



The School of Environmental Sciences

# **The Effect of Animal Personality on Husbandry of Gentoo Penguins (*Pygoscelis papua*)**

a Thesis submitted for the Degree of MSc in Biological Sciences  
at the University of Hull

by

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**Abstract**

In many taxa animals exhibit personality by differing consistently in behaviour across situations and over time in response to stimuli. The study of animal personality has become its own sub-discipline of behavioural ecology and has grown rapidly over the last twenty years. Despite the rapid growth this area of study has received little attention in captive environments. This has resulted in limited understanding of the effects of animal personality on captive animal husbandry. These consistent differences between individuals may necessitate husbandry practices that cater for all personality types. In this study thirteen Gentoo penguins (*Pygoscelis papua*) at The Deep in Hull were investigated over a period of sixteen months using camera and focal observation. Three indicators of boldness were used to determine if personality is present in the population; the responses of penguins to aquarium visitors, aquarists and novel items. How personality was expressed on feeding, site fidelity and individual mating success were then investigated. Gentoo penguins clearly display personality through their behaviour and this was evident from consistent differences in boldness over time, in interactions with aquarium visitors and across situations, shown by similarities in interactions with aquarists and visitors. Boldness was significantly correlated with feeding rates, body weight and choice of site within the enclosure. However, there was no correlation between boldness and mating success. There are, therefore, expressions of personality in this population as bolder individuals fed more, weighed more and spent longer in brighter enclosure areas. However, both shy and bold birds were successful in producing eggs. It is recommended that feeding routines and enclosure design should take into account the requirements of all personality types. It is also suggested that the study be expanded to other populations and species to allow the general applicability of animal personality research on management of animals to be tested.

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## 1. Introduction

### 1.1 Animal Personalities

Behavioural differences between individuals are now known to be widespread throughout the animal kingdom (Wolf & Weissing, 2012). Examples of these behavioural differences include variations in aggressiveness in water striders (*Aquarius remigis*) (Sih & Watters, 2005), differences in boldness in three-spined sticklebacks (*Gasterosteus aculeatus*) (Bell, 2005) and variable sociability in hyenas (*Crocuta crocuta*) (Gosling, 2008a). A well-studied example in birds are great tits (*Parus major*) which differ consistently in their exploratory response towards novel objects with respect to approach distance, approach latency and time spent with the item (Verbeek et al., 1994). Various terms have been used to describe these differences including personality, temperament and behavioural syndromes (Gosling, 2008b; Powell & Gartner, 2011; Sih et al., 2012). However despite the differences in terminology these terms are used to describe behavioural consistency in individuals over time and across contexts (Powell & Gartner, 2011). Although it has long been understood personalities exist in humans (Briffa & Weiss, 2010) it is only recently that it has come to light that these personalities are far more common in the animal kingdom than previously believed (Wolf et al., 2007; Sih et al., 2012). This understanding has developed as studies on animal personalities have flourished over the past twenty years (Gosling, 2008b; Powell & Gartner, 2011) providing an ever growing body of evidence in a range of animal groups including birds, lizards, insects, cephalopods and arthropods (Dall et al., 2004; Sih et al., 2004; Gosling, 2008b). This shows that personality is not just restricted to higher vertebrates (Bell, 2007). Previously these differences between individuals were explained by a number of reasons. These include random variations around the mean value (Rèale et al., 2007; Wolf & Weissing,

2012), curious differences between individuals (Powell & Gartner, 2011) and inaccurate measurements or non-adaptive variation (Groothuis & Carere, 2005). This contributed to individual differences being an underappreciated area of animal science (Bolnick et al., 2003). The relatively recent discovery of widespread animal personalities also comes despite prominent behavioural scientists noting individual variation in behaviour in the 1980s and 90s (Sih & Bell, 2008), for example in studies including those by Clark and Ehlinger (1987), Magurran et al. (1993) and Slater (1981). In addition to this, primatologists have long described distinct social and aggressive behavioural characteristics between individuals (Stevenson-Hinde et al., 1980; Paquette & Prescott, 1988). Indeed those who work with animals regularly, such as zookeepers, have long known animals to exhibit consistent individual differences (Powell & Gartner, 2011) and personalities are attributed to animals by the people who work with them (Groothuis & Carere, 2005). Furthermore the growing number of species studied is an increasing representation of the total species in existence (Gosling, 2008b), showing how common personalities are throughout the animal kingdom. The findings, therefore, that promoted this shift and development in understanding are that behavioural differences between individuals are highly consistent over time and that they occur in a wide range of animal groups (Wolf & Weissing, 2012). This is further supported by evidence that differences in response are not dependent on sex or life history stage (Ellenberg et al., 2009) and the fact that individuals of the same size, sex and from the same population often significantly differ in their behaviour (Bell, 2007). This is the case even when confronted with the same stimuli or within an homogenous captive environment (Herborn et al., 2010). These observations are very similar to those in humans where people of all ages and sexes differ consistently (Dall et al., 2004). Personality has, therefore, been defined as “consistent between-individual differences in the expression of individual behaviour traits” (Mowles et

al., 2012) and this definition is now commonly used in the literature (Dall et al., 2004; Wolf et al., 2007; Briffa & Weiss, 2010; Sih et al., 2012). Despite the term consistent, it does not mean there can be no variation but that differences between individuals largely remain the same (Rèale et al., 2007) and are temporally consistent with little plasticity (Koski, 2011). Commonly investigated personality traits include explorativeness, boldness, aggressiveness, sociability and activity (Rèale et al., 2007; Sih & Bell, 2008). As well as consistency within traits, they can also be closely linked in behaviour syndromes (Godin & Dugatkin, 1996). Despite sometimes being used to define individual differences, the term behavioural syndrome has developed a new meaning with a different definition, when differences in two or more traits are correlated over time (Sih et al., 2004; Bell, 2007; Stamps & Groothuis, 2010). There are a number of examples of behavioural syndromes. One such example is increased aggressiveness in funnel web spiders (*Agelenopsis aperta*) correlating with greater wasteful killing and sexual cannibalism (Maupin & Riechert, 2001). Another instance occurs in sunfish (*Lepomis gibbosus*) with bolder individuals acclimating faster and feeding on more exposed and difficult to capture prey (Sih et al., 2004). Behavioural syndromes have been the subject of much attention because they can result in animals demonstrating sub optimal behaviour (Carter et al., 2012) due to limited behavioural plasticity. For example, explorativeness may be advantageous for finding food in times of shortage but fatal in high predator environments (Sih et al., 2004). In summary behavioural syndromes are correlations between consistent personality traits (Sih & Bell, 2008).

It can thus be seen that in recent years there has been a rapid growth in study of animal personalities (Gosling, 2008b). There has also been significant research into why personalities exist but little study into how individual differences are expressed (Wolf & Weissing, 2012). Furthermore since personality may influence fitness components such as reproduction (Rèale



et al., 2007) there may be clear ecological implications and this is again an area of limited study (Sih et al., 2012). There may, as a result, be important effects of personality on captive animal welfare (Rèale et al., 2007) such as on feeding, space use and reproduction. These implications may also be much more significant than previously thought (Powell & Gartner, 2011). It is therefore important that personality is identified in as many species as possible, both in zoos and in the wild, in order that the effects of personality on welfare can be determined. This in turn will allow the necessary measures to be taken to improve welfare and husbandry techniques.

### 1.2 Previous Welfare Research

The majority of existing research on captive animals has focused on population level studies investigating differences between and within species (Grootuis & Carere, 2005). Captive animals face a range of potential stressors which can be experienced through their auditory, olfactory or visual senses (Carlstead & Shepherdson, 2000; Morgan & Tromborg, 2007). Due to these stressors different species respond differently to captivity (Mason, 2010) including areas such as mating success, activity and enclosure space use (Hosey, 2013). Some species for example live longer, are healthier and more fecund, while the opposite is the case in others. There can also be significant differences between closely related species (Mason, 2010). Variations in mating success have been noted in numerous species. Both forest duikers (*Cephalophus* spp.) (Willette et al., 2002) and African elephants (*Loxodonta africana*) (Clubb et al., 2009) show reduced mating success in captivity compared to the wild. Additionally UK breeding colonies of Humboldt penguins (*Spheniscus humboldti*) have half the chick output of wild populations (Mason, 2010). In contrast the breeding success of the kestrel (*Falco tinnunculus*) is not affected (Kenward, 1974). However, in other species it may be considered

to be improved, for example, the bottlenose dolphin has faster reproductive rates in captivity (Couquiaud, 2005). Animals tend to be less active in captivity and this is related to increased visitor presence (Fernandez et al., 2009). This has been observed in cotton-top tamarins (*Saguinus oedipus*) (Mallapur et al., 2005), ring tailed lemurs (*Lemur catta*) and Diana monkeys (*Cercopithecus diana*) (Chamove et al., 1988). Similarly, space use is affected in numerous species, again in response to visitor presence as animals avoid viewing areas. Examples include lion-tailed macaques (*Macaca silenus*) (Mallapur et al., 2005) and western lowland gorillas (*Gorilla g. gorilla*) (Wells, 2005). Observations of penguin activity and space use show instances of differences between closely related species. In the cases of Little penguins (*Eudyptula minor*) and African penguins (*Spheniscus demersus*), both avoid visitors and have reduced swimming behaviour in the presence of visitors (Ozella et al., 2015; Sherwen et al., 2015) whilst Gentoo penguins exhibit greater pool use in higher levels of visitors (Collins et al., 2016). All this research has, however, been on a population level and responses between individuals within these populations may vary and differences between closely related species may be influenced by the personality composition of the study group. This can lead to a population of bolder individuals being influenced in a different way to a population of less bold animals. There has, therefore, been little research into the individual variation around these behavioural observations (McDougall et al., 2006; Kuhar, 2008). This comes despite the fact that individual differences may greatly impact behavioural studies (Hosey, 2000) and the way individuals interact with their environment (McDougall et al., 2006). Further study of individual differences within captive populations is thus necessary (Kuhar, 2008) especially due to the potential impacts on welfare (Rèale et al., 2007).

