



## Behavioural synchrony in two species of communally housed captive penguins

Preston Foerder<sup>a,\*</sup>, Martin Chodorow<sup>a</sup> and Donald E. Moore III<sup>b</sup>

<sup>a</sup> Hunter College, The City University of New York, Department of Psychology,  
611 Hunter North, 695 Park Avenue, New York, NY, USA

<sup>b</sup> Smithsonian National Zoological Park, 3001 Connecticut Ave. NW,  
Washington, DC 20008, USA

\*Corresponding author's e-mail address: preston-foerder@utc.edu

Accepted 29 May 2013

---

### Abstract

Animals in aggregations such as herds, schools, flocks, or colonies tend to synchronize their behaviour with each other for food acquisition and predator detection. Different species of captive penguins, when housed communally, intermingle more than in their natural habitat. Wild penguins typically divide themselves into separate colonies by species. We predicted that penguins would synchronize their behaviour more with conspecifics rather than interspecifically in a mixed-species zoo exhibit. The subjects were 65 penguins of two different species, chinstrap (*Pygoscelis antarctica*) and gentoo (*Pygoscelis papua*) in the Central Park Zoo, New York, NY, USA. Using instantaneous scan sampling, 359 video scans were taken over 10 days. Scans were analysed for nine different categories of behaviour for both species. Intra-species synchrony scores were calculated using the Kappa coefficient of agreement, and inter-species synchrony was measured by computing cross-correlations. As predicted, overall synchrony was significantly greater within both species of penguins than for randomly aggregated data representing mixed groups. There was also significantly less synchrony between species than between randomly mixed data for six of the nine behaviour categories. The pattern of results indicates that the penguins had organized by behaviour into separate species-specific colonies within the enclosure. They maintained species separation through behavioural synchrony despite the restrictions imposed by captivity.

### Keywords

penguins, behavioural synchrony, captivity.

## 1. Introduction

In a flock or a colony, birds tend to exhibit behavioural synchrony, maintaining similar behaviour at approximately the same time throughout the

group. Domestic geese (*Anser anser*) show synchronized egg-laying patterns within their own flocks. When flocks are combined, within-flock synchrony is maintained with no synchrony between flocks (Kent & Murphy, 2003). Hens (*Gallus gallus domesticus*) have greater egg laying synchrony between pairs within cages than between cages (Webster & Hurnik, 1994).

Wild penguins have exhibited within-group synchrony. African penguins (*Spheniscus demersus*) have been shown to synchronize their diving when foraging for food (Siegfried et al., 1975; Wilson et al., 1986). Little penguins (*Eudyptula minor*) show synchronized parading, tending to leave and return to the colonies with the same individuals in good breeding years (Daniel et al., 2007).

Behavioural synchrony in animal aggregations increases both efficiency of foraging and predator avoidance (Clayton, 1978; Szekely et al., 1991). Many mechanisms have been posited for synchrony including social facilitation (Clayton, 1978), conspecific copying (Wagner & Danchin, 2003), and Hamilton's (1971) 'selfish herd' effect. However, behavioural synchrony may be affected by captivity. It has been shown that captivity can affect the natural behaviour of animals, both wild (Rowell, 1967) and domestic (Scott, 1948). Aggression and stereotypical behaviours may develop or increase (Clubb & Mason, 2003). Hierarchies and other changes in the social system may appear that do not exist outside of captivity (Rowell, 1967).

Some of the synchrony seen in captive animals may be a consequence of regimented schedules. Captive animals are usually fed at a specific time and place with similar food items. Staddon & Simmelhag (1971) observed that pigeons (*Columba livia*) fed at regular intervals, e.g., on a fixed interval schedule, develop two categories of behaviour: interim activities and terminal responses. The interim activities are repetitive behaviours that occur just after the delivery of food and continue up until the start of terminal responses. The terminal responses are behaviours that consistently occur prior to the time of food delivery. Timberlake & Lucas (1985) noted that the behaviours that occur in laboratory conditioning experiments resemble species-specific food gathering behaviour. These pre- and post-feeding repetitive behaviours seen in laboratory pigeons resemble stereotypical behaviour frequently seen in captive animals and may be responsible for the synchrony that appears in captive animal populations.

We examined two species of penguins housed together at the Central Park Zoo in New York City, USA. The exhibit houses both gentoo penguins (*Pygoscelis papua*) and chinstrap penguins (*Pygoscelis antarctica*). In a mixed

species enclosure, animals are far more intermingled than they would be in the wild and have a limited area in which to maintain different territories. Specifically, we investigated whether these two species had organised into a single synchronized group, had maintained separation by synchronizing their behaviour intraspecifically, or showed no synchrony at all.

Chinstrap penguins are the smaller of the two species, 68–77 cm in body length as opposed to 76–81 cm for the gentoo. The two species have different variations in their black and white patterning, as well as the colouring of their beaks and feet. Their wild colonies are found on the Antarctic Peninsula and the subantarctic islands. Although the two species' ranges overlap, the gentoo's natural range extends farther north and not as far south (Müller-Schwarze, 1984; Williams, 1995; del Hoyo et al., 1997).

