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Change in stingray behaviour and social networks in response to the scheduling of husbandry events

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Abstract

Husbandry tasks are often carried out at the same time and in the same manner every day, resulting in the potential for them to become predictable to animals. An unpublished study conducted on a mixed species enclosure of blue-spotted ribbontail rays (*Taeniura lymma*) and blue-spotted maskrays (*Neotrygon kuhlii*), reported increased intra and interspecies aggression preceding training sessions that took place at a fixed time. The current study monitored the behavioural responses of the rays to training events, when training was carried out on either a predictable or an unpredictable schedule. Overall, incidences of aggression on days when training occurred were lower than when no training took place; however, aggression rates varied according to the schedules of training and group composition. Increased activity levels before a training session suggest anticipation of this event. Comparison of social networks for aggressive interactions between conditions showed species and individual differences in aggression. However, these differences may have been in response to a change in social composition of the group in the middle of the study and not due to differences in study conditions. This study will inform management practice by highlighting the importance of husbandry regimes on animal behaviour.

Introduction

The implementation of positive reinforcement training (PRT) can be a highly beneficial management technique used to improve the welfare of captive animals (Corwin 2012). Captive enclosures are often smaller than an animal's natural range and therefore it may not be possible to avoid other individuals or escape from agonistic interactions (Henningsen et al. 2004; Sapolsky 2005). For species known to perform aggression in such captive environments, during key events or life stages, PRT can be implemented to help manage situations; however, the majority of research into the effect of training focuses on mammalian species. As zoos and aquariums aim to maintain high standards of animal welfare, elevated levels of aggression may be deemed an indicator of reduced welfare when compared to typical behavioural repertoires. Training can be used to reduce aggression (Corwin 2012), but in aquarium tanks housing highly dominant individuals, further management techniques may be required, such as the implementation of cooperative feed training. The technique reinforces dominant animals to allow feeding by subordinate animals, with subordinate animals receiving food-based reinforcement for feeding and socially accepting the more dominant individual (Laule and Desmond 1998). Cooperative feeding is adopted in a range of captive environments, commonly in public aquaria, to allow all individuals in a group to gain access to food and reduce aggressive interactions.

When PRT becomes an established part of animal husbandry, the training sessions may be scheduled at a particular time of day. As is the case with other husbandry events, such as feeding, scheduled husbandry can become part of a predictable routine. Predictability can be temporal or signalled, relating to the reliability of the timing of events or the cues before events respectively (Bassett and Buchanan-Smith, 2007) and can affect animal behaviour and welfare. Much of the research on this topic has been conducted on the temporal predictability of feeding times, and predictable feeding schedules have been found to have a number of different behavioural effects in a range of taxa (for review see Bassett and Buchanan-Smith 2007). Specifically in fish, feeding on a temporally predictable schedule has been found to result in increased food anticipatory activity (FAA) (in golden shiners, *Notemigonus crysoleucas*, Reebs and Lague 2000; and goldfish, *Carassius auratus*, Vera et al. 2007); heightened aggression (in Arctic charr, *Salvelinus alpinus*, Brännäs et al. 2005) and in less dorsal fin erosion caused by aggression, compared to unpredictable feeding schedules (in Atlantic salmon, *Salmo salar*, Cañon Jones et al. 2012). Therefore, the importance of monitoring aggression within public aquaria, associated specifically with regard to responses to scheduled husbandry events, is important in terms of welfare and improving animal husbandry.

The position of an individual in a social hierarchy has been shown to influence their food intake. For example, Arctic charr are more dominant and aggressive when given greater access to food (Adams et al. 1995). Aggression is often performed by higher-ranking individuals in social groups, to establish dominance over territories, food and mates (Harwood et al. 2003). This aggression aids in maintaining a stable group structure but can lead to compromised welfare when an individual is repeatedly attacked (Krebs and Davies 1997; Turnbull et al. 1998). Aggressive behaviours (described as bites, nips and chases) have been reported in groups of Atlantic halibut (*Hippoglossus hippoglossus*) at the start of feeding sessions (Greaves and Tuene 2001); however, this aggression may have been due to misdirected feeding attempts and competition for food. Training techniques for specific individuals can result in behaviour changes during training sessions, in subsequent feeding events, and at other non-food related times (Schapiro et al. 2001). Target training has been recommended as a technique to reduce aggression (e.g. Smith et al. 2004); however, if training sessions become temporally predictable, there is potential for them to result in anticipatory behaviour, as has been reported for scheduled feeding times.

