillmich and Burney LeBoeuf for sharing their knowledge and publications on pinnipeds with us. Thanks to all field assistants who collected

sightings presented in this paper. Authors would like to dedicate this work to the memory of Carla Magliocco for her encouragement and support.

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Figures

Figure 1. The first factor plane (Dim 1 and Dim 2) of the MCA which explains 30.6% of the total inertia within the dataset. Species are coloured by their cosine squared (Cos^2) value with larger values suggesting a stronger association with each axis. The categories that represent the greatest contribution to both the Dim 1 and Dim 2 axis are shown in black. (Please see Table 1, and Tables S4-S5 insupplementary material, for a description of each category).

Figure 2. The results of the hierarchical clustering dendrogram using scores derived from the first 8 axis of the MCA. Clusters were determined by finding the optimum level of inertia gain ($p < 0.05$).

Tables

Table 1. The Cosine squared (Cos^2) scores for the most important variables used to characterise the first 2 axes (Dim 1 and Dim 2) of the MCA with variables close to one are best represented by the two dimensions. Also shown is the percentage (%) contribution of the Yes/ No assignments for each category.

Electronic supplementary materials

Supplementary material S1. A) Search terms used in Google scholar searches B) Cases describing death-related behaviours including participant characteristics.

Supplementary material S2. List of social characteristics with references used in the analysis.

411 Supplementary material S3. Histograms showing the number of cases (%) for each (a) cetacean and
412 (b) non-cetacean species, the grieving relationship for (c) cetacean and (d) non-cetacean and the sex
413 for (e) cetaceans for the known cases only. For non-cetaceans the sex has been determined to
414 exclusively Female with only 1 unknown case. Carcass state is shown in (f) for cetacean and (g) for
415 non-cetacean, presence of other individuals involved in (h) for cetacean and (i) for non-cetacean.
416 Supplementary material S4. List of cases describing death-related behaviours and categories used
417 for MCA.
418 Supplementary material S5. Ethogram of death-related behaviours.
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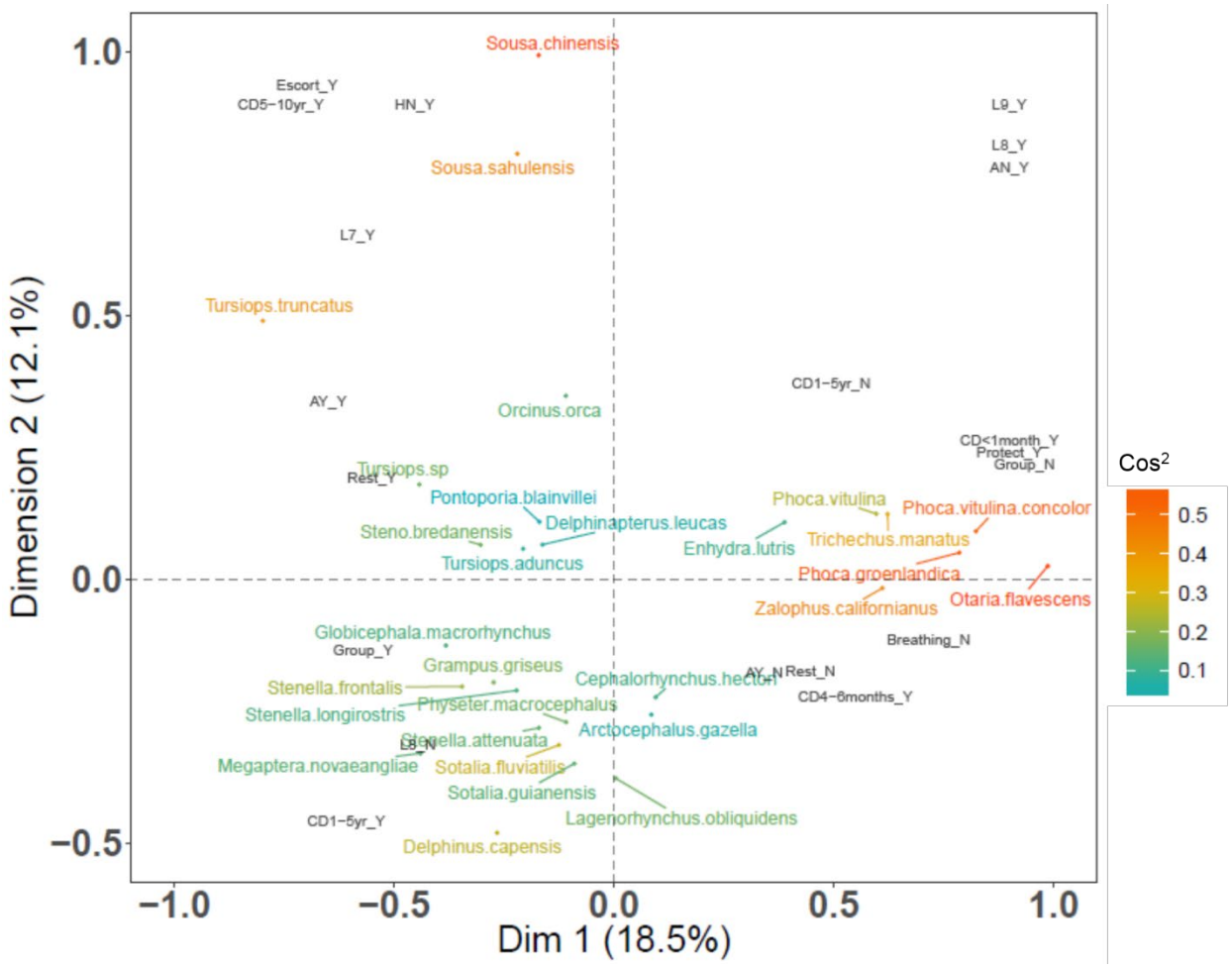