Behaviourally, there are a variety of differences between gentoos and chinstraps. Gentoo colonies are smaller and have a greater distance between nests. Chinstraps use fewer and larger stones in their nest (Volkman & Trivelpiece, 1981). When foraging, gentoos spend more time feeding and less time travelling than chinstraps. They also dive deeper closer inshore than chinstraps (Trivelpiece et al., 1986; Kokubun et al., 2010). Chinstraps are more migratory than gentoos, which tend to spend more of the year in their nesting colonies (Bost & Jouventin, 1990). Chinstrap colonies remain in a single area, but gentoos move their colonies small distances annually, typically less than 150 m per year (del Hoyo et al., 1997). The differing behaviour patterns are affecting the response of wild populations to global warming; the chinstraps, with their greater dependence on sea ice, are declining while the gentoo populations are increasing (Forcada et al., 2006).

In the wild, the two species of penguins would be separated by these differences in migratory behaviour and foraging, which do not segregate them within the captive enclosure. Though there is some rare intermingling of the species in the wild, in general they are separated by their individual nesting choices. The gentoos stay in the flat areas while the chinstraps nest on the steep slopes and cliffs (Müller-Schwarze, 1984). Ackerman (1997) found that the birds in the Central Park Zoo his exhibit maintained their natural nesting sites. The exhibit has areas of flat beach on which the gentoos nest and a low cliff where the chinstraps nest. Based on this previous research and preliminary observations, we hypothesized that even though captivity may enforce a certain amount of synchrony on the group as a whole, the

two species will maintain behavioural separation by synchronizing their behaviour more within species than between species. This hypothesis would be supported if more intraspecific than interspecific behavioural synchrony is observed.

## **2. Materials and methods**

### *2.1. Subjects and housing*

The subjects were 65 penguins on exhibit at the Central Park Zoo, New York, NY, USA: 42 chinstrap penguins (*Pygoscelis antarctica*), 22 m, 20 f; 23 gentoo penguins (*Pygoscelis papua*) of two subspecies (7 *P. p. papua* and 16 *P. p. ellsworthii*), 8 m and 15 f. The birds ranged in age from 1 year to over 16 years. At the time of the study, the entire colony had been in existence for 16 years. The subjects' natural yearly light cycles have been reversed to coordinate with the northern hemisphere. Daily and seasonal light shifts occur gradually and are timed to simulate day and night periods and seasonality. L:D cycles range from extremes of 7 h of light daily from December 2nd to January 13th to 18.5 h of light on June 24th with equal L:D periods at the vernal and autumnal equinoxes. Subjects were fed individually by hand twice daily at approximately 10:30 am and 2:30 pm. Feedings took approximately 30–60 min.

The penguins are housed in an interior, enclosed naturalistic habitat. The habitat is divided between a 108 m<sup>2</sup> artificial rocky cliff and beach area at the back two thirds of the exhibit and a 181 700-l fresh water filled pool at the front. Underwater viewing is enabled through a glass wall that runs the length of the exhibit and bisects the pool. Only the top third of the pool is visible through the glass. The lower portion of the pool, along with hiding places behind rocks and cliffs, provide the birds with areas where they cannot be seen from the public viewing area. Various enrichment devices, such as balls, plastic toys, recorded sounds, and piles of ice cubes, are used in the enclosure at different times.

### *2.2. Procedure and apparatus*

The penguins were observed using instantaneous scan sampling. Observation periods did not include feeding times, cage cleaning or other interventions by keepers. Due to the schedule imposed by daily feeding and habitat maintenance, observation times were limited to approximately 3 h between the

first and second feedings and 30–60 min between the second feeding and cleaning of the enclosure. Approximately 10–15 min after the second feeding water sprayers are turned on throughout the exhibit. Observations were stopped before the afternoon cleaning and whenever a keeper was in the enclosure. The study was done during the pre-breeding period in January 2005, 3 days per week for a total of 10 observation days and 359 scans in total. All observations were made from the public viewing area. The winter observation period was chosen to ensure less interference by fewer spectators than attend the zoo at other times of the year. However, this also meant lower light levels in the exhibit than at other times. The observations during this study were discontinued when one subspecies of gentoo was transferred to another facility.

The habitat was scanned every 5 min with a hand-held Sony DCR-TRV140 Digital 8 Camcorder. To maximize the number of birds visible to the camera, scans were conducted in two stages. First the pool was scanned from right to left, raising the camera at the end in a continuous movement to scan the beach and cliff from left to right. Mean time of total scan was 65.80 s (SD = 8.60 s). Mean time of the pool scan was 27.42 s (SD = 3.73 s). Mean time of the land scan was 38.29 s (SD = 6.25 s).