Social network analysis (SNA) has been used since the 1930s to discern direct and indirect relationships between humans (Wasserman and Faust 1994). Wilson (1975), and more recently a number of additional researchers (Krause et al. 2007; Coleing 2009; Krause et al. 2009), have applied SNA to animal behaviour in a range of areas most commonly involving non-human primates (Krause et al. 2007). Social network analysis has been conducted in a range of aquatic species including guppies (*Poecilia reticulata*, Croft et al. 2004), Atlantic salmon (Cañon Jones et al. 2010; Cañon Jones et al. 2012), and bottlenose dolphins (Tursiops truncatus, Lusseau and Newman 2004; Lussaeu et al. 2006). Cañon Jones et al. (2012) used SNA to investigate the effects of changing the predictability of feed schedules on Atlantic salmon behaviour and fin damage, and found that the differences in aggression and fin damage were related to changes in the social networks of the individuals as a result of the different feeding conditions. In response, determining the social network of captive groups can assist in the investigation of the effect of scheduled husbandry events on behaviour.

This study documents the influence of PRT on levels of aggression and investigate the effects of conducting training on a predictable and unpredictable routine. In addition, the study investigates differences in the social network of individuals in the tank in response to husbandry training and changes in social group composition.

Materials and method

Study animals consisted of three adult female blue-spotted ribbontail rays (*Taeniura lymma*) (numbered 1 to 3) and three adult female blue-spotted maskrays (*Neotrygon kuhlii*) (numbered 4 to 6), housed in a mixed species exhibit with six silver moonies (*Monodactylus argenteus*) and one blue-striped snapper (*Lutjanus kasmir*) at Living Coasts, Torquay, UK. The tank was 12,500 litres in volume at a depth of 82.5cm. The tank was divided by a footbridge running along the middle of the tank. All species were able to swim under the bridge and access all areas; however, visitors were unable to see the animals when under the bridge. The water temperature was maintained between 22 and 26°C and the salinity between 31–34ppt. There was a layer of 1–2 cm of fine coral sand covering the base of the tank, with some rocks placed throughout. Artificial mangrove roots protruded from above the water into the tank. Visitors can view the surface of both tanks and two sides of the larger tank through the glass.

The rays were fed three scatter-feeds per day. The first was at 0845 hours and consisted of 45g of New Era Marine Pellets, the second and third feeds were both 150g of chopped mixed wet food (squid, sandeel, sprat, smelt and mackerel or herring) at approximately 1230 and 1600 hours (+/− 10 minutes). The second feed also incorporated a guest educational talk.

Target training was carried out with two of the blue-spotted ribbontail rays, which were identified as the two most dominant

Table 1. Training conditions.

Training condition	Duration	Training days	Training time	Individual trained
No training	12 days	No training	No training	None
Predictable 1	25 days	Monday, Wednesday and Friday	1530 hours	Dominant female
Unpredictable	16 days	Random days, 3 times per week	Random times between 0845 and 1500 hours	Second most dominant female
Predictable 2	16 days	Monday, Wednesday and Friday	1530 hours	Second most dominant female

Table 2. Descriptions of aggressive event behaviours.

Behaviour	Description
Chasing	Actively following another swimming animal, with one or both animals exhibiting aggression or submission
Biting	Gripping another animal with mouth
Retreat	Actively moving away from another animal by more than one body length
Collision	Swimming into a mobile or stationary animal, resulting in displacement of the target animal

Table 3. Number and description of the different data collection sessions throughout each data collection day in the different training conditions.

Training condition	Pre-feed (20 minutes prior to feeding).	Post-feed (20 minutes after feeding).	Before predictable training time*	After predictable training time**	Before unpredictable training time*	After unpredictable training time**	General (20 min sessions at varying times of day to ensure all sessions in the day were observed)
No training	3	3	1	1	-	-	2
Predictable 1 and Predictable 2	3	3	1	1	-	-	2
Unpredictable	3	3	1	1	1	1	2

*20mins prior to actual, or equivalent predicatable training time; **20mins after actual, or equivalent predictable training time.

animals at the start of the study, based on the amount of aggression they both initiated and received. The rays had been trained for approximately 12 months prior to the start of the study, but had not been actively trained for six months. Training involved the focal ray pressing their body up against the target and immediately receiving a piece of fish (from the day's quota) as a reward from the trainer. Each animal had a personalised target. Pre-training preparations and equipment set-up (laying out food and targets) were performed in the same way for each training session, in order to keep signals and cues consistent across all conditions and hence to control for signalled predictability.