Figure 1. The first factor plane (Dim 1 and Dim 2) of the MCA which explains 30.6% of the total inertia within the dataset. Species are coloured by their cosine squared (Cos^2) value with larger values suggesting a stronger association with each axis. The categories that represent the greatest contribution to both the Dim 1 and Dim 2 axis are shown in black. (Please see Table 1 for a description of each category).

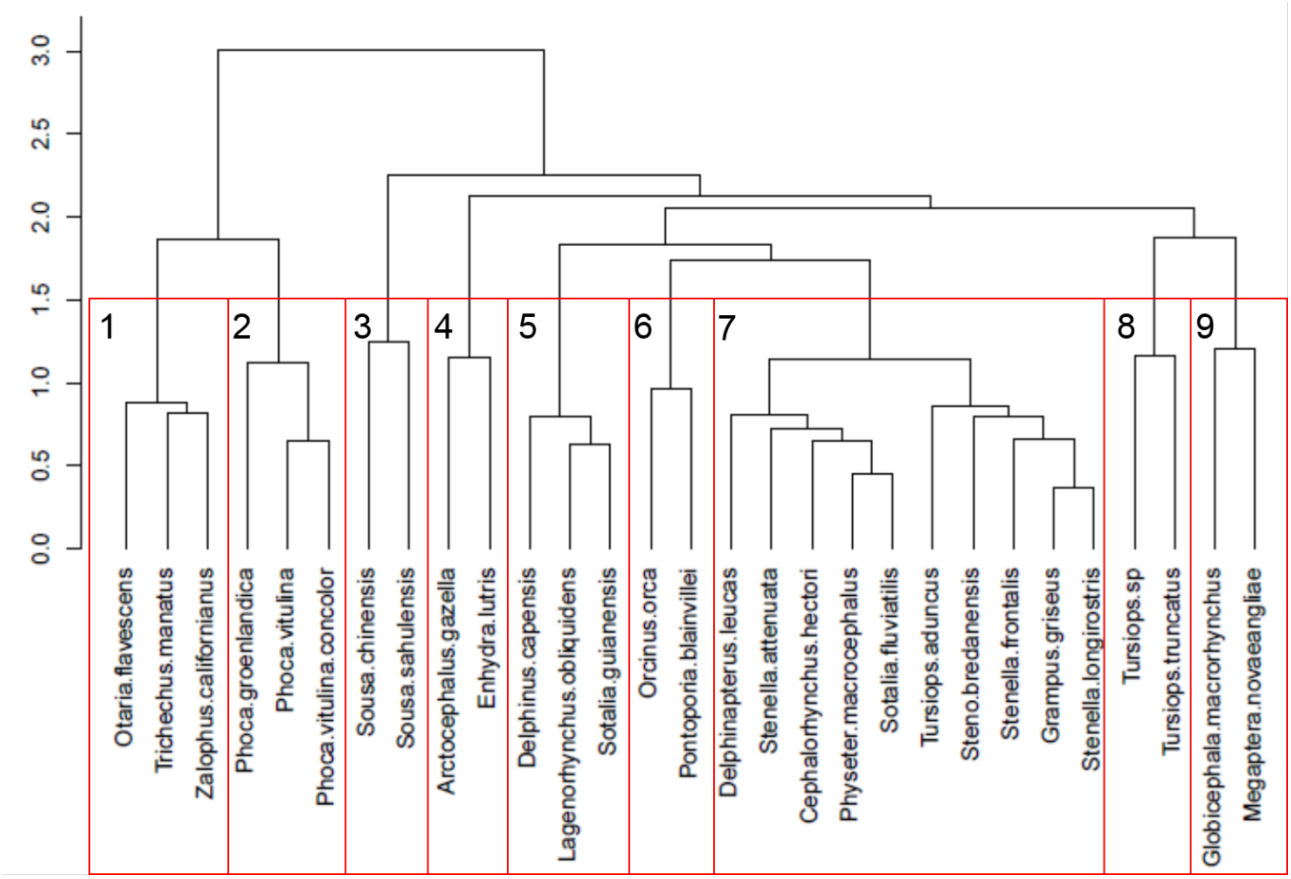

Figure 2. The results of the hierarchical clustering dendrogram using scores derived from the first 8 axes of the MCA. The resulting 9 clusters were determined by finding the optimum level of inertia gain ($p < 0.05$).

Table 1. The Cosine squared (Cos^2) scores for the most important variables used to characterise the first 2 axes (Dim 1 and Dim 2) of the MCA with variables close to one are best represented by the two dimensions. Also shown is the percentage (%) contribution of the Yes/ No assignments for each categories.

