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CO-VARIATION IN THE PROBABILITIES OF SIGHTING HARBOR PORPOISES AND BOTTLENOSE DOLPHINS

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Evidence of violent interactions between bottlenose dolphins (*Tursiops truncatus*) and harbor porpoises (*Phocoena phocoena*) has now been found in several parts of their range, but the factors underlying this behavior remain unclear (Jepson and Baker 1998, Ross and Wilson 1996). Whatever the function of the bottlenose dolphins' aggression, the potentially fatal consequences suggest that there could be selection for avoidance behavior by harbor porpoises. As a result, finer-scale segregation in either time or space may occur where the geographical ranges of these two species overlap (*e.g.*, Durant 1998).

In this study we used data collected from commercial dolphin-watching trips to determine whether there was any relationship between the probabilities of sighting bottlenose dolphins and harbor porpoises. Surveys were conducted from a 16-m converted trawler that has been used for wildlife-watching trips in northeast

Scotland since 1997. All trips were made in the southern part of the Moray Firth, within the area where aggressive interactions between bottlenose dolphins and harbor porpoises were first observed (Ross and Wilson 1996) and continue to be recorded.[1] All trips left from Buckie Harbor (57°40.91′N, 02°57.6′W), and the vessel traveled east within 2 km of the coast. Typically, trips started between 1100 and 1500, lasted for approximately 2 h (mean = 115 min, range 40–220 min) and covered approximately 10 km of coastline.

In the summers of 2000, 2001, and 2002, the Moray Firth Wildlife Centre (MFWC) used these trips as a platform for photo-identification studies of bottlenose dolphins. Throughout this period, at least one MFWC staff member was present on each trip, acting as an interpreter for between 2 and 12 passengers and collecting data on cetacean sightings. During each of these trips, the start and end time of the trip was recorded, together with an estimate of sea state on the Beaufort scale, the GPS location, and time of all encounters with bottlenose dolphins or harbor porpoises.

Trips were made from May to September, on between 87 and 110 d in each year. Where several trips were made on a single day, we randomly selected just one of these to avoid pseudoreplication. Overall, dolphins or porpoises were seen on 147 (50%) of the 295 trips. On 63 trips (21.4%) we encountered only bottlenose dolphins, on 76 trips (25.8%) we saw only harbor porpoises, and both species were encountered on just 8 trips (2.7%). However, the probability of sighting each of these two species is expected to differ in relation to factors such as sea state, because harbor porpoises are inherently more difficult to detect in rough conditions (Hammond *et al.* 2002). Similarly, there are known to have been seasonal (Wilson *et al.* 1997) and interannual (PMT, unpublished data) changes in the relative abundance of bottlenose dolphins in other parts of the Moray Firth, which may also influence sighting probability in this study area. We used logistic regression to explore how a positive sighting of one species during the trip influenced the probability of seeing the second species, while controlling for these other factors. Using forward stepwise models, we determined whether month, year, sea state, trip duration, and the presence of the other species had a significant influence on the probability of sighting (a) bottlenose dolphins and (b) harbor porpoises on each survey. We also checked for interactions between these variables. These analyses used only data on the presence or absence of sightings of each species on each survey, and do not therefore include information on the size of groups or number of encounters. All analyses were carried out using SPSS (Mathsoft Inc.).

Our final model for bottlenose dolphins included only month and the presence of harbor porpoises as significant influences on the probability of sighting (Table 1), with sightings peaking in the middle of the summer (Fig. 1). On the other hand, a broader suite of factors influenced the probability of sighting harbor porpoises (Table 1). As anticipated, the probability of sighting porpoises dropped markedly at higher sea states, and also increased slightly during longer trips. As seen for bottlenose dolphins, sighting probabilities differed through the season, but the

[1] Personal communication from R. Reid, Scottish Agricultural College Veterinary Laboratory, 6 December 2002.

Table 1. Results of the logistic regression models used to determine which factors influenced the probability of sighting (a) bottlenose dolphins and (b) harbor porpoises on each boat trip. The change in deviance refers to removing the term from the final model, with *P* values calculated using a chi-squared approximation.