The species of each penguin along with its behaviour according to the ethogram in Table 1 was coded from the videos. As both species are sexually monomorphic, sex of the birds was not included in this analysis. The

**Table 1.**  
Ethogram of penguin behaviours.

Behaviour	Description
Swimming	Bird locomoting or floating in water.
Standing	Bird in an erect position.
Preening	Bird using beak to straighten feathers anywhere on body.
Wing flapping	Bird standing with head down, while flapping wings.
Locomoting	Any form of movement on land from place to place; i.e., running or walking.
Lying	Bird with belly on ground in a prone position.
Diving	Bird moving from land into water.
Single display	Bird standing with head up, flapping wing, while possibly vocalizing. Bird bowing.
Mutual display	Single display behaviours performed along with one or several other birds. Also aggressive behaviours.

primary difference between the subspecies is height (*P. p. papua* are, on average, slightly taller). This difference was also not discernible from a video recording of moving birds in various postures; thus, both subspecies were included in the analysis as a single species. Precautions were taken against counting birds twice by never counting birds exiting the water. As the penguins were capable of swimming much faster than the scan speed, swimming through the scan, turning around and coming back into the scan, birds in the water were only counted swimming in one direction depending on which direction the majority of birds were swimming. Mean swimming duration of birds was much greater than scan time based on random samples of 10 birds of each species; chinstrap:  $M = 9.89$  min,  $SD = 13.43$  min; gentoo:  $M = 6.40$  min,  $SD = 8.27$  min.

In preparation for statistical analysis, the coded behavioural data were used to construct three tables, one for all the penguins combined, one for chinstraps, and one for gentoos. In each data table, each of the 359 rows represented a scan and each of the nine columns represented a type of behavioural activity. Cell<sub>*ij*</sub> of the table contained  $n_{ij}$ , the number of penguins during scan *i* that were engaged in activity *j*. The total number of penguins in view during scan *i* is represented by  $n_{i.}$ , the sum of the counts in row *i*.

### 2.3. Statistical analysis

Our analysis of the data compares intra- and inter-species synchrony using two measures, Kappa (Fleiss, 1971; Siegel & Castellan, 1988; Rook & Penning, 1991) and cross-correlation (Bjørnstad et al., 1999). Unlike some other synchronization measures (e.g., Engel & Lamprecht, 1997; Walker et al., 2010), neither of these requires that the birds be individually identified.

Kappa can provide an index of overall synchronization within a population by using the ratio of the number of pairs of individuals engaged in a common activity to the total possible number of pairs. In terms of the data table, there is maximal synchronization in scan *i* when one of the cells in row<sub>*i*</sub> contains  $n_{i.}$ , the total number of individuals for that row. This represents a scan in which all of the animals are engaged in the same activity. When there is less synchronization in a scan, the individuals are engaged in many different activities and, therefore, their counts are distributed among many cells of the row. Of course, activities that are more prevalent overall (summed over the whole table), such as standing, would be expected to have higher counts in any given scan than less frequent activities, such as wing flapping. Kappa

takes overall prevalence of activities into account by computing an expected level of synchronization due to chance (see Rook & Penning (1991) for the formulas for computing Kappa based on the arrangement of the data tables described in the previous section).

Recently, Asher & Collins (2012) compared Kappa to three other measures of behavioural synchrony (proportion of observations 100% conforming, proportion of conforming individuals, and Ruckstuhl's group mean) in a computer simulation study that varied the number of behaviours, the number of individuals, and the degree of synchrony. They concluded that, of the four measures they tested, Kappa was the most accurate because it is the only one of the four that takes into account the expected degree of synchrony due to chance.

Kappa can indicate if the overall activity pattern within chinstraps is more synchronized than expected by chance alone, and, similarly, if the overall activity pattern within gentoos is more synchronized than expected solely by chance. By contrast, the other metric in our analysis, cross-correlation, can be used to measure the synchrony between two populations (Bjørnstad et al., 1999). A simple form of this measure is the Pearson product-moment correlation coefficient (i.e., the Pearson  $r$  statistic) calculated over  $x, y$  pairs consisting of the proportion of individuals in population X and the proportion of individuals in population Y engaged in a particular activity (e.g., swimming) during each observation period. In terms of the data table, it is the correlation between the proportions ( $n_{ij}/n_{i.}$ ) of individuals in column  $j$  of the table for chinstraps and the proportions of individuals in column  $j$  of the table for gentoos.

Kappa and cross-correlation are complementary measures of synchrony in the following ways: Kappa can be used to analyze the entire data table for a group and produce a single number representing its synchrony. If the Kappas for chinstraps and gentoos are significant, it means that there is overall synchrony within both groups, but it does not tell us if the groups' activity patterns are the same or different, or, if different, where they differ from each other. On the other hand, cross-correlation can directly compare the activity of the two groups over time for a specific behaviour, such as swimming. If the cross-correlation between chinstraps and gentoos for a particular activity is significantly *less* than expected by chance, then there is asynchrony between the two species for that behaviour. However, in contrast to Kappa, a single cross-correlation cannot provide an overall picture.