### 1.3 Indicators of Personality

Commonly investigated personality traits include aggressiveness, sociality and boldness (Sih & Bell, 2008). Boldness, in comparison to other personality traits, is not so easy to define as it is subjective. Numerous varying definitions along a similar theme appear in the literature with response to novelty being key, along with reaction to risk (Bell, 2005; Toms et al., 2010). Boldness in this study will therefore be defined as an active response to novel and risky situations. Individuals can be bold or shy with fast or slow exploration and these traits often result in conflicts between curiosity and risk (Herborn et al., 2010). Visitors to zoos can be a source of enrichment, stress or can have neutral impact (Birke, 2002; Fernandez et al., 2009; Ozella et al., 2015). As a result visitors can provide novel stimulation to animals provided their behaviour is appropriate (Collins et al., 2016). There are examples of this in felids (Margulis et al., 2003) and a captive long billed corella (*Cacatua tenuirostris*), with the latter spending significantly longer at the front of its cage in the presence of visitors (Nimon & Dalziel, 1992). Cases of stress, however, are far more common with avoidance of visitors in animals including jaguars (*Panthera onca*) and Indian leopards (*Panthera pardus*) (Mallapur & Chellam, 2002; Sellinger & Ha, 2005). The majority of these studies, however, do not take into account individual variation. This is an important omission because variation in response to human disturbance between individuals has been observed in penguins in the wild (Ellenberg et al., 2009). The fact that penguins have good vision, hearing (Penguin Taxon Advisory Group, 2005) and high levels of curiosity (Sherwen et al., 2015) means that there may be differences in response to visitors. Furthermore, increased vigilance has been observed in response to visitors in both captive (Sherwen et al., 2015) and wild penguins (Warren et al., 2003; Holmes et al., 2005; Walker et al., 2006). This response may, in the case of some individuals, be due to stress while in others potentially a curiosity behaviour towards novel items or individuals

outside the enclosure. As with visitors, staff members can also be enriching or stressful to animals (Morris, 1964; Claxton, 2011) so there may also be differences in response to these familiar individuals (Collins et al., 2016). Therefore, observing individual variations in response to both familiar (staff) and non-familiar (visitors) people may be a potential indicator of personality in penguins. Penguins also respond with curiosity to novel objects (Penguin Taxon Advisory Group, 2005) and careful observation of how animals react to novel enrichment may give an insight into their personality (Powell & Svoke, 2008). Environmental enrichment using novel items is commonly used by zoo staff to create a more complex and stimulating environment (Skibieli et al., 2007). These novel items encourage natural behaviour and activity patterns (Renner & Lussier, 2002) and when exposed to familiar and novel objects individuals spend more time exploring novel objects (Antunes & Biala, 2012). In chimpanzees (*Pan troglodytes schweizfurtii*) for example, bolder individuals monopolise novel objects (Paquette & Prescott, 1988). Therefore, observing how a penguin population responds to novel items may give further knowledge into their personality by noting differences between bold and shy individuals. In conclusion, the level of boldness shown by different individuals towards visitors, aquarists and novel items may all be indicators of whether personality exists in captive penguins. This is the case because when confronted with the same environmental stimuli individuals of the same species often differ in their response.

#### 1.4 Expressions of Personality

Since an animal's personality, when it is identified, can be used to predict how it will respond to different situations (Vazire et al., 2007) it can also be used to understand and promote welfare. For this reason, it is important to determine the potential effects of personality in a captive population so that welfare and husbandry decisions can be made that take into

account differences in temperament between individuals. Potential expressions of personality in captive Gentoo penguins include differences in feeding habits, site fidelity and mating success. Firstly, the fact that individuals respond differently to keepers because they are enriching or stressful (Careau et al., 2008; Claxton, 2011; Collins et al., 2016) may result in different levels of feeding between individuals due to varying responses to these familiar individuals. This is especially important as the penguins at The Deep are hand fed and feeding requires close proximity interactions with keepers. In addition to this, more explorative and bold individuals may expend more energy so have greater food requirements (Careau et al., 2008). Crucially the most significant aspect of daily animal husbandry is meeting the energy demands of the animals (Worthy, 2001). Therefore, better understanding of different individual's feeding habits and requirements will help aid husbandry practice in this area. Secondly, how individuals use space within the enclosure may also be influenced by their personality. This may be the case as their ability to occupy different areas within an enclosure may be determined by their boldness in response to human proximity (Martin & R  ale, 2008). An example of this is seen in chipmunks (*Tamias striatus*) which are not distributed randomly with respect to human visitation (Fraser et al., 2001), with more explorative individuals occupying areas closer to human visitor areas (Dingemanse et al., 2003). Therefore, in a population of Gentoo penguins their personality may influence their choice of site within the enclosure and have a part to play in welfare practice by showing the need for locations within an enclosure that suit all individuals (Sherwen et al., 2015). Finally, there may also be effects on mating success due to personality potentially impacting reproductive strategies (Powell & Gartner, 2011). Stress is a major barrier to captive reproduction (Mason, 2010) and increased boldness has been seen to result in higher mating success (Smith & Blumstein, 2007). This may be because bolder animals have higher resilience to stress than shyer animals (Powell &

Gartner, 2011). Examples of this can be seen in a number of species including bighorn sheep (*Ovis canadensis*) where bold ewes have a higher weaning success (Dingemanse & Réale, 2005). Therefore an understanding of personality may be used to improve captive breeding success by reducing stress through providing good breeding conditions for all individuals (McDougall et al., 2006). This may be achieved by taking personality into account during enclosure design so as to provide for both shy individuals with places to hide and bold individuals with objects to explore (Kuhar, 2008). This will be especially important in species where captive breeding is important (Araki et al., 2007) and as zoos and aquaria work to maintain genetically diverse populations (Powell & Gartner, 2011). In summary, understanding how personality is expressed in individual feeding habits, use of space within the enclosure and breeding success will aid husbandry, welfare and conservation respectively.

### 1.5 Aims of Study

The aim of this study is to identify indicators of personality in a population of captive Gentoo penguins using repeatability and consistency in response to visitors, members of staff and novel items as measures of boldness, with boldness being a commonly investigated personality trait (Sih & Bell, 2008). The effects of the consistent differences between individuals on feeding, site fidelity and mating success will be identified. The study hypothesises that (i) personality will be present in the population and expressed through differences in response to visitors, staff and novel items, (ii) personality will influence (a) individual feeding preferences and weight, (b) choice of site within the enclosure and (c) mating success.

This research is significant as little work has been done on the consequences of personality (Réale et al., 2007; Powell & Gartner, 2011). A better understanding of the consequences of

personality may improve husbandry practice, animal welfare and conservation efforts (Vazire et al., 2007). Examples of areas that may be improved include future feeding regimes and enclosure design. Working with small populations of sometimes rare animals that did not evolve in their new captive environment requires the ability to predict how the animals will respond to different situations (Powell & Gartner, 2011) and research that aids this understanding is important for animal welfare as a whole. This research may also be applied to species from other taxa giving it further importance.

## **2. Ethics**

The project received ethical approval from the University of Hull and The Deep's ethics committee. No ethical considerations are associated with this project as the majority of the project's experiments are based on data records, external observations or discreet cameras inside the enclosure. For the most part the experiments also monitored the natural behaviours of the birds without attempting to create responses. One exception to this, however, was with the indicators of personality section of the study when placing novel items in the enclosure. The aim of this was to generate a response from the birds but this is a common practice at The Deep and in zoos/aquaria for enrichment purposes. This in turn has a positive impact on animal welfare (Wells, 2009) and all the items placed in the enclosure were approved by The Deep's science officer. There was also limited physical contact with the birds throughout the investigation. This occurred during weighing and was carried out by aquarists. This contact was minimal as the penguins were encouraged to stand on scales of their own accord during feeding and enrichment. An acclimatization period of two weeks was also completed so the penguins got used to the researcher's presence outside the enclosure when the focal observations were carried out.

