Group Size and Behavioural Ecology in the Superfamily Delphinoidea (Delphinidae, Phocoenidae and Monodontidae)

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Contents

Zusammenfassung

Bei Begegnungen mit Delphinen ist es auffallend wie unterschiedlich gross die Gruppen sind, in denen diese Tiere beobachtet werden können. In dieser Studie wurde die Gruppengrösse der Delphinoidea Arten (Delphinidae, Phocoenidae, Monodontidae) auf ihre Abhängigkeit von Variablen der physikalischen Umwelt, der Nahrung und von 'life-history' Variablen untersucht. Zusätzlich wurde ein Versuch unternommen, die Delphinoidea Arten aufgrund dieser ökologischen Variablen und der Gruppengrösse zu kategorisieren.

Die Variabilität in der Gruppengrösse ist enorm: sie reicht von den ein bis zwei Individuen in den Gruppen von Schweinswalen bis zu mehreren Tausend Tieren in den Gruppen einiger Hochseedelphine. So ist die Idee naheliegend, dass diese verschiedenen Gruppengrössen als Reaktion auf unterschiedliche ökologische Gegebenheiten und unterschiedliche zwischen- und innerartliche Beziehungen entstanden sind. Es kann angenommen werden, dass dieser Selektionsdruck noch immer in den heutigen ökologischen Nischen erkennbar ist.

Ein zwischenartlicher Vergleich konnte zeigen, dass die Gruppengrösse hauptsächlich von den phylogenetischen Variablen Art und Subfamilie abhängt, die den Grossteil der Variabilität in den Gruppengrössen erklären können. Die Gruppengrösse wuchs auch mit zunehmender Offenheit des Habitates und zeigte eine u-förmige Beziehung mit der Temperatur. Andererseits halfen die life-history Variablen und die Nahrung kaum zur Schätzung der Gruppengrössen.

Innerartliche Vergleiche der drei grossen Delphinidae Schwertwal, Grindwal und Rundkopfdelphin, der drei kleineren Delphinidae grosser Tümmler, gemeiner Delphin und blauweisser Delphin und der zwei Phocoenidae Schweinswal und Dall's Hafenschweinswal führten zu statistischen Modellen, die Gruppengrössen für jede Art korrekt voraussagen konnten. Die Form der Abhängigkeit, die biologische und die statistische Bedeutung konnte für die erklärenden Variablen der physikalischen Umwelt, der Nahrung und der Life-history bestimmt werden. Es wurde dabei jedoch kein allgemeines Muster sichtbar und jede Art zeigte ihr eigenes Muster von Abhängigkeit der Gruppengrösse von den erklärenden Variablen.

Die Delphinoidea Arten können erfolgreich klassifiziert werden, wenn ein schrittweises Verfahren angewandt wird. In einem ersten Schritt können die Delphinoidea Arten in drei Grössenklassen eingeteilt werden: die kleinen Delphinoidea, die grossen Delphinoidea und die Schwertwale. Die grossen Delphinoidea Arten können dann mit einem Klassifizierungsfehler von etwa 10 % kategorisiert werden. Um einen ähnlich kleinen Fehler bei den kleinen Delphinoidea zu erreichen, müssen diese zuerst nach geographischer Region aufgetrennt werden. Obwohl alle Arten des Nordatlantiks auch im Nordpazifik vorkommen, zeigen die Kategorisierungen der getrennten Regionen deutlich kleinere Klassifizierungsfehler. Dies ist ein Hinweis darauf, dass die Nischen klarer innerhalb der Regionen getrennt sind als insgesamt und dass einige Arten des Nordatlantiks ähnliche Nischen besetzen wie andere Arten im Nordpazifik. Körpergrösse war aufs Neue die wichtigste Variable in der Klassifizierung der kleinen und grossen Delphinoidea: verschiedene Modelle mit ähnlichem Klassifizierungsfehler enthielten alle die Variable Grösse,

und die Klassifizierungsfehler kamen hauptsächlich zwischen Arten mit benachbarter Grösse vor.