Term	df	Coefficient	SE	Deviance	*P*
(a) Dolphin sighting probability					
Month	5			18.20	<0.01
Porpoises	1			17.22	<0.001
Total model	288			292.1	
(b) Porpoise sighting probability					
Sea state	1	−0.60	0.178	12.93	<0.001
Trip duration	1	0.035	0.01	14.19	<0.001
Month	5			14.48	<0.05
Year	2			2.05	>0.1
Dolphins	1			15.53	<0.001
Month × Year	10			20.77	<0.05
Total model	277			261.34	

significant interaction between year and month indicates that the nature of this relationship varied between years. In general, sightings of porpoises tended to increase later in the season, but the precise timing of this increase varied between years. Controlling for these other factors, the presence of dolphins remained a highly significant negative influence on the probability of sighting harbor porpoises (Fig. 1).

These results suggest that there are relatively fine-scale differences in the distribution of bottlenose dolphins and harbor porpoises in this study area. Previous surveys conducted throughout the entire Moray Firth have shown that harbor porpoises are often found in more offshore areas, whereas bottlenose dolphins occur most regularly within 5 km of the coast (Hastie *et al.*, in press). Segregation within the small area used in this study could result from different temporal patterns in their use of these coastal waters. Previous studies have highlighted the importance of tidal currents for bottlenose dolphins feeding in adjacent areas (Mendes *et al.* 2002), and it is possible that the two species use such features in slightly different ways. We explored this possibility by comparing the number of sightings of each species in each hour either side of high tide, but there was no significant difference in the timing of encounters with the two species in relation to the tidal cycle (chi-squared = 10.47, 11 df, $P = 0.48$). Alternatively, there could be more subtle differences in habitat use that result in spatial segregation. However, data on survey effort in different parts of the study area were not available to determine whether there were species differences in habitat preference. Nevertheless, the locations of encounters with each species can be compared, and these suggest that the observed pattern could result from fine-scale segregation in both time and space. Figure 2 shows that there is overlap in the distribution of encounters over much of the area, pointing to possible temporal segregation, but there is also an indication of spatial segregation at the western and eastern extremes of the survey area.

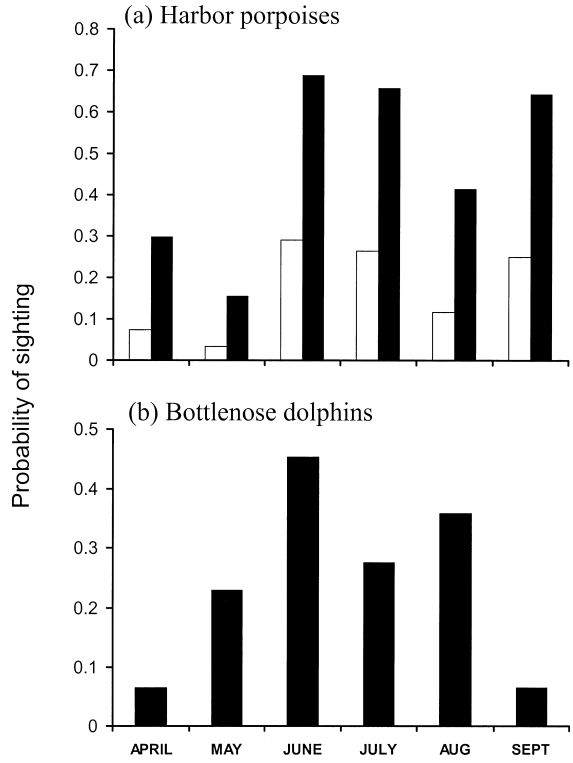

Figure 1. Variation in the predicted probabilities of seeing (a) harbor porpoises and (b) bottlenose dolphins in different months, based upon the logistic regression models in Table 1. Estimates for harbor porpoises are presented for trips on which dolphins were seen (open bars) or were not seen (solid bars), and are standardized for 2002, a trip duration of two hours, and sea state 2. Estimates for bottlenose dolphins are for trips in which porpoises were not seen.

The midsummer peak in the probability of sighting bottlenose dolphins was similar to that seen in adjacent parts of the Moray Firth, and it has been suggested that this may be a response to movements of migrating salmonids through the area (Wilson *et al.* 1997). In contrast, harbor porpoise sightings increased later in the season (Fig. 1a), a pattern also seen in other Scottish coastal waters (Northridge *et al.* 1995). Together, these results highlight that segregation of these two species may be occurring at both large and small scales, and that this should be considered when developing further studies to investigate the interactions between the two species. This finding also has implications for the design and interpretation of line-transect surveys that are used to estimate harbor porpoise abundance (Smith 1981, Dahlheim *et al.* 2000, Hammond *et al.* 2002). Often, these surveys collect multi-species data, but estimates for individual species are generally considered independent. Our results indicate that this is not the case, as the probability of sighting harbor porpoises is lower in presence of bottlenose dolphins. Efforts to improve line-transect estimates by accounting for factors such as environmental