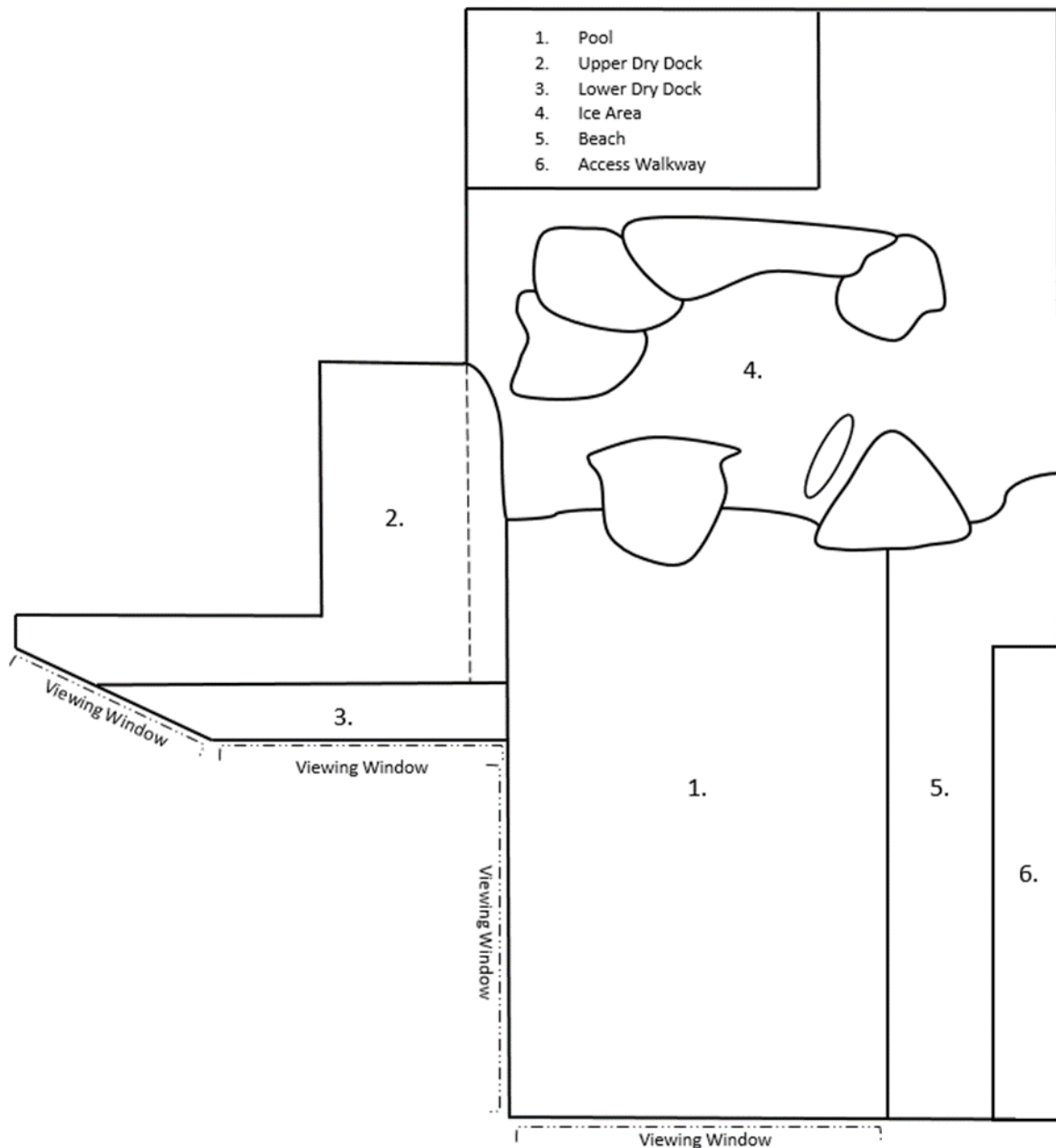
### 3. Methods

#### 3.1 Study Animals and Enclosure

Thirteen Gentoo penguins (*Pygoscelis papua*) form the study population at The Deep, comprising of six females and seven males, with each individual being easily identifiable by their coloured wing band around the humerus (upper wing). As of June 2017, the age range of the population was one to seven years old. Two chicks hatched in 2016 increasing the population size from 11 to 13. The initial group of 11 arrived at The Deep from two zoological institutions (Calgary Zoo, Canada and Moody Gardens, Galveston Island Aquarium, Texas USA) and are housed in an enclosure with 70m<sup>2</sup> of land area and a 42.5m<sup>2</sup> (60,000 litre) pool with a deep (2m) and shallow (1.25m) section. The land space is divided into a dry dock area with shallow water section, an ice shelf and beach area (Figure 1). This allows penguins to partake in their lifestyle activities (Dawkins, 2004) therefore meeting the requirements of a penguin enclosure as it must have land space and a pool for swimming (Penguin Taxon Advisory Group, 2005; N/A). A full repertoire of natural behaviours is therefore possible, which is vital for animal welfare (Fernandez et al., 2009), as being prevented or unable to perform these activities is a form of stress (Sellinger & Ha, 2005). In addition to public visitor presence, the penguins have at least three close contact interactions with aquarists each day. These follow a fixed routine and occur between 08.45-10.00h to clean the enclosure, and during feeding at 11.30-12.00h and 15.30-16.00h. The penguins are hand fed predominantly capelin (*Mallotus villosus*), with European sprat (*Sprattus sprattus*) and Atlantic herring (*Clupea harengus*) also composing part of the diet. Antarctic krill (*Euphasiia superba*) is also scatter fed in the pool three to five times a week. Hand feeding the birds allows careful monitoring of individual feeding as this is a good indicator of health. The birds are fed *ad libitum* with



fluctuations in feeding amount daily and per feed. In addition, individual birds have different food preferences (Penguin Taxon Advisory Group, N/A). The penguins are exposed to two types of contact; unfamiliar (public) and familiar (the 5 aquarists). This contact with people makes up a significant part of the lives of these captive penguins (Hosey, 2013).



**Figure 1.** Penguin enclosure at The Deep, showing main enclosure areas and public viewing windows.

### 3.2 Analysis of Behaviour

Three indicators of boldness were chosen for this study, boldness towards aquarists, interactions with the public and responses to novel items. Three effects of boldness were studied, on feeding and weight, site fidelity and mating success.

#### 3.2.1 Boldness Towards Aquarists

The first indicator, boldness towards aquarists, was obtained by questioning the aquarists, who work with the penguins on a daily basis, to rate each penguin's boldness towards them. The ratings of each aquarist were independent of the others as each person was unaware others were also rating the birds. In addition, all the data was obtained over the course of a day in both years so there was no chance to discuss ratings with other aquarists. A scale of 1-13 was used, with 13 being most bold and 1 the least bold. Proximity when feeding and ease of handling (during medical treatment or wing band replacement) were selected as criteria. The birds that fed closer to aquarists and responded best to handling received higher values in the ranking. The five aquarists rated the birds once in both 2015 and 2016, with one change of personnel between the two sets of ratings. The ratings from 2015 were from a previous study by the author (undergraduate research project) and the 2016 ratings include the two 2016 chicks. The birds were then ranked on their boldness from their average rating over the two years. The ranking of 1-13 was again used and this was correlated with the consequences of personality.

#### 3.2.2 Penguin-Public Interactions

The second indicator investigated was penguin-public interactions at the pool viewing window, while penguins were in the water. This was studied between 11.30-12.00h and

15.30-16.00h during the two daily half hour feeds. The times were chosen as this was when aquarists were present in the enclosure ensuring conditions were always the same within the enclosure during observations. This was also the time of highest pool activity by the birds, as shown in the previous study by the author, allowing the maximum possible interactions to be observed. The number of interactions lasting longer than one second by each penguin was noted to give a total for each penguin for every half hour observation period. Only interactions carried out at the water surface, when birds held position in front of a visitor(s) at a distance of less than 50cm, were counted. All observations were continuous (all interactions by all penguins noted over the half hour period), with the researcher positioned at one end of the public viewing window, so the whole window could be observed (Figure 1). Continuous observation was important, as due to the short nature of the interactions in this study some interactions could be missed. This was the case in the studies of Kuhar (2008) and Wells (2005) which only observed behaviours occurring at set time intervals. Birds were identified by coloured wing bands, making it possible to always identify the bird interacting with the public.

A total of 110 observation periods were carried out studying interactions at the viewing window. These were split equally between periods of low (<100 people) and high (>100 people) visitor numbers at the viewing window in the observation period, to take into account the variable visitor numbers at The Deep. Visitors were counted by the observer at five minute intervals during the observation period, to give a total over the half hour, as this was a method which worked effectively for Sellinger and Ha (2005). The data were collected over a period from November 2015 to March 2017 and includes data from the previous study by the author on the same population using identical methods. This sixteen month period allowed changes in behaviour over time to be observed. The two chicks that hatched at The Deep in 2016 are

included in the study. The eight months with greater than ten observation periods per month were then used to create an average number of interactions per half hour for each bird in each of these months. This was used in the repeatability analysis of personality. The average number of interactions across the sixteen months was used to rank the birds (1-13, as with aquarist boldness ratings). These rankings were correlated with the aquarist boldness ratings.

### 3.2.3 Responses to Novel Items

Responses to novel items was the final indicator of personality studied. Four novel items were introduced to the enclosure for four consecutive days each (Sunday to Wednesday), over a period of four weeks. The items recommended by The Deep's science officer were a soft toy penguin (30cm), a water filled plastic bowl (80cm) with floating rubber duck (10cm), a plastic turtle children's toy (25cm) and a mirror ball (15cm). These objects were placed on the ice shelf for half an hour and the responses of individuals were filmed using a GoPro Hero4Silver camera. Two methods to analyse repeatability were used. First, BORIS (Behavioural Observation Research Interactive Software) (Friard et al., 2016) was used to observe the time duration spent by each penguin (identifiable by coloured wing bands) at the novel objects during the half hour observation periods. The GoPro footage was uploaded into BORIS and an ethogram was created in the program with a state (duration) event set for each individual. This was activated when the bird reached the novel object and stopped when the bird left. The interaction area around the object was a circle centred on the object with a diameter of 1.5m. More than one visit could also be completed by each bird over each half hour and multiple concurrent interactions could take place at once, as this was permitted in BORIS. This allowed the total duration spent at the item and the average duration of each individual visit to be calculated. In the second method the number of orientations with the object by each

penguin was observed. Orientations were defined as the beak of the bird orienting directly at or touching the object. This is important as birds may spend time around the object within the 'interaction distance', but not be interacting at all (Skibieli et al., 2007). By observing direct contacts, it can be confirmed the individual was investigating the novel object and this method was adopted from the work by Antunes and Biala (2012). Therefore, between these two methods, the average total duration spent at the item, average duration of visits at each item and average number of orientations to each object were collected for repeatability analysis.