Es scheint, dass die Gruppengrössen der Delphinoidea Arten hauptsächlich das Resultat eines historischen phylogenetischen Prozesses ist. Diese Feststellung wird dadurch unterstüzt, dass die Gruppengrösse einerseits am besten durch die Variablen Art und Familie vorausgesagt werden kann und auf der anderen Seite jede Art der innerartlichen Vergleiche ein anderes Reaktionsmuster gegenüber den gleichen Nischenvariablen zeigte. Zusätzlich gibt es Hinweise darauf, dass der Prädationsdruck einen kleinen Einfluss auf die Gruppengrösse hat, indem Gruppen in offeneren Gebieten grösser sind. Auch die Ernährung kann direkt und indirekt via die Temperaturvariablen einen schwachen Einfluss auf die Gruppengrösse haben.

Trotzdem sind die Gruppengrössen der Arten nicht spezifisch genug, dass diese damit vorausgesagt werden können. Das bedeutet, das mehrere Arten ähnliche Gruppengrössen haben. Tatsächlich unterscheiden sich die Arten hauptsächlich in ihrer Körpergrösse. Das ist überraschend, weil man annehmen würde, dass Arten von ähnlicher Grösse grundsätzlich ähnlichere Nischen besetzen würden, da sie ähnliche physikalische constraints mit sich bringen, und sich dann durch Konkurrenz in klar abgetrennte Nischen verdrängen.

Möglicherweise bringen die Delphinoidea Arten alle ein ähnliches biologisches Erbe bezüglich der Verhaltensmechanismen mit sich, und die sozialen Muster entstehen dann in einer Interaktion zwischen diesen Mechanismen und der Umwelt. Basierend auf den vorliegenden Daten müsste man dann annehmen, dass nicht einmal eine solche Interaktion zu einer klaren Differenzierung in den verschiedenen Arten führt, wahrscheinlich weil die Umwelt recht uniform ist und durch einen historischen Prozess teilweise verdeckt wird.

Summary

Encountering groups of dolphins, it is striking how variable they are in size. In this study, group size of Delphinoidea species (Delphinidae, Phocoenidae, Monodontidae) was investigated in relationship to parameters of the physical environment, the diet and the life-history variables of the Delphinoidea. Additionally an attempt was made to categorise the Delphinoidea species using the same set of variables together with the group size measures.

Variability in group size is enormous, ranging from one or two animals in harbour porpoises to several thousand animals in herds of some offshore dolphins. Thus the idea is straight forward to assume that these different group sizes have evolved in reaction to different environmental conditions, different inter- and intraspecific relationships. These selective forces can be assumed to be still visible in the ecological niches that the different species occupy today.

An interspecific analysis revealed that group size most strongly depends on the phylogenetic variables species and subfamily which can account for most of the variability in group size. Group size also increased with openness of the habitat and showed a u-shaped relationship with temperature. On the other hand life-history variables and the diet could hardly help in predicting group size.

Intraspecific comparisons of the three larger Delphinidae killer whale, pilot whale and Risso's dolphin, the three smaller Delphinidae bottlenose dolphin, common dolphin and striped dolphin and the two Phocoenidae harbour porpoise and Dall's porpoise lead to statistical models that could predict group size for each of these species. The shape of dependence, the biological and the statistical significance could be assessed for the variables of the physical environment, the diet and the life-history of the species. No general pattern was found, and each species showed its own pattern of dependence of group size on the explanatory variables.

The Delphinoidea species can be successfully categorised using discriminant analysis in a step-wise procedure. In a first step the Delphinoidea species can be split in three groups according to (body) size: small Delphinoidea, large Delphinoidea and the killer whales. The large Delphinoidea can then be categorised on their own with a remaining classification error of about 10 %. To achieve a similar result for the small Delphinoidea they have to be split according to geographic region. Though all the species of the North Atlantic also occur in the North Pacific these categorisations have much lower misclassification rates. This indicates that niches are more strictly separated within a region than between regions and thus some species in the North Atlantic may occupy similar niches to those of other species in the North Pacific. Size was also the most important variable in the discriminant analyses on the three species subsets: different models that reached a similar misclassification error all include the variable size, and misclassifications mainly occured between species of adjacent size.