In the current study, assessing the significance of Kappa and cross-correlation poses a challenge for the standard parametric approach to statistical significance. For example, Rook & Penning (1991) note that if the number of scans is large, then Kappa will be approximately normally distributed, and this can provide a basis for hypothesis testing. However, the *p*-values of such a hypothesis test, or a comparable one for cross-correlation, assume, among other things, independence between observations or scans, an assumption that is not met here. Specifically, our data are temporally non-independent (autocorrelated), a condition that can occur in the sampling of behaviour, especially when scans are taken at regular and closely spaced intervals (Dow et al., 2006). To measure the lack of independence, autocorrelations were calculated for both species for the nine behaviours that we recorded. Over lags ranging from 1 to 36, representing temporal separations from 5 to 180 min (the duration of an average day's recording period), all nine behaviours of each species showed significant autocorrelation at one or more lags. Randomly sampling from the 359 scans did not entirely ameliorate this problem, even when only a single scan was selected from each day's data. Clearly, there are considerably fewer degrees of freedom in the data than indicated by the number of recorded scans (359), and this poses a problem for assigning statistical probabilities to outcomes.

As an alternative to the parametric approach, we used a randomization test (Edgington & Onghena, 2007) to compare the observed synchrony measures (Kappas and cross-correlations) to the measures that are found when group membership is the result of randomly assigning penguins to groups without regard to their species (a similar use of group randomization can be found in Walker et al. (2010), where it is used to test the significance of a measure of synchrony in subgroups of sheep within a flock). Random assignment will result in mixed groups, each consisting of some chinstraps and some gentoos. There are more than  $2.27 \times 10^{17}$  ways in which the 65 penguins of the current study can be partitioned into groups of 42 and 23, the maximum count of chinstraps and gentoos, respectively. This number of possibilities is too great to be examined exhaustively, but a large random sample of the partitions makes it possible to construct distributions of Kappas and cross-correlations for these partitions and compare them to the observed values. In this manner, we can ask how likely it is for a random partition to have Kappas like those actually observed for chinstraps and gentoos, or cross-correlations like those measured between our two species. Because of



**Table 2.**

An example of hypothetical activity data randomly partitioned into two groups.

Scan	Combined groups					Group X				Group Y					
	Activities				Total (X's + Y's)	Activities				Total	Activities				Total
	A	B	C	D		A	B	C	D		A	B	C	D	
1	5	2	2	1	10 (6 + 4)	4	0	1	1	6	1	2	1	0	4
2	4	0	5	0	9 (5 + 4)	3	0	2	0	5	1	0	3	0	4
3	3	6	1	1	11 (6 + 5)	2	4	0	0	6	1	2	1	1	5
Total	12	8	8	2		9	4	3	1		3	4	5	1	

the non-independence problem in time-series data, randomization tests have been used by researchers in a number of fields to test the statistical significance of their measures of temporal synchrony. For example, Feldman et al. (2011) examined the synchrony of heart rhythms in mother-infant pairs by comparing the cross-correlations between each mother and her own infant to cross-correlations between the data of randomly paired mothers and infants.

There are many possible ways to randomize data. The procedure that we used kept all aspects of the data the same except for the assignment of individuals to groups, which was done randomly. Table 2 illustrates the process using hypothetical data. In scan 1, for the combined groups, there were 5 individuals engaged in activity A, 2 in activity B, 2 in activity C, and 1 in activity D. For the randomization, these 10 individuals' behaviours were represented as AAAAABBCCD and were placed in an array, which was then randomized in terms of its order, producing, for example, ACAAD-BACAB. Next, the array was partitioned based on the number of individuals in group X and in group Y that were observed in scan 1, in this case, 6 X's and 4 Y's. This meant the randomized array was split between the first 6 and last 4 elements, resulting in the partition [ACAADB] [ACAB], which was tallied and is shown for scan 1 in the sections of the table labelled Group X and Group Y, respectively. The same procedure was applied to scan 2 and to scan 3. In our actual randomization test using the combined penguin data, the activity counts in each of the 359 scans were partitioned into two groups, with the number of individuals in Group X equal to the number of chinstraps and the number of individuals in Group Y equal to the number of gentoos that were observed on that scan (as noted earlier, on any given scan, it was generally the case that some penguins were out of view). This resulted in a