### 3.2.4 Effects of Boldness on Feeding and Weight

Feeding records at The Deep were analysed between 1<sup>st</sup> January and 31<sup>st</sup> December 2016. This was possible due to the comprehensive and extensive daily feeding records at The Deep. These records note the number and type of fish consumed by each penguin every day. By using the average weight of each food type, the weight in grams eaten every day by all penguins can be calculated. This value, however, does not include krill feeds in the pool but krill feeds make up a minimal part of the diet at The Deep. For this study, the average daily feed in grams by each penguin was calculated for 2016. The two chicks average is, however, just for the days following the end of their crèche period (22<sup>nd</sup> August 2016). The penguins are also regularly weighed (Kg) by the aquarists using scales (Marsden model V-20) in the enclosure, which the penguins have to stand on to be fed or during enrichment. The weights for each bird used in this study were all taken on the 2<sup>nd</sup> January 2017. Penguins were ranked from 1-13 on both their average daily feed and weight. From the average daily food intake and the penguin's weight it was possible to calculate the daily food intake as a percentage of the penguin's body weight. This gives a more accurate record of a penguin's food intake as it

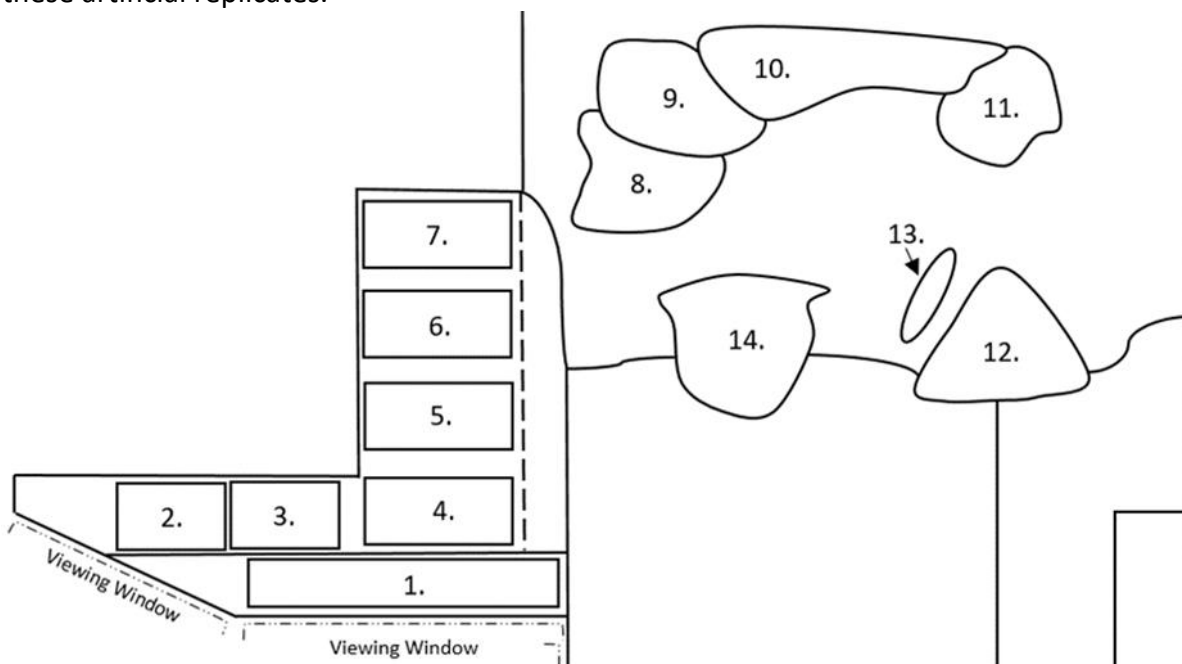
takes into account the weight of the birds (Hinke & Trivelpiece, 2011), with penguin daily food consumption being 10-14% of body weight (Penguin Taxon Advisory Group, N/A).

In addition, tray feeds were carried out to observe how individuals feed from this method. A tray (50 x 30 x 20cm) with that day's food type (30-40 fish on crushed ice) was placed in the enclosure at 13.45h, halfway between the morning and afternoon feed, and left unattended for half an hour. This gave the penguins the opportunity to feed with no aquarists present. The number of fish taken by each bird was observed over the half hour period, using footage taken with a GoPro camera and coloured wing bands for identification. Four of these tray feeds were carried out over one month at weekly intervals, the number of tray feeds selected so as to not interfere with The Deep's feeding routines. This allows comparison between how penguins feed from aquarists and trays and to identify any influences of personality.

### 3.2.5 Analysis of Site Fidelity

GoPro footage was used but using time lapse photography to take a photo every five minutes between the hours of 10.00-11.30h, 12.30-15.30h and 16.00-18.00h. This covered all daylight hours that aquarists were not in the enclosure. Two cameras were used to cover the ice area and the dry dock and were started simultaneously at 09.45h. The enclosure was divided into fourteen areas, sites one to seven in the dry dock and eight to fourteen on the ice shelf (Figure 2). The location of each individual was recorded at five minute intervals to determine total percentage use of each of the areas. The fourteen areas used in the study were not all of equal size but were chosen due to their defined edges clearly visible in the contours of the enclosure. This was carried out over five days to calculate an average use of each area and to determine the site predominantly used by each bird. The distance (in cm) from the centre of each site to the nearest viewing window was then measured using a tape measure and the

light intensity at each site was determined using a Hanna (HI 97500) luxmeter. Measurements were taken at 10.00h on two days to create an average. However, light levels were found to be highly consistent. There was no change in light levels between days due to the dominance of controlled artificial lighting that mimics the natural light cycle of these birds. Therefore, the penguins using each site were identified, as well as the distance from visitors and light intensity at each site. The site parameters could then be correlated with the boldness of the penguins occupying each location in the enclosure. The fact that ten of the thirteen birds occupy the same sites in five pairs was taken into account by creating an average boldness for the pair of birds occupying the site. This resulted in eight data points instead of thirteen and removed the effects of pseudoreplication. Pseudoreplication is the process of artificially increasing the number of samples or replicates and the outcome is often more significant results. By carrying out the analysis on eight data points once the fact that paired individuals occupied the same sites was taken into account prevented pseudoreplication by removing these artificial replicates.



**Figure 2.** Close up of penguin enclosure at The Deep showing the fourteen sites used in the site fidelity study.

### 3.2.6 Effects of Boldness on Mating Success

The mating success (occurrence of at least one egg per pair) of the adult birds in the population was observed. Nests are regularly checked for eggs during breeding season. The population at The Deep has had two successful breeding seasons, 2016 and 2017. The birds that reproduced in 2016 and 2017 were noted, and from this individual mating success calculated, 100% for breeding in both years, 50% in one and 0% for no breeding. The chicks were not included in this part of the study as they had not reached sexual maturity.

### 3.3 Statistical Analysis

All of the data collected during the four investigations was analysed using R software (R Core Team, 2015). The figures required for the study were also generated in R.

All penguins were considered to be behaviourally independent despite several penguins being related. For example, the population includes offspring from two adult pairs and a full brother and sister. This assumption is supported as heritability in personality is only low to moderate, ranging in a number of taxa (excluding primates) from 0-0.4 (Brent et al., 2014). Personality is also influenced by a number of factors including genetic, environmental, developmental or situational factors (Stamps & Groothuis, 2010; Wolf & Weissing, 2012). These factors combined allow all individuals to be considered as independent data points.

To assess consistency in aquarist ratings Kendall's (W) coefficient of concordance was used. Kendall's W assesses agreement among observers and therefore gives a value of consistency across the rankings of the aquarists towards each penguin. This method was chosen ahead of other methods of assessing consistency such as the omega coefficient (Dunn et al., 2014).



To analyse repeatability in the indicators of personality (public interactions and novel items), consistency repeatability ( $R_C$ ) was used.  $R_C$  is a variance estimate and illustrates how strong individual consistency is (Rèale et al., 2007) and shows how much of the behavioural variation is due to differences between individuals (Bell et al., 2009).  $R_C$  takes into account and allows for mean level changes in all individuals over time whereas these changes are not factored in when using agreement repeatability ( $R_A$ ) (Biro & Stamps, 2015).  $R_C$ , consistency repeatability, was analysed using a generalized linear mixed model approach in a Bayesian context (Monte Carlo Markov Chain GLMM; Package MCMCglmm in R). For public interactions, by using the variance estimates from a linear model containing average interactions (per month) by the penguins with the public as the dependent variable, observation day as fixed effects and individual as random effect, an  $R_C$  value was generated. Following the work of Biro and Stamps (2015) observation day was used as a fixed factor. To satisfy normal (Gaussian) distribution in the test when analysing public interactions, the average number of penguin interactions with visitors were transformed using the log10 function. Identifying whether the data was normally distributed or equally variant around the means was achieved using screening tests. These were Shapiro and Levene's test respectively. Q-Q plots were also used as visual representations of distribution. Further to this posterior distribution plots of the intercept and variance components were inspected visually to determine that models converged and that the algorithms were valid. Autocorrelation was evaluated using plots of residuals and models were chosen depending on deviance information criterion (DIC). A non-informative prior was used to choose the best unbiased model ( $V=1$ ,  $n = 0.002$ ). The chain length was 1300000 which was "thinned" by a factor of 1000 giving an effective sample size of 1300 (1300000/1000). Burnin was set at 300000. Burnin is the process of choosing the best starting point for the chain by discarding early simulations, this is done to remove

unrepresentative data. The posterior mode for fixed and random effects along with their 95% confidence intervals (CIs) was reported.

For study of novel items using repeatability the same process was used. The dependent variable was exchanged for number of orientations, average duration of visits and total duration spent at the novel item. Exponential distribution was used in the analysis in all three cases, as the data was of this distribution even following transformation.

When analysing site fidelity, a multiple linear regression was used. All assumptions of this test were met; the relationship between independent and dependent variables was linear (scatterplot), normal distribution was observed between predicted and observed values (Q-Q plot), there was no multicollinearity between the independent variables (correlation coefficient  $<0.8$ ) and finally there was no clear pattern (homoscedasticity) in the distribution of residuals versus predicted values (cone-shaped pattern in scatterplot). This method takes into account the effect of two independent variables on the dependant variable. In this case, distance from visitors and light intensity as the independent variables and boldness as the dependant variable. This allows determination of the independent variable that has greatest effect on the dependent variable. This was determined to be light intensity and further analysis was then completed on this, with the fact that birds had formed pairs and occupied the same site also being taken into account. The correlation being run for eight data points (five pairs and three individuals) instead of thirteen (thirteen individuals).