		Dim1	*Dim 2*	*% Contribution*		
Category	**ID**	**Cos^2**	**Cos^2**	**Total**	**Yes**	**No**
Dispersal	D8	0.52	0.26	0.78	16.9	6.16
Calf Dependence	CD5-10yr	0.18	0.44	0.62	16.44	5.23
Herding (No)	HN	0.02	0.54	0.56	20.01	2.39
Escorting	Group	0.53	0.03	0.56	5.16	8.44
Calf Dependence	CD1-5yr	0.3	0.17	0.47	7.56	6.14
Alloparental (No)	AN	0.31	0.13	0.44	10.05	2.49
Death related Behaviour	Protecting	0.4	0.01	0.41	8.63	2.21
Escorting	Helper	0.13	0.23	0.36	9.49	2.42
Calf Dependence	CDless3m	0.34	0.01	0.35	7.35	1.9
Calf Dependence	CD4-6m	0.34	0	0.34	7.22	2.64
Death related Behaviour	Breathing	0.31	0.01	0.32	2.9	4.74
Death related Behaviour	Rest	0.25	0.04	0.29	3.97	3.22
Alloparental (Yes)	AY	0.22	0.06	0.28	4.94	1.92
Dispersal	D9	0.15	0.07	0.22	6.07	2.87