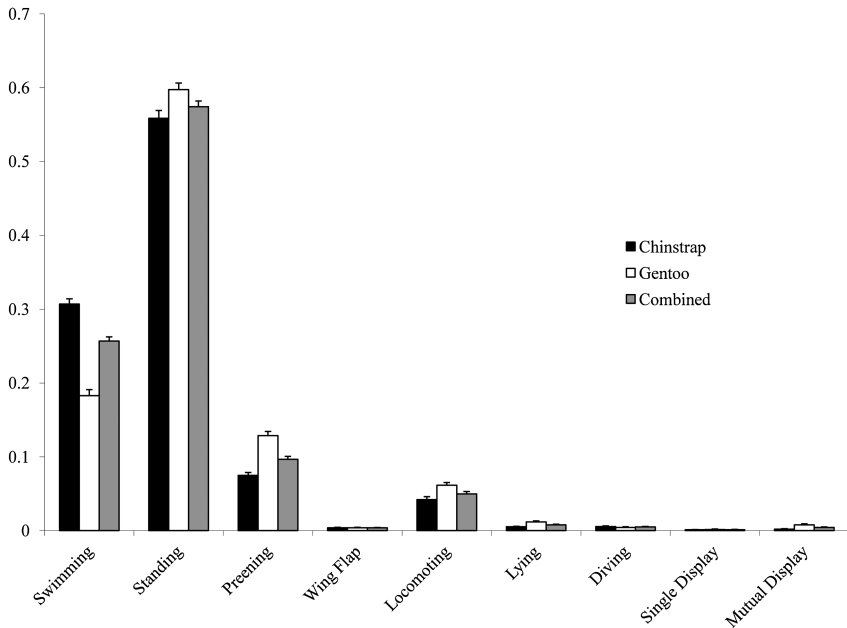
randomized scan for each group, as shown in Table 2. Once all 359 scans had been partitioned in this manner, the values of the test statistics, Kappa and cross-correlation, were computed. Once again, it is important to note that the number of activities and the group sizes were constrained to match those of the observed data, and the temporal structure of the combined data was retained; only the assignment of individuals to groups was randomly varied.

For the Kappa tests, the randomization of the data table was repeated 10 000 times, yielding 10 000 Kappas for each group. These were used to construct two distributions of Kappa, one for the chinstraps and the other for the gentoos. Standard statistical packages generally assume that the number of subjects (the row totals in the tables) is constant when computing Kappa, but since this was not the case for our data, we computed the Kappas by using a custom-written program in Perl that did not make this assumption. For the cross-correlation tests, the randomization of the data table was repeated 1000 times, yielding in a total of 9000 cross-correlations (1000 for each activity type). From these, a distribution was constructed for each kind of behaviour. The cross-correlations were computed in Microsoft Excel. To calculate the  $p$ -value for an observed measure (Kappa or cross-correlation), the measure was compared to the appropriate distribution produced through randomization. The  $p$ -value was the proportion of cases in the distribution that were equal to or more extreme than the observed measure.

### **3. Results**

The average proportions of birds engaged in each behaviour are shown in Figure 1. For both species, standing was the most frequent behaviour followed by swimming, preening and locomoting.

Table 3 shows the values of Kappa for the two species combined and for the chinstraps and gentoos separately. The table also shows the means, standard errors and ranges of the two distributions of Kappa produced by randomization. The observed Kappa for the chinstraps, 0.0645, was greater than all 10 000 of the Kappas in the distribution of Group X, the random group whose size matched that of the chinstraps and, therefore, the probability that this difference is due to chance is  $p < 0.0001$ . Similarly, the Kappa for the gentoos, 0.0714, was greater than all 10 000 Kappas in the distribution of Group Y, the random group whose size matched that of the gentoos, and hence,  $p < 0.0001$ .



**Figure 1.** Average proportion of birds engaged in each behaviour for chinstrap ( $N = 26.18$ ), gentoo ( $N = 17.50$ ) and combined ( $N = 43.68$ ) + SE, 359 scans.

Table 4 shows the values of the observed cross-correlations between species for the nine behaviours, as well as their  $p$ -values, and the means, standard errors, and ranges for the cross-correlation distributions produced by randomization. The cross-correlations for the four most frequent be-

**Table 3.**

Numbers of penguins, proportions of observed and expected synchronization and values of observed Kappa, by group; characteristics of randomization test distributions of Kappa.

Group	Mean number observed per scan	Proportion of synchronization		Observed Kappa	Randomization test distributions of Kappa (based on 10 000 randomizations)		
		Observed	Expected		Mean	SE	Range
Combined	43.68	0.444	0.415	0.0500			
Chinstrap	26.18	0.460	0.423	0.0645*	0.0507	0.0028	0.0382–0.0617
Gentoo	17.50	0.458	0.417	0.0714*	0.0494	0.0039	0.0350–0.0664

\*  $p < 0.0001$ , based on randomization test.

**Table 4.** Observed cross-correlations between chinstraps and gentoos engaged in each of 9 activities; characteristics of randomization test distributions of cross-correlation for 9 activities.