Finally, the correlation between aquarist rating and visitor interactions plus all analysis on consequences of personality were completed using correlation tests. Spearman's correlation was used when using ranked non-parametric data (aquarist boldness rank against ranked daily feed and ranked weight plus reproductive success against boldness rank from aquarists

and boldness rank from public interactions). Pearson's correlation was used when using parametric data (aquarist boldness rating against average interactions, average daily feed against percentage body weight daily food consumption, percentage body weight daily food consumption against number of fish taken from trays, light intensity of site against boldness rank from aquarists). Screening tests were used to determine whether parametric tests could be carried out.

## 4. Results

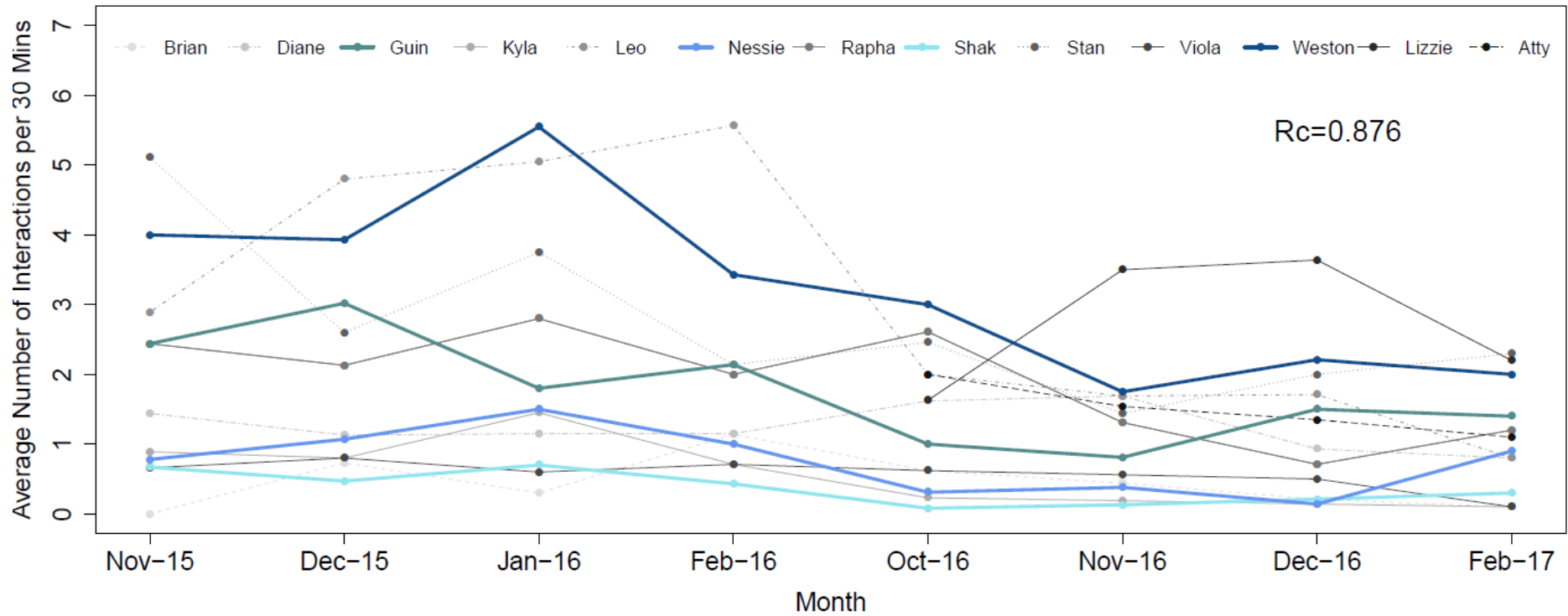
### 4.1 Indicators of Personality

There is high consistency between aquarists in the boldness ranking of the birds across the two years of the study (Table 1.) and this was analysed using Kendall's W. Consistency was high in both 2015 (Kendall's  $W=0.817$ ,  $df=10$ ,  $p<0.001$ ) and in 2016 (Kendall's  $W=0.724$ ,  $df=12$ ,  $p<0.001$ ). There was a change in personnel between the two years and this was aquarist five. There are no ratings from 2015 for the two chicks that hatched in June 2016.

**Table 1.** Aquarist boldness ratings of each penguin by the five penguin keepers in 2015 and 2016 including overall average across both years. 2016 includes the two chicks hatched in that year and Aquarist 5 was also a different person in this year.

Penguin	2015					2016					Mean
	Aquarist 1	Aquarist 2	Aquarist 3	Aquarist 4	Aquarist 5	Aquarist 1	Aquarist 2	Aquarist 3	Aquarist 4	Aquarist 5	
Weston	10	11	11	10	10	12	13	12	13	13	11.5
Leo	11	10	10	11	11	13	12	11	12	12	11.3
Atty	-	-	-	-	-	11	11	6	11	11	10.0
Diane	7	7	9	9	9	7	10	13	7	5	8.3
Lizzie	-	-	-	-	-	10	7	2	10	10	7.8
Stanley	9	9	6	7	2	9	8	9	8	8	7.5
Viola	8	8	8	8	8	8	9	5	5	4	7.1
Rapha	5	4	5	6	3	5	4	7	6	9	5.4
Brian	4	3	7	5	4	2	2	10	9	7	5.3
Kyla	6	6	3	4	7	6	6	8	4	3	5.3
Guinevere	2	2	2	3	6	1	5	4	3	2	3.0
Nessie	3	5	1	1	5	3	3	1	2	1	2.5
Shackleton	1	1	4	2	1	4	1	3	1	6	2.4

Individual penguins were also consistently different in their average number of interactions with visitors, as seen in the highlighted examples of Guinevere (Guin, green), Nessie (light blue), Shackleton (Shak, turquoise) and Weston (dark blue) (Figure 3). This is shown by high repeatability ( $R_c = 0.876$ ,  $CI = [0.731, 0.944]$ ). The  $R_c$  value of repeatability takes into account the apparent changes in interaction averages over time within the population, observable as a negative trend, with a decrease in average interactions as the study progressed.



**Figure 3.** Average visitor interactions for each of the thirteen individuals.  $R_c$  value shows consistency within individuals using repeatability. The four bold coloured lines show (green, light blue, turquoise, dark blue) highlight four individuals which demonstrate the highly consistent differences between individuals. Data points for the two chicks (Lizzie and Atty) begin in October 2016.

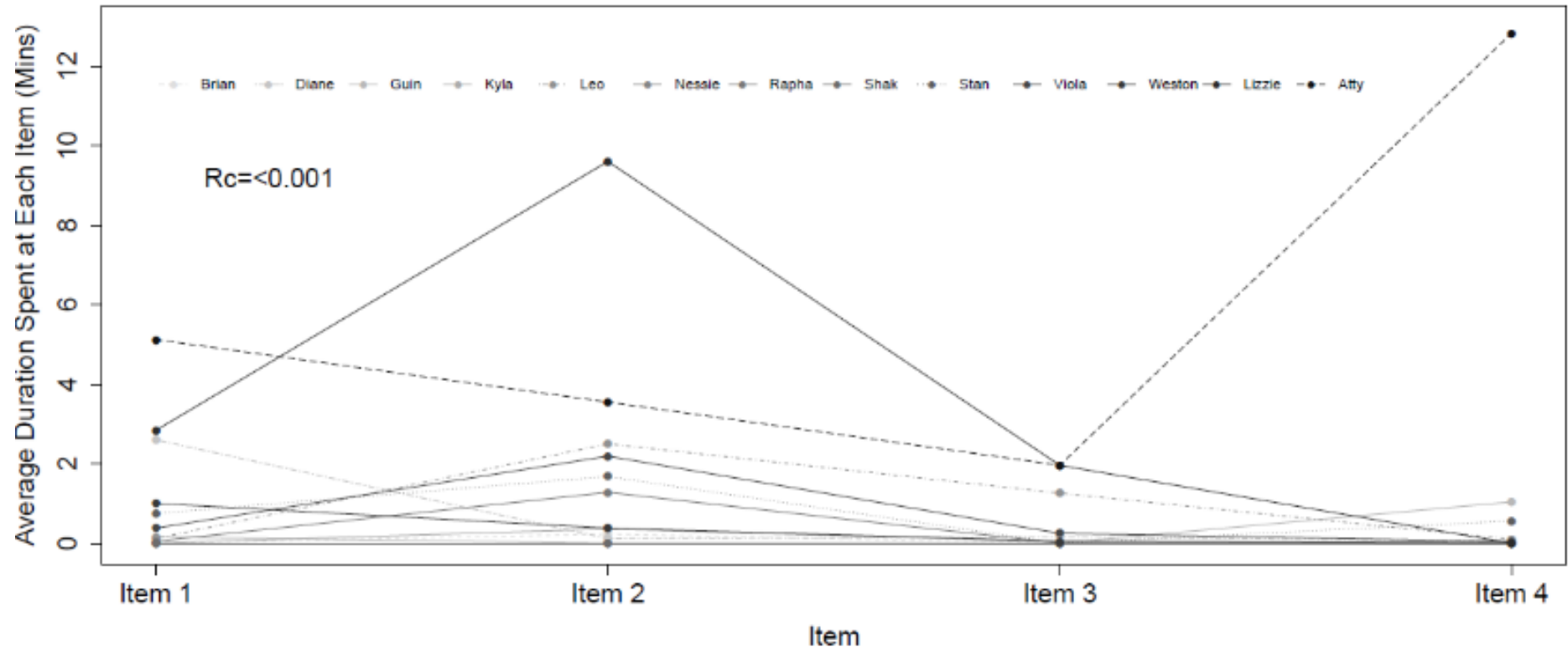
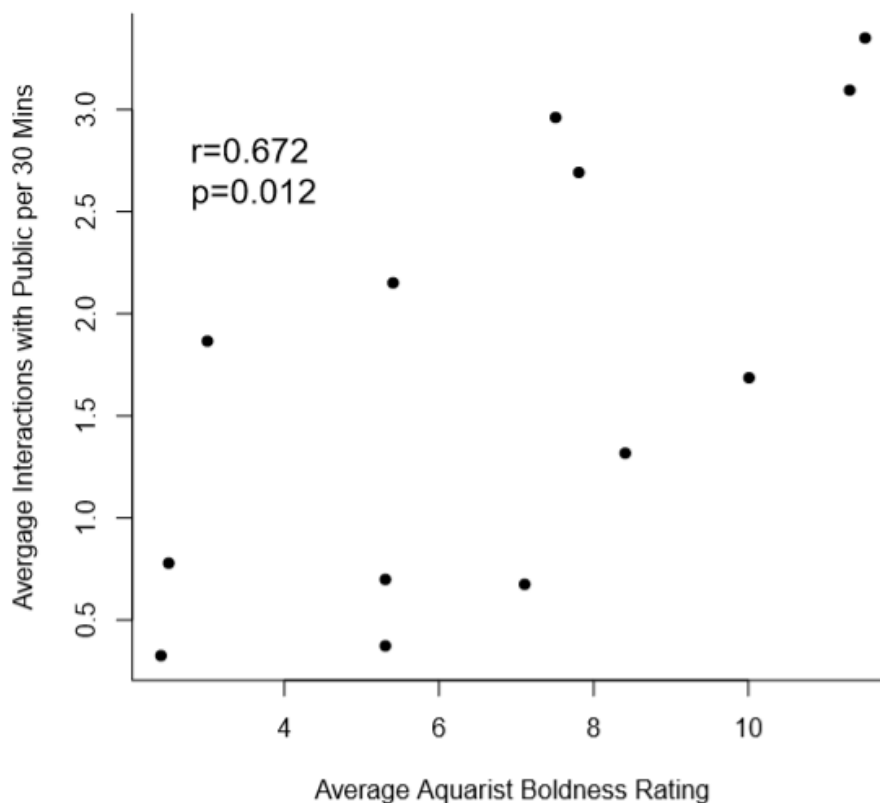