It seems that group size in Delphinoidea is the result of a mainly historical phylogenetic process. This is supported by the fact that group size in the interspecific comparison has been predicted best by the variables species and family and that the different species in the

intraspecific comparisons showed different reactions to the same variables that describe their niche. There is a slight indication that predation has some influence on group size in that groups tend to be slightly larger in more open habitat. Diet may also have a direct and an indirect weak influence via the temperature variables.

Nevertheless, though the species can predict the group size, the inverse is not true: species cannot be differentiated on the basis of group size because this variable is not sensitive enough to do so. Thus several species do have similar group sizes. Species differ mainly in the variable (body) size. This is quite surprising in that it would be assumed a priori that species of similar size tend to occupy similar niches, because they have similar physical limitations, and would thus displace each other through high competition into ecological niches that differ markedly.

Possibly the Delphinoidea species have a similar biological heritage and a similar predisposition regarding behavioural mechanisms in common. Then, different social patterns would emerge in an interaction of these mechanisms with the environment. With the current data it would have to be assumed then that not even this interaction leads to clearly different ecological patterns in the different species. This is most likely the case because the environment is rather uniform and a historical process partly hides the evolutionary adaptations.

General Introduction

Dolphins and their lives are fascinating to human beings. It is hard to tell what draws us towards these species. Is it the myth of the gentle helpers in the sea, that has recently been questioned (Connor *et al.*, 1992b, 1999; Patterson *et al.*, 1998; Ross and Wilson, 1996), is it the harmony that one feels seeing these creatures move so gracefully through a medium that is so foreign and sometimes threatening to us, or is it the evolutionary memory of an aquatic phase that we may have shared with other now terrestrial mammals (Morgan, 1989; Gaeth *et al.*, 1999)? Another part of the fascination may lie simply in the fact that dolphins live in groups. This simple fact may stir our interest being such social animals ourselves that even the evolution of language is suggested to be based in our social lifes (Dunbar, 1993, 1996). Thus we may simply wonder how other animals organise their social day-to-day interactions and how they came to be such social species in the first place. Thus we are interested in the origin and maintenance of social systems, both for its proximate mechanisms, that we ourselves experience in day-to-day life, as well as for its ultimate (evolutionary) reasons. The latter is mainly addressed in this current study.

It is undeniable that the Delphinoidea (Delphinidae, Phocoenidae, Monodontidae) display an unbelievable diversity in appearance (Perrin, 1991, Fig. 1). The variability is not only visible in appearance, though, but also in many ecological and behavioural characteristics. Some species are specialist for cold waters like the Monodontidae (Brodie, 1989; Hay and Mansfield, 1989) others solely occur in tropic waters such as e. g. common dolphins or spinner dolphins (Evans, 1994; Norris *et al.*, 1994). Group sizes are also very variable ranging from the more or less solitary harbour porpoises (Evans, 1980; Heide-Jørgensen *et al.*, 1993; Palka, 1995) to the Stenella species that are observed in herds of up to several hundreds and sometimes even thousands of animals (Kasuya *et al.*, 1974; Miyazaki and Nishiwaki, 1978; Perryman and Lynn, 1994). The social system varies from the relatively rigid matrilines of killer whales (Bigg *et al.*, 1987, 1990) to the fission-fusion system of the bottlenose dolphins (Scott *et al.*, 1990; Smolker *et al.*, 1992; Wilson, 1995; Félix, 1997).

Such variety is usually viewed as an evolutionary adaptation to specific niches. This is the starting point for this current research in which I attempt to find ecological correlates of group size that can explain (part of) this variability.