	Activity								
	Stand	Swim	Preen	Locomote	Wing flap	Lie	Dive	Single display	Mutual display
Observed cross-correlation	0.311**	0.340**	0.403*	0.368**	0.053	0.234**	0.114*	0.222	0.011**
Randomization test distributions of cross-correlation (based on 1000 randomizations)									
Mean	0.518	0.528	0.489	0.623	0.056	0.085	0.379	0.157	0.353
SE	0.027	0.028	0.031	0.031	0.047	0.043	0.079	0.099	0.086
Max	0.597	0.605	0.602	0.717	0.169	0.227	0.576	0.422	0.679
Min	0.425	0.437	0.390	0.513	-0.056	-0.043	0.105	-0.022	0.134

\*  $p < 0.01$ , based on randomization test.

\*\*  $p < 0.001$ , based on randomization test.

haviours — standing, swimming, preening and locomoting — were all significantly *less* than those of the randomizations ( $p < 0.001$  for standing, swimming and locomoting, and  $p < 0.01$  for preening), showing less synchrony between chinstraps and gentoos than expected by chance. The five lower frequency behaviours — wing flapping, lying, diving, single display and mutual display — show a less uniform pattern. Diving and mutual display are significantly less correlated between the species ( $p < 0.01$  and  $p < 0.001$ , respectively), while wing flapping and single display are not significantly different from the cross-correlations in the randomizations, and, surprisingly, lying is more strongly cross-correlated between chinstraps and gentoos than it is between randomized groups ( $p < 0.001$ ).

#### 4. Discussion

The results are consistent with the view that there is overall synchrony in behavioural activity within both species of penguins and that their activity patterns are different from each other for six of the nine types of behaviour recorded, including the four most frequent types. The values of Kappa in Table 3 appear to be quite small, but as Asher & Collins (2012) note from their simulation studies, Kappa decreases as the number of behavioural categories increases. When the Kappa values of the chinstraps and gentoos were compared to those calculated for groups of the same size that were formed by random assignment, the results showed greater synchrony within the same-species groups than within the mixed-species groups. When cross-correlations were used to measure synchrony between groups, the results for most of the behaviour categories showed significantly less synchrony between chinstraps and gentoos than between randomly assigned groups of comparable sizes.

The methods we have used to analyse synchrony in our data can be applied more generally to any situations in which animals can be classified in terms of their group membership (e.g., in some cases by species, sex, or age) but cannot be identified individually. The reason for this is that Kappa and cross-correlation, our measures of synchrony, can be computed over groups rather than individuals. Furthermore, the combination of a measure of within-group synchrony, such as Kappa, and a measure of between group synchrony, such as cross-correlation, provides a much better picture of species distinctiveness through behavioural synchrony than either measure alone. As noted earlier,

the randomization analysis presented here is similar to that of Walker et al. (2010), who measured synchrony of grazing in subgroups of sheep. Their results showed that there was significantly greater synchrony within an all-male subgroup and within an all-female subgroup than in groups formed by random assignment, but the same was not true for subgroups based on the animal's size (large or small). The Walker et al. study differed from the current one in a number of ways: (a) it used a measure of synchrony related to network analysis which required that the individual animals be identifiable, (b) it measured only a single activity, grazing and (c) it did not directly compare the synchrony between two groups.

Returning to the current study, less roaming space within the exhibit than in the wild increases intermingling that may facilitate the synchrony of the group. Yet within the exhibit, species differences keep them separated to some degree in behaviour if not in space. The reasons for these differences may derive from both behaviour and physiology. The birds have shown that they maintain their species-typical nesting sites. This behaviour indicates that their innate behaviours are still in play even though all of the birds were hatched in captivity and have never been in the wild (Ackerman, 1996). Ruckstuhl (1999) theorized that synchrony is influenced by body size, which determines foraging needs and activity budgets. In a sexually dimorphic species, such as bighorn sheep, synchrony will happen within sexes as well as within age groups. In a fast maturing, sexually monomorphic species, such as penguins, one would expect greater synchrony across individuals. The differences in synchrony between the gentoo and chinstrap penguins may be a consequence of the different body sizes of the two species.

Some of the synchrony observed in this study may be due to species-specific circadian rhythms. Penguins utilize a circadian clock that follows day length to aid in navigation and regulation of breeding cycles. Both gentoo and chinstrap show diurnal activity patterns that correlate with light/dark cycles and reduced activity during periods of least light intensity. However, chinstrap and gentoo, in the wild, have different foraging schedules (Cockrem, 1990). The birds' innate circadian cycles could account for some of the synchronized behaviour. The light schedules in the Central Park Zoo exhibit duplicate seasonal light changes to approximate the bird's native latitudes to aid in breeding. Other zoos have reported breeding success using this lighting technique as well (AZA, 2005).

While the dim exhibit lighting in January may have affected observation, video adjustments during behaviour coding were able to compensate for the lower light levels. The zoo setting imposed other practical observation problems: video scans blocked by the public, varying daily schedules, and hidden animals. All of these can affect the accuracy of the observations. Obviously, observations without these impediments would be ideal, but impractical in a working zoo setting. To some extent, the limits of these constraints have been compensated for in the statistical analysis. Other interventions by the keepers happened during the study as a part of the everyday operations of the zoo. As the analysis was based on synchronization, either the animals had a synchronized or unsynchronized response to these interventions that would not have greatly affected the results.