Figure 4. Average duration (mins) spent by each individual at each of the four novel items.  $R_c$  value shows consistency within individuals using repeatability.

Penguins did not show individually consistent responses towards novel objects. This was seen across all three response variables observed; number of orientations, average duration of visits and average total duration spent at each novel item, in all cases  $R_c < 0.001$ . Average duration spent at each item is shown as an example (Figure 4). Large variability was present between and within individuals across all three variables of response to novel objects. In addition, many individuals made very few to no interactions with the novel objects. The two individuals that spent the greatest average time with the novel objects were Atty and Lizzie.

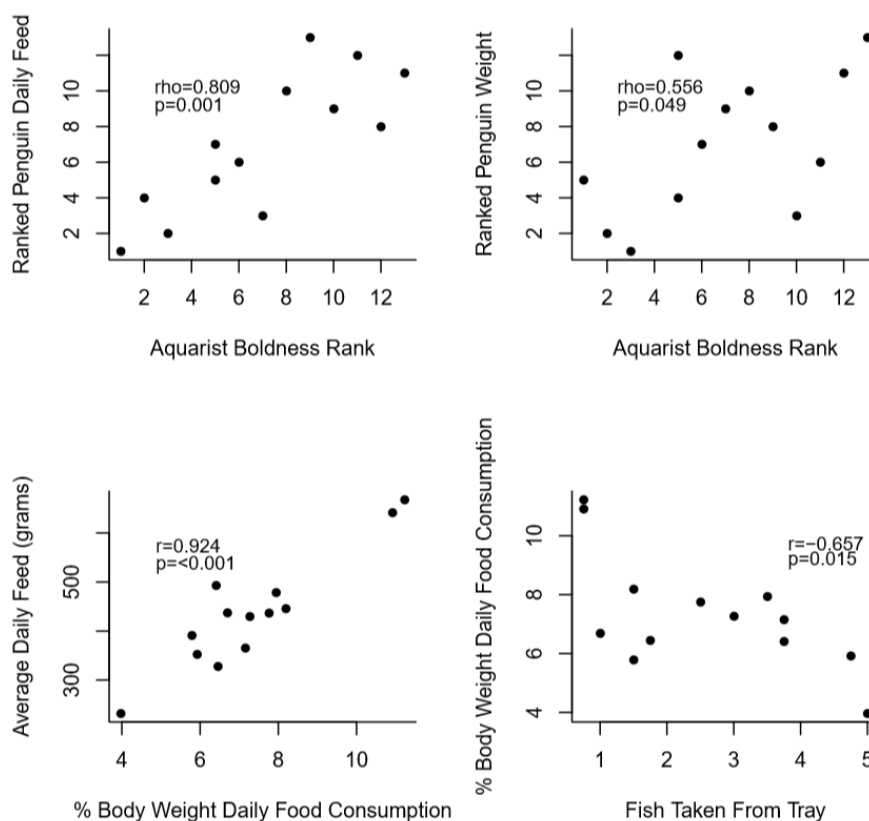
Mean boldness towards aquarists and the average interactions with visitors over the whole study significantly correlate ( $r(11)=0.672$ ,  $p=0.012$ ; Pearson correlation). Individuals that are bolder towards the public, due to spending greater time with the public at the pool viewing window, were also the individuals with consistently higher aquarist ratings (Figure 5).



**Figure 5.** Correlation between average aquarist boldness rating and average interactions with the public over the half hour observation periods, Pearson's correlation coefficient ( $r$ ) and  $p$  values shown.

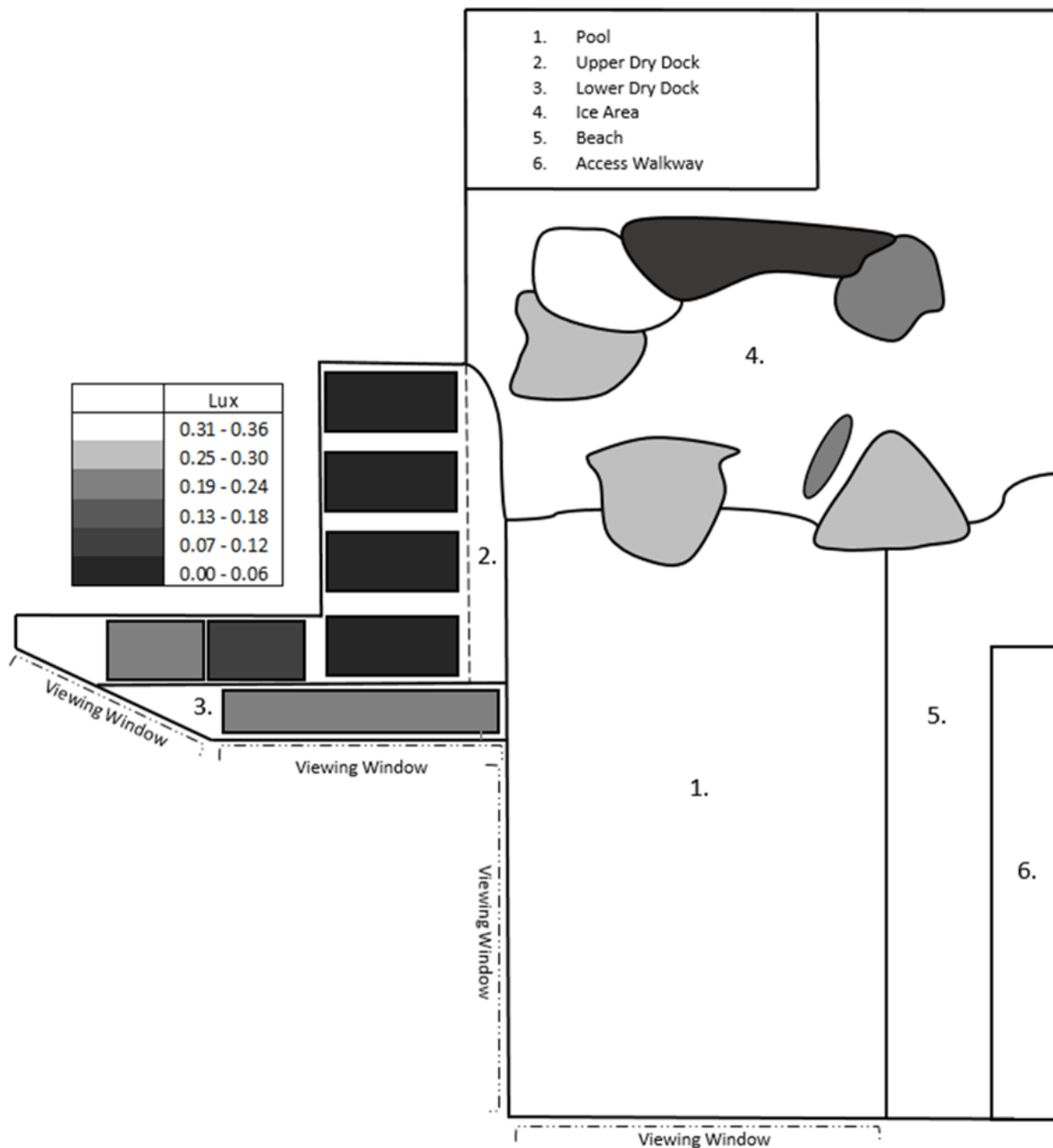
#### 4.2 Expressions of Personality

When the penguins are ranked using their average aquarist ratings, significant positive correlations are found with both the ranked average daily feed ( $\rho=0.809$ ,  $df=11$ ,  $p=0.001$ ; Spearman correlation) and ranked weight ( $\rho=0.556$ ,  $df=11$ ,  $p=0.049$ ; Spearman correlation) of individuals (Figure 6). The mean daily feed of each bird significantly correlates positively with each individual's percentage body weight daily food consumption ( $r(11)=0.924$ ,  $p<0.001$ ; Pearson correlation). However, when daily food consumption is correlated with food taken from tray feeds, the correlation is negative ( $r(11)=-0.657$ ,  $p=0.015$ ; Pearson correlation), with birds that eat a smaller percentage of their body weight from aquarists, eating a greater number of fish from tray feeds (Figure 6).