Data collection

Data were collected during four training conditions (Table 1). Behavioural data were collected using instantaneous scan sampling of state behaviours (locomotion, feeding, resting, digging and interacting with the environment) at one-minute intervals, and all occurrence sampling of aggressive event behaviours (Table 2), over 20-minute observation sessions. For each aggressive event, the initiator and receiver were recorded. Observations were conducted before and after each tank feed, before and after each training session, and for two random sessions (general observations) per day, to provide data for seven conditions (Table 3).

Statistical analysis

To investigate aggression before and after feeding and training events for all four conditions, the total occurrences of aggression were compared. Data for the No training and Predictable 1 conditions, and the Unpredictable and Predictable 2 conditions, were compared separately due to the death of the most dominant and aggressive *T. lymma* (ray number 3) between the Predictable 1 and Unpredictable conditions.

Negative binomial Generalised Linear Models (GLM) were run in R studio (R Studio Team 2018) to compare aggressive behaviours between and within conditions. The models revealed an overdispersion statistic of >2, therefore a series of zero-inflated GLM models were carried out. All sessions were weighted according to duration (of time in sight) and models included the variables of condition and individual. High overdispersion values indicated that zero-altered Poisson (ZAP) and zero-altered negative binomial (ZANB) models should be applied. Multiple link functions were tested, and these were compared using their Akaike information criterion (AIC) values.

To determine whether the timings of repetitive events (feeding and training) had an effect on behaviour, state behaviours were grouped into active and inactive behaviours and the mean number of minute scans these behaviours were observed, in each 20-minute session, was calculated.

To analyse social networks of the group, directed and weighted association matrices were created for aggressive event behaviours, and social network diagrams of these interactions were produced for each condition using SOCPROG (Whitehead 2009). To determine whether asymmetric agonistic interactions were reciprocated between individuals or unidirectional in each of the four conditions, Mantel Z-tests (absolute reciprocity) and Hemelrijk Kr-tests (relative reciprocity) were run with 1000 random permutations.

De Vries' test for linearity was carried out for each condition, with 1000 random permutations. The dominance indices 'proportion of contests won' and 'modified David's scores' (de Vries et al. 2006) were calculated. The 'I&SI' dominance ranking method (de Vries 1998) was then used to rank each ray in the four conditions.

Results

Overall, incidences of aggression between the rays were significantly different between conditions (Figure 1). More

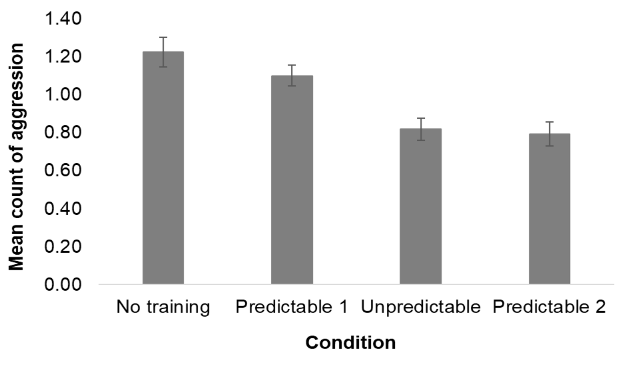

Figure 1. Mean count of aggressive interactions performed by all subjects in each of the four training conditions (the No training condition did not involve training, the two Predictable training conditions involved target training at the set time of 1530 hours and the Unpredictable condition involved target training at random times between 0845 and 1500 hours).