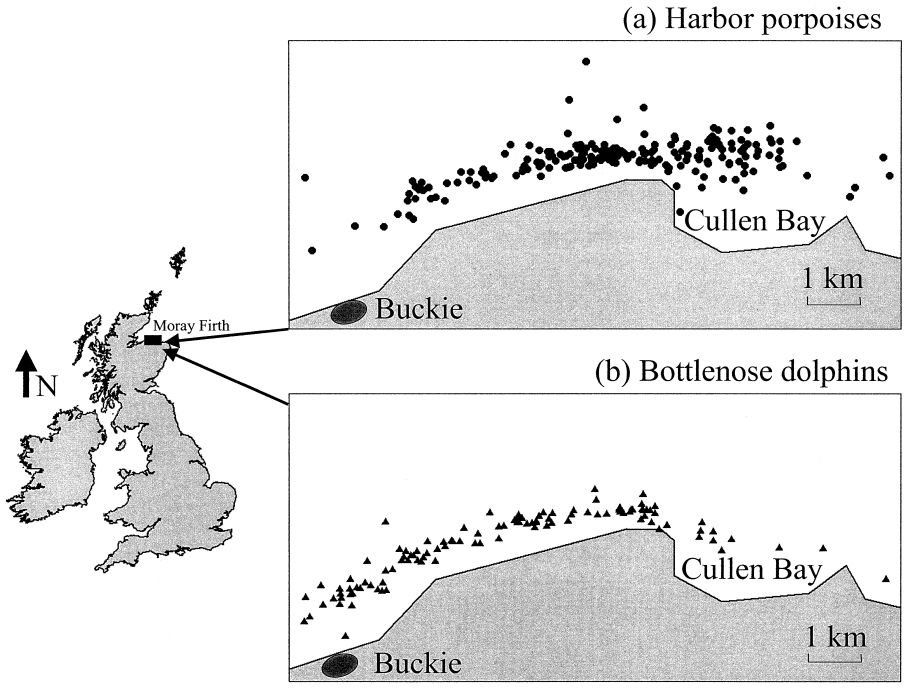

Figure 2. A map of the UK showing the position of the study area, together with locations of the start of encounters with (a) harbor porpoises and (b) bottlenose dolphins.

variation (Forney 2000, Palka and Hammond 2001) and behavioral responses to survey vessels (Palka and Hammond 2001) should, therefore, also consider potential responses to other species present in the sampled area.

More generally, these findings illustrate the value of commercial wildlife-watching trips as a platform for cetacean research. This permitted intensive survey effort over three seasons, greatly increasing the power of our study to detect factors that might be influencing the probability of sighting these two species. This approach builds upon the earlier role that commercial dolphin-watching trips originally played in gathering direct video evidence of the bottlenose dolphins' aggressive attacks upon porpoises (Ross and Wilson 1996). In future, the value of information from commercial trips would be greatly enhanced if GPS data loggers were used to record exact survey routes, thereby permitting quantitative assessments of habitat selection by the two species. In using data of this kind, we assume that sighting effort does not decline through the trip, or following a successful encounter with dolphins. In general, the presence of a regular observer and interpreter should minimize this, particularly as these trips endeavor to detect a range of different wildlife species to maintain passenger interest. On the few surveys on which there were encounters with both species, the initial encounter was with dolphins on four out of ten occasions. Consequently, a positive sighting of bottlenose dolphins did not appear to reduce search effort for harbor porpoises,

indicating that there is a genuine ecological basis to our finding that the probabilities of sighting bottlenose dolphins and porpoises are not independent.

While this study has shown that there is covariation in the probability of sighting these two species, the causes underlying these patterns remain unclear. The occurrence of violent attacks by bottlenose dolphins on harbor porpoises provides one possible cause for this fine-scale segregation, but there are others. Such attacks may lead to avoidance behavior by porpoises. Alternatively, there could be mutual avoidance by individuals of both species, for example, to minimize direct or interference competition for food. Similarly, the two species could be occupying subtly different ecological niches that we were unable detect at the sampling scales used in this study. Nevertheless, whatever the ultimate cause, these data do suggest that further studies at relatively fine scales, targeted at comparing the temporal and spatial distribution of bottlenose dolphins, harbor porpoises, and their potential prey, may provide further insights into the factors driving the interactions between these two species.

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