It is especially interesting to conduct such research on the Delphinoidea as they are aquatic species. Many theories have been put forward for the evolution of group sizes in terrestrial mammals (see an overview in the introduction of the interspecific comparison, page 21) and thus the aquatic environment is an independent test for these ideas (Marino, 1997; Connor *et al.*, 1998). It is independent in the sense, that we can test the ideas on mammalian species which are not closely related and have faced a completely different evolutionary history as they developed in an environment with different physical properties (see also the discussions of the inter- and intraspecific comparisons, pages 39 and 50).

In the first main chapter an interspecific comparison of group size is conducted in relation to the phylogeny, the physical environment, the diet and the life-history of the Delphinoidea species. In the second chapter intraspecific variation of group size is investigated and related to the interspecific differences. In the third chapter the ecological knowledge is used in an attempt to categorise the Delphinoidea species.

Appendix A gives a more detailed overview of the database on which the three chapters are based and Appendix B reports the history of the statistical evaluations and more statistical details on the final models. Appendix C presents two short papers that are directly based on field data gathered by the author and his assistants. The initial motivation of the field work had been to collect data on parameters for individual-based models on Delphinoidea social systems. Unfortunately the killer whales were seen very rarely in the two years of field work (1996, 1997) but the statistical analysis of the data from the literature offered more opportunities than had been expected when I set out for this study.

Thus, welcome to a tour through the fascinating variability of group sizes in the Delphinoidea which, once again, may open a whole lot of new biological questions.