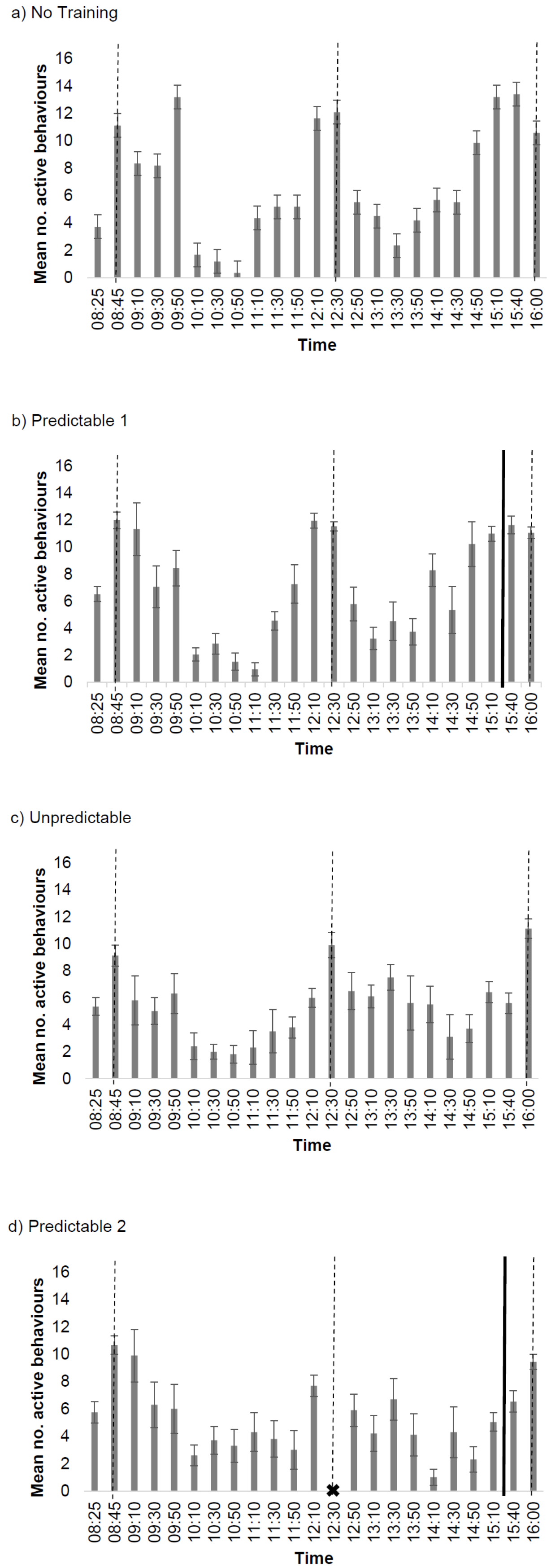

Figure 2. Mean number of active behaviours in 20-minute observation sessions throughout the day during the four training conditions. The dotted lines show the feeding times of 0845, 1230 and 1600 hours, the solid black line shows the training time of 1530 hours. Cross indicates that no data were collected at 1230 during the Predictable 2 condition.

aggression was performed before training commenced, compared to the Unpredictable (Z=3.70, P<0.001) and Predictable 2 (Z=3.93, P<0.001) conditions. Significantly more aggression was performed when training was offered in the Predictable 1 condition compared to an Unpredictable schedule (Z=3.37, P<0.001) and more in the first compared to the second Predictable training schedules (Z=3.67, P<0.001).

Behaviours before and after training events

We found significantly higher aggression rates before training events in the first Predictable condition compared with the equivalent time in the No training condition (X^2_1=18.31, P<0.001, Z=4.21, P<0.001). There was also a significantly higher aggression rate before the equivalent time of predictable training in the Unpredictable condition compared with the second Predictable condition (X^2_1=67.98, P<0.001, Z=6.39, P<0.001).

After training events, rates of aggression were significantly higher at the equivalent time in the No training condition compared to a Predictable training event (X^2_1=37.76, P<0.001, Z=6.26, P<0.001). In the Predictable 2 condition, aggression performed after the training event time was significantly higher when training was conducted on an Unpredictable than a Predictable schedule (X^2_1=41.03, P<0.001, Z=5.96, P<0.001).

Aggression within the Predictable conditions

In the first Predictable condition, aggression rates were higher before training events than after training events (X^2_2=244.19, P<0.001, Z=5.06, P<0.001) and higher before and after training sessions compared to a random time of day (Z=13.22, P<0.001 and Z=6.27, P<0.001, respectively). However, in the Predictable 2 condition, aggression rates were higher after than before training events (X^2_2=42.26, P<0.001, Z=4.20, P<0.001), and higher at a random time compared to before training periods (Z=5.48, P<0.001). There was no significant difference in aggression when comparing after training to a random time of day (Z=1.90, P=0.057). Models for the Unpredictable condition were non-significant (X^2_2=2.76, P=0.096).