**Figure 6.** Feeding and boldness relationship correlations. a. Aquarist boldness rank against daily average feeding rank. b. Aquarist boldness rank against ranked penguin weight. c. Percentage body weight daily food consumption against average daily feed. d. Average fish taken from feeding tray against percentage body weight daily food consumption.  $\rho/r$  and P values shown.

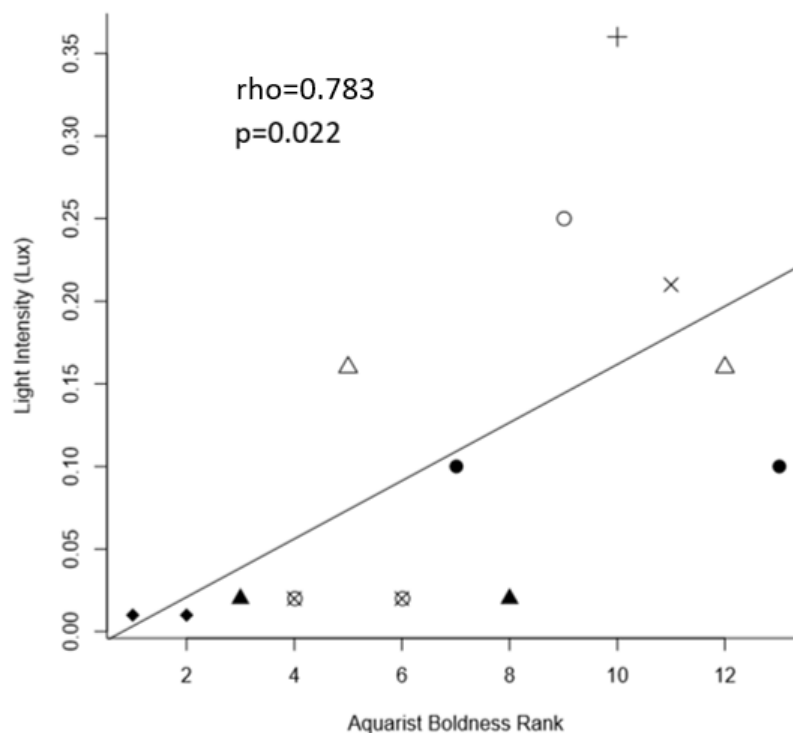




**Figure 7.** Penguin enclosure at The Deep, showing main enclosure areas and the light levels (Lux) of each of the fourteen sites with the enclosure.

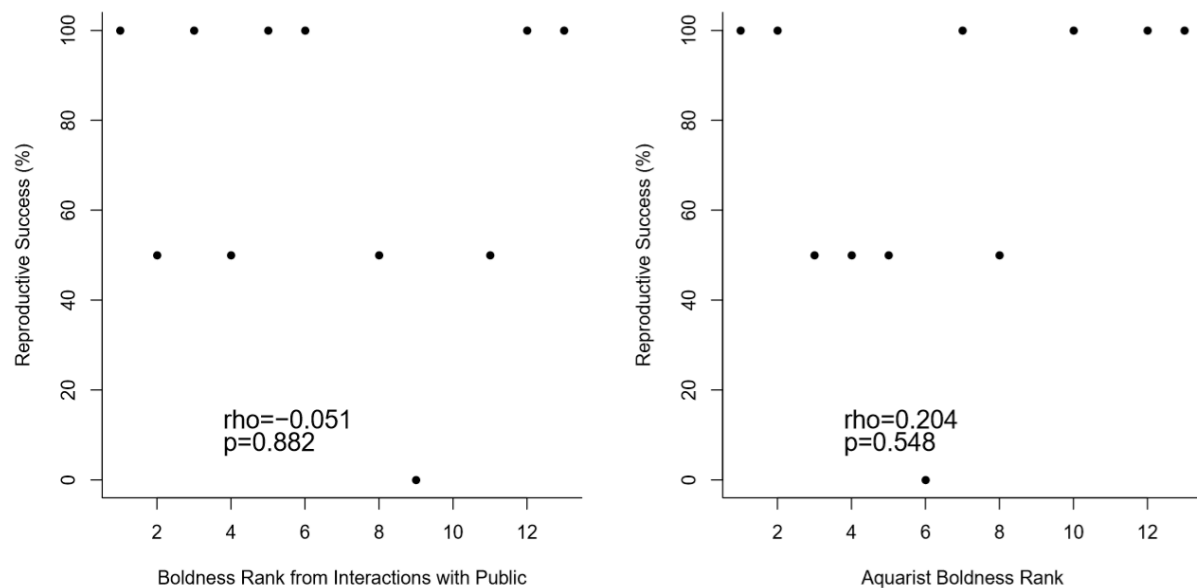
Following multiple linear regression analysis, it was found that there was a relationship between environmental parameters (light and distance to nearest viewing window) and boldness ( $R^2=0.756$ ,  $F(2, 10)= 4.745$ ,  $p=0.036$ ). However, only light intensity ( $t=3.081$ ,  $df=10$ ,  $p=0.012$ ) had a significant relationship with boldness by aquarist rating. There was no relationship with distance from visitors ( $t=-1.391$ ,  $df=10$ ,  $p=0.195$ ). The aquarist boldness rank

of the penguins correlated with the light intensity at the site within the enclosure predominantly used by each penguin. Analysis took into account the fact that five pairs of birds occupy the same sites. This allowed an average boldness to be created from both birds for each site. Bolder penguins occupy sites with higher light intensity ( $\rho=0.783$ ,  $df=6$ ,  $p=0.022$ ; Spearman correlation) (Figure 8). Light intensity across the sites used ranged from 0.01-0.36 Lux, darker sites in the dry dock and predominantly lighter sites on the ice area (Figure 7). Eleven of the thirteen birds in the population have greater than 70% site fidelity, while the two chicks are more plastic (Atty 42.31% and Lizzie 37.11%). However, their site fidelity is higher than if an even distribution was exhibited across sites (7.14%). The other sites occupied by the chicks have very similar light intensities to the site that they occupy predominantly.



**Figure 8.** Aquarist boldness rank of the birds correlated against the light intensity (Lux) of the site occupied by each penguin, best fit line shown. Pairs occupying the same sites within the population are shown by matching symbols. The two chicks are shown by the symbols  $\times$  (Atty) and  $\circ$  (Lizzie). Regression analysis done on boldness averages of pairs occupying the same sites,  $p$  and  $\rho$  values shown.

Finally, aquarist ranking of boldness does not correlate with individual mating success across the two breeding seasons ( $\rho=0.204$ ,  $df=11$ ,  $p=0.548$ ; Spearman correlation; Figure 9). This is also the case when individual mating success is correlated against the ranking of average public interactions ( $\rho=-0.051$ ,  $df=11$ ,  $p=0.882$ ; Spearman Correlation; Figure 9). In the population, six birds had 100% breeding success, four birds had 50% and one individual did not breed over the two years. This bird, however, did not pair in either year of the study. There was a substantial increase in the percentage of birds that reproduced from 2015 (54%) to 2016 (91%).



**Figure 9.** Percentage individual mating success over the two breeding seasons at The Deep, against rank of interactions with public and aquarist boldness, rho and p values shown.

## 5. Discussion

The Gentoo penguins that make up the population at The Deep exhibit consistent individual differences. This is demonstrated both by the significant repeatability over time in interactions with members of the public and the lack of variance in aquarist ratings over the two year study period. These individual differences, in two very different scenarios, also correlate, showing personality across different situations. This is shown as penguins that are bolder towards the public also have higher ranks in boldness by aquarists. These consistent differences mean this is the first study to show personality in this species. Personality traits that are of relevance for husbandry are also present in this group, with variations in feeding preferences and site choice within the enclosure. Bolder birds feed more from aquarists and have a higher weight, while shyer members of the population feed more from tray feeds. The bolder individuals also occupy sites with higher light intensity. However, in comparison to these two areas, personality has no influence on mating success in this population with high mating success present in both bold and shy individuals.

### 5.1 Personality

The two main criteria required for personality to be present in a population are consistency over time and across contexts or situations (Dingemanse & Réale, 2005; Wolf et al., 2007; Bergmüller & Taborsky, 2010; Sih et al., 2012; Beekman & Jordan, 2017). Contexts are functional behavioural categories (e.g. feeding, dispersal, predator response). Situations are given sets of conditions at a single point in time (e.g. different levels of predation risk), or different conditions across time (e.g. non-breeding season versus the breeding season) (Sih et al., 2004). There can, therefore, be behavioural differences in the same context but different situations (e.g. feeding activity in the absence or presence of predators), or in

different contexts in different situations (e.g. intraspecific aggression in the absence of predators versus feeding behaviour when predators are present) (Sih et al., 2004). The population at The Deep satisfies both of these two requirements of personality. First, the penguins show high repeatability in interactions with the public over time. Second, these differences are across the same context but in different situations (response to predators in curiosity towards unfamiliar individuals and reaction to husbandry care from familiar individuals; feeding and treatments), with bold and shy individuals responding the same to both aquarists and visitors. This evidence of personality in this population supports the literature that personalities are common (Bolnick et al., 2003; Gosling, 2008b) both in humans (Sih et al., 2004) and in a wide variety of species, including mammals, fish, birds, reptiles, amphibians, arthropods, insects, cephalopods and molluscs (Bell et al., 2009). However, the current collection of studied species is far from representative, with 84% of studies being carried out on mammals and the remaining 16% covering all other animal groups (Gosling, 2008b). Although this study was nine years ago, it highlights the need for further study into other species and animal taxa. Gentoo penguins can now be added to this list, as no previous study has investigated personality in this species and this provides further evidence that personalities are common in birds (Gosling, 2001).