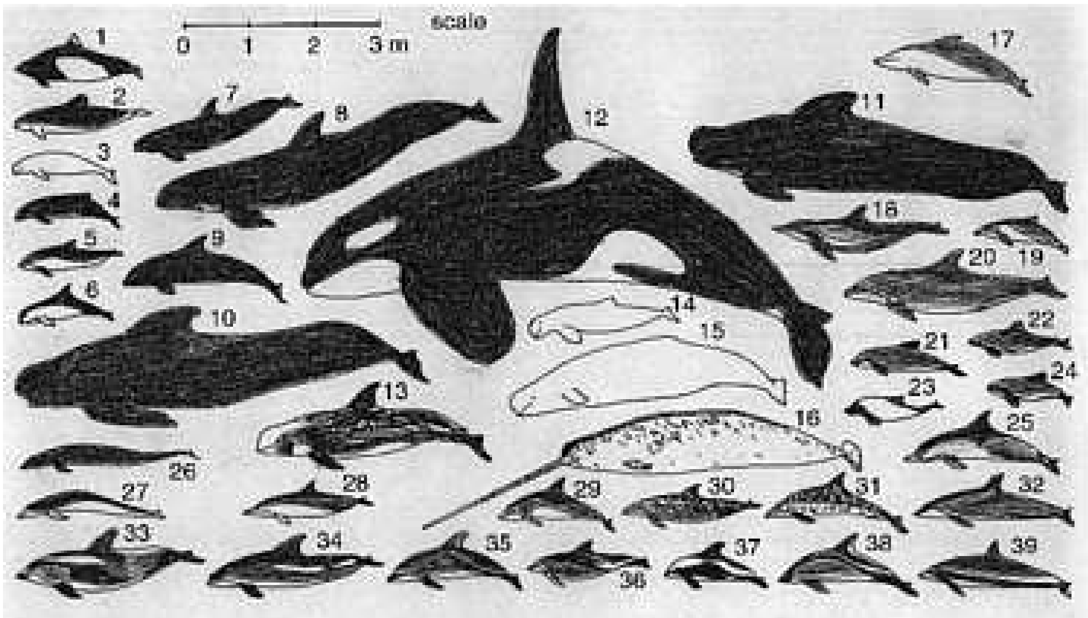

Figure 1: The Variability of the Delphinoidea species (after Folkens, 1991). Species: 1: Phocoenoides dalli, 2: Australophocoena dioptrica, 3: Neophocoena phocoenoides, 4: Phocoena spinipinnis, 5: Phocoena phocoena, 6: Phocoena sinus, 7: Feresa attenuata, 8: Pseudorca crassidens, 9: Peponcephala electra, 10: Globicephala melas, 11: Globicephala macrorhynchus, 12: Orcinus orca, 13: Grampus griseus, 14: Orcaella brevirostris, 15: Delphinapterus leucas, 16: Monodon monoceros, 17: Sousa spp., 18: Steno bredanensis, 19: Sotalia spp., 20: Tursiops truncatus, 21: Cephalorhynchus eutropia, 22: Cephalorhynchus heavisidii, 23: Cephalorhynchus commersonii, 24: Cephalorhynchus hectori, 25: Delphinus delphis, 26: Lissodelphis borealis, 27: Lissodelphis peronii, 28: Stenella longirostris, 29: Stenella clymene, 30: Stenella frontalis, 31: Stenella attenuata, 32: Stenella coeruleoalba, 33: Lagenorhynchus albirostris, 34: Lagenorhynchus acutus, 35: Lagenorhynchus obliquidens, 36: Lagenorhynchus obscurus, 37: Lagenorhynchus cruciger, 38: Lagenorhynchus australis, 39: Lagenodelphis hosei

General Conclusions

In the interspecific comparison of group sizes a two step model was found that can describe the group size in Delphinoidea species. The most important predictor of group size was the phylogeny reflected by the variables species and subfamily. In addition, predation pressure (reflected by the openness of the habitat) might slightly increase group size and diet might also slightly influence group size.

In a series of intraspecific comparisons the dependence of group size on ecological parameters could be successfully modelled (statistically) for common dolphin, striped dolphin, bottlenose dolphin, Risso's dolphin, pilot whale, killer whale, harbour porpoise and Dall's porpoise. It is striking that group size seems to depend on different sets of variables in each species.

Delphinoidea species can be predicted based on group size, physical environment, diet and life-history information in a step-wise procedure. First all species are split in three (body) size groups of which one only contains the largest killer whales. The small Delphinoidea have to be additionally split according to region to enable a successful classification. These categorisations seem to be mainly based on body size.

Several reasons may account for this picture (see also the discussions of the inter- and intraspecific comparisons, pages 39 and 50):

- The ideas on how group sizes evolve in terrestrial animals cannot be generalised to the aquatic environment. Thus, aquatic mammals face different evolutionary pressures and thus adapt differently. This is not very likely as, even though the physical environment is different, one would expect a strong mammalian heritage that leads to similar reactions if faced with similar problems on land as well as in the water.

- Group size is the result of a process of historical progression within the different species, possibly based on adaptations of a monophyletic precessor rather than a detailed adaptation to the specific (present) niches of these species. If this were the case one can only guess why the different species have evolved in the first place. It could be that this pattern of differing group sizes but similar niches is connected to the relatively fast and contemporaneous radiation of the Delphinoidea species. If, at the beginning of the radiation process, the (few) dolphin species experienced their new niche(s) in the marine habitat as if they were empty, then one can imagine a radiation process fanning out into the(se) empty niche(s) possibly following many (random) evolutionary steps on the way which may have been different for the different species. Once the niche(s) were occupied by the new Delphinoidea species, the radiation stopped, but the different species could (obviously) not displace one another even if the niches were quite similar.

- Delphinoidea might currently face a relaxed evolutionary pressure regarding group size, especially as it seems, that the different species have quite similar or largely overlapping ecological niches. There does not exist a theory, though, which could explain how such a relaxed evolutionary pressure can be maintained over time.

- It may be that the current biological species are not well defined. It is possible that many of the species form local or even sympatric ecotypes that should be differentiated in an analysis as has been conducted here.

- Different species follow different strategies to solve similar problems. This is in principal possible and we are currently learning more about this. Nevertheless this would not alter the conclusion that the evolution of the Delphinoidea is a largely historical (and thus partly accidental) process.

- The shape of the influence of ecological parameters on group size may not be linear and also impossible to bring into a linear form through transformation and thus difficult to capture in an additive statistical model.

These results may lead to the notion that the evolutionary process in Delphinoidea is much more a historical process (with random moves and constraints) than a specific ideal adaptation to current or recent ecological circumstances.