Activity patterns

Comparing daily patterns in active behaviours between the four conditions, there was a general trend in the mean number of active behaviours, all increasing towards the feeding times of 0845, 1230 and 1600 hours (Figure 2). Peaks were seen at all three feeding times, with troughs of activity in between feeds. Slightly less variation in activity level is seen throughout the day in the Unpredictable condition (c), where training took place at random times. This was particularly apparent between the second and third feeds, with there being a less pronounced decrease in activity than seen between the morning period (0845 to 1230 hours) and other conditions.

Social network analysis

No significant reciprocity was found in all of the conditions, suggesting that aggressive interactions were unidirectional throughout the study (all P>0.90) (Figure 3).

The dominance hierarchies for the Predictable 1 condition (*h'*=0.886, P=0.068), Unpredictable condition (*h'*=1.000, P=0.114), and Predictable 2 condition (*h'*=0.950, P=0.051) were not significantly linear. However, the hierarchy was significantly linear in the No training condition (*h'*=1.000, P<0.05).

In all four conditions, the blue-spotted ribbontail rays (*T. lymma*) were dominant over the blue-spotted maskrays (*N. kuhlii*) (Table 4). However, the positions of individual rays in the hierarchy were not fixed across conditions. One of the *T. lymma* (number 3) was most dominant in the No training and Predictable 1 conditions,

Table 4. Proportion of contests won (PCW), modified David's scores (Mod DS) and dominance ranks (Dom rank) for the rays in each condition.

Ray	No training			Predictable 1			Unpredictable			Predictable 2		
	PCW	Mod DS	Dom rank	PCW	Mod DS	Dom rank	PCW	Mod DS	Dom rank	PCW	Mod DS	Dom rank
1	0.88	12.25	2	0.92	13.08	2	0.96	7.62	1	0.94	7.39	2/1
2	0.76	8.58	3	0.64	7.99	3	0.96	6.91	2	0.91	7.23	1/2
3	0.76	5.03	1	0.80	4.84	1	n/a	n/a	n/a	n/a	n/a	n/a
4	0.11	-7.58	6	0.10	-7.99	5/4/6	0.39	-1.98	5	0.30	-3.66	5
5	0.13	-8.06	5	0.12	-7.96	4/6/5	0.21	-5.86	3	0.20	-4.22	4
6	0.14	-10.22	4	0.12	-9.95	6/5/4	0.16	-6.69	4	0.13	-6.73	3

followed by the other two *T. lymma* animals (numbered 1 and 2). After the death of ray number 3, the two remaining *T. lymma* became the most dominant animals in the tank, sharing the top rank in the final (Predictable 2) condition. The maskray ranks varied more, with one of the animals (number 4) being the least dominant in all conditions except in the first Predictable condition, when all *N. kuhlii* were ranked in reciprocal positions with shared rankings.