It may be argued that because of the scanning procedure, averaging 65 s per scan, that the behaviour is not exactly synchronized. Many of the behaviours analysed were states, such as standing and swimming, which tended to last much longer than the scans. Other event behaviours would have happened within a close enough period of time that they were nearly synchronous if not exactly so. The scanning was done in the fastest method possible to cover the entire exhibit, while still being able to view as many penguins as possible. A 'snapshot' photo would have given an actual synchronous scan but would not have been able to differentiate moving behaviours. Also due to the length of the exhibit and the narrowness of the viewing area, one photo could not show the entire area and would still have to be aided by other photos, removing the precise synchrony. Penguins tend to be very sedentary, as shown by their most frequent behaviour: standing. Swimming was shown to last much longer than the scan. Taking all this into account, we believe that the scanning method was the best possible under the constraints of the exhibit.

Observations of the birds during the study seemed to indicate that space-usage was partially divided by species. Future research could investigate the actual space usage of the exhibit, time budgets, and synchrony over the course of the year to see how it is affected by light variation and breeding cycle. A comparative study with a wild population of the same species could also determine the amount of synchronization maintained by these penguins in the wild and that could be compared to captive populations as a measure of the effect of captivity on their behaviour.

Housing multiple species of penguins together in a single exhibit is a common strategy in many facilities (AZA, 2005). Mixed species penguin exhibits similar to the Central Park Zoo can be seen in facilities ranging from the Tennessee Aquarium and SeaWorld San Diego in the USA to the Rotterdam Zoo in the Netherlands (P. Foerder, personal observation). When behavioural problems arise in a mixed-species exhibit, knowledge of behavioural synchrony can aid in determining the exact treatment of each species in an exhibit, contributing to animal welfare. Differences in the rhythm of activity and rest periods may lead to incompatibility in mixed species exhibits (Hediger, 1950). Part of the husbandry of maintaining animals in a mixed-species exhibit should be ascertaining their social relationships. This knowledge can guide care of the animals and assist in introductions of same or different species. It is necessary to take temporal and social relationships among animals into consideration in exhibit design (Nuttall, 2004). In mixed species zoo exhibits, these relationships may be hard to ascertain. Our research showing that penguins maintain species-specific behavioural synchrony within the confines of captivity may aid in communal housing of different penguin species.

### Acknowledgements

We would like to thank the staff at the Central Park Zoo for their help in conducting this study: John Rowden, Yula Kapetanacos and Rob Gramzy. Diana Reiss, Sheila Chase, Mark Hauber and Sarah Webb are acknowledged for their editorial comments and suggestions.

### References

- Ackerman, C. (1996). Nesting preferences of gentoo and chinstrap penguins at the Central Park Wildlife Center, New York. — Draft copy, Central Park Wildlife Center, New York, NY.
- Ackerman, C. (1997). Nest-site preferences, pair-fidelity and site-fidelity in gentoo and chinstrap penguins. — *Int. Zoo News* 44: 327-333.
- Asher, L. & Collins, L. (2012). Assessing synchrony in groups: are you measuring what you think you are measuring? — *Appl. Anim. Behav. Sci.* 138: 162-169.
- AZA (2005). Penguin taxon advisory group penguin husbandry manual, 3rd edn. — Available online at: [http://marineanimalwelfare.com/images/Penguin\\_HB.pdf](http://marineanimalwelfare.com/images/Penguin_HB.pdf).
- Bost, C. & Jouventin, P. (1990). Evolutionary ecology of gentoo penguins (*Pygoscelis papua*). — In: *Penguin biology* (Davis, L.S. & Darby, J.T., eds). Academic Press, New York, NY, p. 85-108.