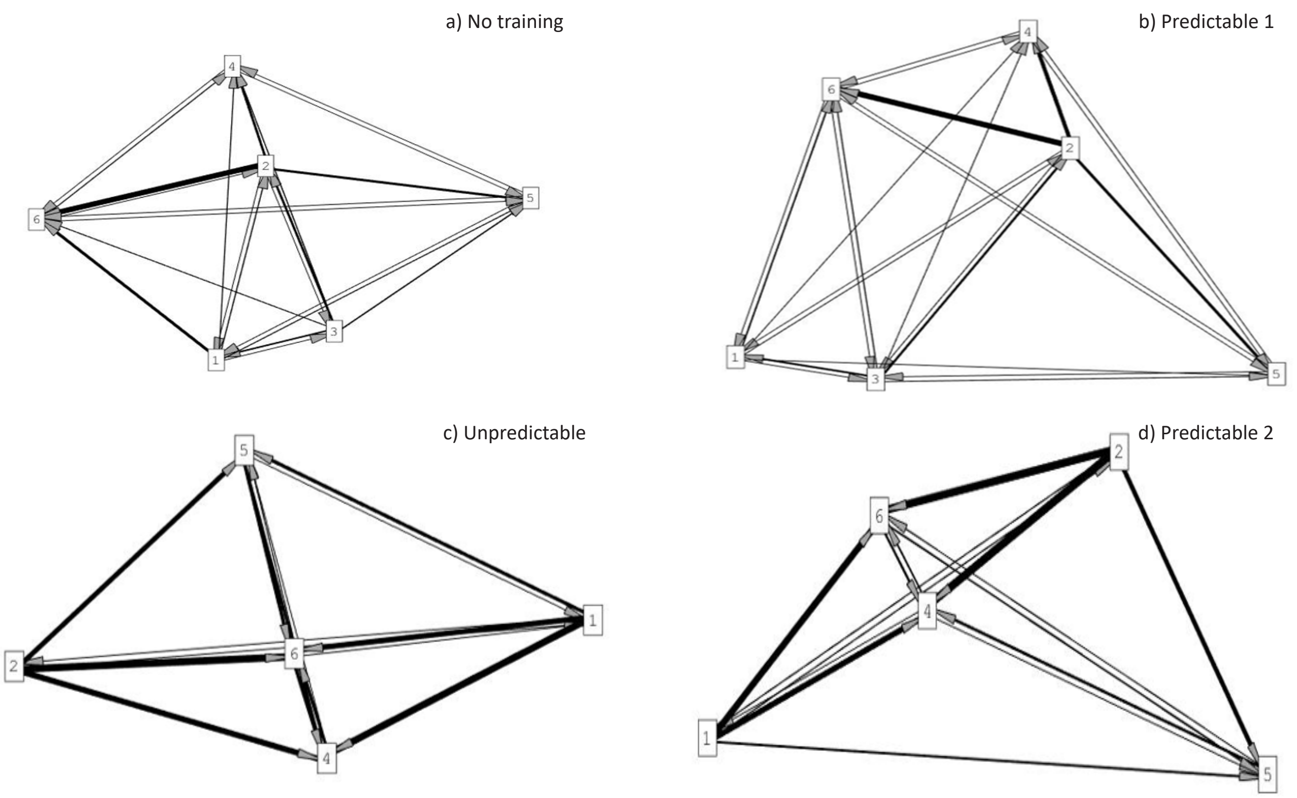

Figure 3. Social network diagrams of aggressive interactions in the four training conditions. Each node is labelled with a number that represents a ray (1–3 are blue-spotted ribbontail rays; 4–6 are blue-spotted maskrays). Individuals 1 and 3 were trained. The thickness of the edges showing the weight of the interactions and the arrows denoting the direction of the interactions, from aggressor to receiver.

Discussion

Overall, incidences of aggression in the tank decreased over the course of the study, with higher overall levels performed in the period in which no training was carried out. Although aggression was generally low in occurrence, the implementation of PRT may be beneficial to the welfare of the individuals in the exhibit by reducing overall levels of aggression. Anecdotally, from keeper reports, biting is still occurring, mainly overnight; therefore, aggression should continue to be monitored. As suggested by Semeniuk and Rothley (2008), while studying southern stingrays (*Dasyatis americana*), the occurrence of biting could be accidental, due to the position of the mouth being on their underside, resulting in inadvertent biting when searching for food. At Living Coasts, persistent biting may also be due to aggression, not in response to resource competition, but due to the high carrying capacity of the tank. The marginally lower levels of aggression in the Unpredictable and Predictable 2 conditions in comparison to the first two conditions (No training and Predictable 1), are most likely due to the change in group composition, as the most dominant female died between the two sets of conditions. The death of one of the blue-spotted ribbontail rays has likely impacted the results of this research. Although this could not have been foreseen, it would be beneficial to repeat the study with the remaining group, now that more time has passed since the death and the social structure is likely to have stabilised allowing for full comparisons between all of the conditions. This is the main reason for conducting separate analyses for the conditions and therefore, the discussion will explore differences between specific conditions, not comparing the data set as a whole.

This study found differences in the rates of aggression performed around training sessions, depending on the schedule of the training event. In the first Predictable condition, animals were more aggressive before training compared to non-training days and around training events (both before and afterwards) than at a random times of day. These findings suggest anticipation of the training event and that there may be negative implications of training being carried out at a set time. Anticipation can manifest as behaviours that may be considered negative, such as increased aggression (e.g. Brännäs et al. 2005). It has also been suggested that predictability enables a preparatory response, whereby the animal is able to prepare itself for a forthcoming event, which has been suggested to be a reason for an animal's preference for predictable events found in some studies (e.g. Prokasky 1956).

Conversely, the higher levels of aggression after training compared to a random time in the first Predictable condition, and higher aggression after training than before training in the second Predictable condition may be related to anticipation of daily feeding, which occurred shortly after training. Indeed, the daily patterns in active behaviours suggest that activity is linked to feeding events, with peaks observed around feed times. This finding was expected as active behaviours, including agonistic behaviours, have been seen in other species of ray when there is a valuable resource, such as food, to compete over (Semeniuk and Rothley 2008). Both species of stingray in the study were observed to be highly inactive when food was not present, spending long periods of time resting and/or buried in the tank substrate. Levels of active behaviours started to increase in the observation sessions prior to feeding time, suggesting some level of FAA, as reported in other fish species (e.g. Reebs and Lague 2000; Vera et al. 2007), potentially in anticipation of the feeding event.

This study also suggests that there could be individual differences in the ability to predict the timing of events. It was anecdotally observed that the most dominant of the ribbontail rays (who was trained in the Predictable 1 condition), would swim up and down the side of the enclosure at the location at which the individual was first target-trained 12 months previously. This behaviour was not exclusively observed before a training event, but the individual was generally more active at this time of day. The next ray to be trained (in the latter half of the study) was not seen to do this, which could be due to a reduced ability to predict the events and/or a difference in personality, which has been shown to affect behavioural responses in fish (Frost et al. 2006; Castanheira et al. 2013). Increased activity in the area near feeding stations before set feeding times has been reported in other elasmobranch species (Smith et al. 2004). The contrasting results of the two Predictable conditions means that the current study is inconclusive regarding the effects of predictable or unpredictable training on levels of aggression in rays. The most likely reason for variation is the death of the most dominant female between the first Predictable and the Unpredictable training conditions; therefore, further research is needed to determine the effect of predictability on a stable social group.

The reduced variation in activity throughout the day in the Unpredictable condition suggests that providing food at a random time of day may increase activity levels at times when the rays would otherwise be inactive. The provision of choice to animals is reported to be highly beneficial for welfare (Ross 2006); however, the natural daily rhythm of a species, that is, typical periods of inactivity and rest, must be considered. Wild *T. lymma* are known to spend the day hidden inside caves or underneath ledges, emerging at night to feed (Scott 1993). Encouraging animals to be active at times of the day that they would usually be inactive may be detrimental to their welfare, and thus the effect of unpredictable routines may have a stronger influence on some species in captivity. The reason that the tank in the present study is provided with three daily feeds is due to a previous study concerning feed regularity, which found that the group fed and foraged more when provided with three feeds per day (Edgar et al. 2012). In this study, predictable training events were carried out close to the scheduled 1600 hours feed and this may have unknowingly influenced the amount of aggression seen and masked any anticipatory behaviour related to the training time. Therefore, if the study were repeated, the predictable training time should be at a time that is not followed by an already established feeding event.

Blue-spotted ribbontail rays (*T. lymma*) were found to be dominant over the blue-spotted maskrays (N. kuhllii) throughout all conditions; however, no linearity of relationships were found in the three training conditions. All six study animals were subjected to aggression from other individuals; however, aggression levels between the two species and between individuals varied dramatically. The death of the most dominant *T. lymma* resulted in some changes in dominance ranking and less aggression being directed towards the remaining *T. lymma* as this female had been the main performer of aggression. The amount of aggression observed in the second half of the study (Unpredictable and Predictable 2 conditions), particularly during the Unpredictable condition, may have been due to the new group structure and not the change of condition, with a period of instability resulting due to the death of the dominant individual. In addition, the low rates of aggression observed during the study may have resulted from an unnatural social grouping of the two ray species housed in the exhibit. The two species may not interact in the wild and a female-only group is unlikely to be seen in situ as these species of ray are suggested to only form groups briefly, to mate (Semeniuk and Rothley 2008). Sexual segregation has been observed in other elasmobranch species to avoid the costly, aggressive interactions between sexes (dogfish, *Scyliorhinus canicula*, Sims et al. 2001). In response, some of the aggression observed may have been due to females competing for dominance within the group. To test whether the predictability of training does have an effect on aggression, the Unpredictable and Predictable conditions should be repeated with the new group now that some time has elapsed, as the group is likely to be more stable and a No training condition should also be carried out for comparison.

In conclusion, the inclusion of PRT was beneficial in reducing the occurrence of aggressive behaviours within the tank and it is suggested that training should be continued as part of the husbandry routine. In terms of anticipatory behaviours, higher rates of aggression and increased activity levels indicate that the group may be experiencing anticipation before a training event, which was more pronounced in the first predictable schedule condition than the second. The change in aggression may be due to the death of the most dominant animal in the tank in the middle of the study, which also had a strong influence on the dominance rankings of the animals in the exhibit.

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