- Bjørnstad, O., Ims, R. & Lambin, X. (1999). Spatial population dynamics: analyzing patterns and processes of population synchrony. — Trends Ecol. Evol. 14: 427-432.
- Clayton, D.A. (1978). Socially facilitated behavior. — Q. Rev. Biol. 53: 373-392.
- Clubb, R. & Mason, G. (2003). Animal welfare: captivity effects on wide-ranging carnivores. — Nature 425: 473-474, DOI:10.1038/425473a.
- Cockrem, J.F. (1990). Circadian rhythms in Antarctic penguins. — In: Penguin biology (Davis, L.S. & Darby, J.T., eds). Academic Press, New York, NY. p. 319-339.
- Daniel, T.A., Chiaradia, A., Logan, M., Quinn, G.P. & Reina, R.D. (2007). Synchronized group association in little penguins (*Eudyptula minor*). — Anim. Behav. 74: 1241-1248.
- Del Hoyo, J., Elliott, A. & Sargatal, J. (eds) (1997). Handbook of the birds of the world, Vol. 1: ostrich to ducks. — Lynx Edicions, Barcelona.
- Dow, S., Engel, J. & Mitchell, H. (2006). Autocorrelation, temporal independence, and sampling regimen. — In: Zoo research guidelines: statistics for typical zoo datasets (Plowman, A., ed.). Biza, London.
- Edgington, E.S. & Onghena, P. (2007). Randomization tests, 4th edn. — Chapman & Hall, London.
- Engel, J. & Lamprecht, J. (1997). Doing what everybody else does? A procedure for investigating behavioural synchronization. — J. Theor. Biol. 185: 255-262.
- Feldman, R., Magori-Cohen, R., Galili, G., Singer, M. & Louzoun, Y. (2011). Mother and infant coordinate heart rhythms through episodes of interaction synchrony. — Inf. Behav. Dev. 34: 569-577.
- Fleiss, J.L. (1971). Measuring nominal scale agreement among many raters. — Psychol. Bull. 76: 378-382.
- Forcada, J., Trathan, P.N., Reid, K., Murphy, E.J. & Croxall, J.P. (2006). Contrasting population changes in sympatric penguin species in association with climate warming. — Global Change Biol. 12: 411-423.
- Hamilton, W.D. (1971). Geometry for the selfish herd. — J. Theor. Biol. 31: 295-311.
- Hediger, H. (1950). Wild animals in captivity. — Butterworth Publications, London.
- Kent, J.P. & Murphy, K.J. (2003). Synchronized egg laying in flocks of domestic geese (*Anser anser*). — Appl. Anim. Behav. Sci. 82: 219-228.
- Kokubun, N., Takahashi, A., Mori, Y., Watanabe, S. & Shin, H. (2010). Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. — Mar. Biol. 157: 811-825.
- Müller-Schwarze, D. (1984). The behavior of penguins: adapted to ice and tropics. — State University of New York Press, Albany, NY.
- Nuttall, D.B. (2004). An animal-as-client (AAC) theory for zoo exhibit design. — Landscape Res. 29: 75-96.
- Rook, A.J. & Penning, P.D. (1991). Synchronisation of eating, ruminating and idling activity by grazing sheep. — Appl. Anim. Behav. Sci. 32: 157-166.
- Rowell, T.E. (1967). A quantitative comparison of the behaviour of a wild and caged baboon group. — Anim. Behav. 15: 499-509.
- Ruckstuhl, K.E. (1999). To synchronise or not to synchronise: a dilemma for young bighorn males? — Behaviour 136: 805-818.

- Scott, J.P. (1948). Dominance and the frustration–aggression hypothesis. — *Physiol. Zool.* 21: 31-39.
- Siegel, S. & Castellan, N.J. (1988). *Nonparametric statistics for the behavioral sciences*. — McGraw-Hill, New York, NY.
- Siegfried, W.R., Frost, P.G.H., Kinahan, J.B. & Cooper, J. (1975). Social behavior of Jackass penguins at sea. — *Zool. Afr.* 10: 87-100.
- Staddon, J.E.R. & Simmelhag, V.L. (1971). The “superstition” experiment: a reexamination of its implications for the principles of adaptive behavior. — *Psychol. Rev.* 78: 3-43.
- Szekely, T., Sozou, P.D. & Houston, A.I. (1991). Flocking behavior of passerines: a dynamic model for the non-reproductive season. — *Behav. Ecol. Sociobiol.* 28: 203-213.
- Timberlake, W. & Lucas, G.A. (1985). The basis of superstitious behavior: chance contingency, stimulus substitution, or appetitive behavior? — *J. Exp. Anal. Behav.* 44: 279-299.
- Trivelpiece, W.Z., Bengtson, J.L., Trivelpiece, S.G. & Volkman, N.J. (1986). Foraging behavior of gentoo and chinstrap penguins as determined by new radiotelemetry techniques. — *Auk* 103: 777-781.
- Volkman, N.J. & Trivelpiece, W. (1981). Nest-site selection among Adelie, Chinstrap and Gentoo penguins in mixed species rookeries. — *Wilson Bull.* 93: 243-248.
- Wagner, R.H. & Danchin, E. (2003). Conspecific copying: a general mechanism of social aggregation. — *Anim. Behav.* 65: 405-408.
- Walker, D., Carmeli, C., Perez-Barberia, F., Small, M. & Perez-Fernandez, M. (2010). Inferring networks from multivariate symbolic time series to unravel behavioural interactions among animals. — *Anim. Behav.* 79: 351-359.
- Webster, A.B. & Hurnik, J.F. (1994). Synchronization of behavior among laying hens in battery cages. — *Appl. Anim. Behav. Sci.* 40: 153-165.
- Williams, T.D. (1995). *Bird families of the world: the penguins (Spheniscidae)*. — Oxford University Press, Oxford.
- Wilson, R.P., Wilson, M.T. & McQuaid, L. (1986). Group size in foraging African penguins (*Spheniscus demersus*). — *Ethology* 72: 338-341.