Despite the reliance on consistency, this does not imply that individual behaviour is fixed (Rèale et al., 2007; Biro & Stamps, 2008). There can be changes in behaviour over time, but differences between individuals must remain consistent (Mathot et al., 2012). Differences in behaviour over time occur in both humans and non-human animals (Beekman & Jordan, 2017). An example of this is shown by Adriaenssens and Johnsson (2013), when despite an overall increase in activity among the brown trout (*Salmo trutta*) studied, the individuals most active in the first test were still the most active in the second test following recapture. This is

also the case in this study, where the overall trend is a decrease in interactions among the population, but the individuals that interact the most at the start of the study, are still the individuals with the most interactions at the end of the study. This decrease suggests habituation, as animals do eventually come to ignore visitors (Chamove et al., 1988) as they lose their novelty (Paquette & Prescott, 1988). However, personality research has also shown animal behaviour to be less flexible than previously believed (Wolf et al., 2007). This is supported by this study and that by Adriaenssens and Johnsson (2013), because although there are changes in behaviour over time, the trends among individuals remain the same and no individual has a large change in behaviour towards a set stimuli.

## 5.2 Indicators of Personality

Two of the three indicators used in this study have been shown to be effective identifiers of personality. Studying three indicators of personality was important as it is vital not to focus on one single behaviour (Bell, 2007). This is because studying multiple behaviours reduces the risk of indicators not being successful in identifying personality, as was found in this study. The first of the effective indicators was responses towards visitors. This is supported by this study, as penguins were found to respond differently to the visitor presence. Personality impacts on how animals react to challenging situations (Rèale et al., 2009) such as enriching or stressful visitors (Ozella et al., 2015) and this stimulus can vary in intensity and volume (Chamove et al., 1988), with busy and quiet days being present in all zoos and aquariums (Hosey, 2000). Animals can interact with visitors, as shown through the studies by Cook and Hosey (2005) and Nimon and Dalziel (1992) on chimpanzees (*Pan spp.*) and a captive long billed corella (*Cacatua tenuirostris*) respectively. However, a large amount of animal visitor interactions often result in avoidance behaviour (Davey, 2007). Since these interactions, in

species where they occur, make up a significant part of a captive animal's life (Hosey, 2013) and individuals respond differently to humans dependant on their personality (McDougall et al., 2006; Davey, 2007), this is an effective indicator of personality. These factors also help facilitate data collection over long time periods, allowing repeatability analysis as shown by this study. This also allows personality not to be confused with non-repeatable behaviours caused by environmental conditions or recent exposure to stimuli (Careau et al., 2008; Briffa & Weiss, 2010). This is an issue that may arise due to lack of data, one off or rare behaviours possibly being confused for common ones, when in fact they are not repeatable.

Therefore, personality influences how individuals interact with individuals of other species, including humans (Powell & Gartner, 2011) such as keepers (Careau et al., 2008). An example of this is the fact that the way tigers (*Panthera tigris tigris*) interact with keepers is influenced by their personality (Phillips & Peck, 2007). However, little other study has been carried out in this area (Hosey, 2008). Keepers possess the ability to accurately and consistently rate the personality of animals in their zoos/aquaria (McDougall et al., 2006). This has been demonstrated in a number of studies showing high correspondence between keeper ratings and behavioural observations (Wielebnowski et al., 2002; Carlstead & Brown, 2005; Gosling, 2008a; Koski, 2011). This is supported by the results of this study, with the high consistency of ratings and the strong correlation between the behavioural interactions with the public and the aquarist ratings. The reliability of these ratings also understandably increases over time with experience of working with the animals (Powell & Svoke, 2008). Furthermore, the effort to keep ratings as independent as possible between aquarists adds further weight to their reliability. Therefore, keeper ratings of animals can be a reliable indicator of personalities and can be used to add further strength to behavioural repeatability observations.

Measuring the response to novel items was not found to be an effective indicator of personality in this study. This is demonstrated by the low repeatability in all three response variables measured; number of orientations, average duration of visits and average total duration spent at each novel item. This method (repeatability across the four novel items) was chosen as the initial method was unsuccessful. The original method was observing the order of approach to each item. Some items were not approached the first time they were placed in the enclosure or not by all penguins, even after the four days. The average responses to each item, across the four times they were placed in the enclosure, gave a better representation of each individual's reaction to them. Therefore, although this includes responses when the item lost its novelty (days 2-4), an accurate representation of responses was not achieved when just observing the responses when the items were truly novel (on first encounter). Novel items have been used in many previous studies to assess personality in a diverse range of species (Briffa & Weiss, 2010). The results of this study are in opposition to the current understanding that careful observation of an animal's response to novel items gives an insight into its personality (Powell & Svoke, 2008). A large range of novel objects have been used in previous studies including Lego, Playmobil, tennis balls, bottles, etc. (Antunes & Biala, 2012). Novel items may, however, cause an avoidance stress response in birds as seen in great tits and blue tits (*Cyanistes caeruleus*) (Briffa & Weiss, 2010). In this study, the choice of items used may have caused a similar stress response in the birds preventing them from interacting with the object immediately, or not at all due to the low exposure time to each object. This is shown by the low overall interaction with the objects by a large proportion of the population and is subsequently a limitation of this aspect of the study. Faster habituation to weak novel item stimuli (Paquette & Prescott, 1988) may also play a part in the lack of repeatability, due to varying responses to different items (Antunes



& Biala, 2012), some of the items chosen perhaps having a lower effect and this could be due to size, colour or interaction potential. This is supported as the object most interacted with (water filled plastic bowl with floating rubber duck) was the largest and offered the greatest interaction potential to the birds. Furthermore, the time and location that the objects were introduced to the enclosure may not have been appropriate to gain the required data for repeatability. This could be the case as the penguins have varying activity levels during different times of the day and can also spend large amounts of time swimming at certain periods. Therefore, introduction of the item during lower activity periods (preening following a swim or the beginning of roosting behaviours at night) or when swimming, may significantly reduce attention towards the novel item. Therefore, a more robust method, through better selection of items and/or a different time of introduction, may have provided better results, allowing novel items to aid identification of personality in this study. The unsuccessful use of this technique as an indicator, despite the significant previous success achieved with novel items outlined in the literature, highlights the need to study more than one behavioural response when studying personality.

### 5.3 Expression of Personality on Feeding and Weight

The penguins at The Deep show different feeding strategies dependent on their personality. This is displayed in either bolder individuals feeding more from aquarists or shyer individuals from tray feeds. This difference in feeding strategy is supported by the literature as individuals often vary consistently in their responses to environmental and social challenges such as feeding (Dingemanse & Réale, 2005; Bergmüller & Taborsky, 2010). Significant evidence exists that feeding strategies are dependent on personality (Sih & Watters, 2005), with resulting conflicts between feeding and predator avoidance (Sih et al., 2004; Carter et al., 2012). As

shown by this study and others, individuals differ in their response to keepers (Careau et al., 2008; Claxton, 2011). In addition to this, animals such as penguins can view humans as predators (Herborn et al., 2010). Therefore, this can explain the difference in feeding strategies in this population, with bolder individuals being prepared to feed from the keepers in a more risky scenario than the less risky tray feeds preferred by the shyer individuals. There is support for this in the literature as individuals can be placed on a proactive to reactive axis (Sih & Bell, 2008) with proactive individuals taking more risks for higher productivity, while reactive individuals are risk averse to enhance survival (Aplin et al., 2014). This axis is common across multiple taxa (Aplin et al., 2014) with proactive individuals being bolder. These individuals have the greater resource intake but higher mortality risk (Sih & Bell, 2008). For example, in great tits reactive individuals flock trading safety for greater resource competition, while bold proactive individuals forage alone but face greater predation risk (Aplin et al., 2014). The same distribution in feeding strategies has also been noted in zebra finches (*Taeniopygia guttata*) (Aplin et al., 2014) and barnacle geese (*Branta leucopsis*) (Kurvers et al., 2012). In addition to this, shy individuals also take longer to feed in a captive environment than bold individuals (Herborn et al., 2010) decreasing the time available to feed from aquarists. This is an area that could be investigated in future studies. Furthermore, bolder individuals, due to being more active and exploratory (Sih & Bell, 2008), may have greater energy expenditure and subsequently greater food requirements (Careau et al., 2008). This may further reinforce the need to feed in risky, more productive situations (Aplin et al., 2014). The difference in feeding strategies in this population due to personality, highlights the need to provide food using a range of feeding techniques to suit all individuals in a captive environment. The need to keep the number of familiar individuals (aquarists) to a minimum is also important to maintain human-animal relationships (Hosey, 2008). This in

turn reduces the potential predation stimulus of unfamiliar keepers (Claxton, 2011). An example which illustrates this is a study on clouded leopards (*Neofelis nebulosa*) which showed higher stress levels in individuals exposed to greater numbers of keepers (Wielebnowski et al., 2002). Taking these factors into account is especially important in this population because shyer individuals eat significantly less than the 10-14% of body weight advised daily food consumption for penguins (Penguin Taxon Advisory Group, N/A) and it is imperative in captivity to meet the energy needs of the animals (Worthy, 2001). However, this is not the only possible indicator of health, other examples include observed variations in body size and direct health assessments. These are potential areas for further study when determining effects of personality on the energy intake and health of penguin individuals.

Conditioning of behaviours and potential hierarchies in the population were not considered to have an impact on feeding amounts by the individual birds. Firstly, in the case of conditioning, in the experience of the researcher and other aquarists who feed the penguins, there has been no change in individual feeding levels or behaviour over the course of the study by individual penguins. The birds all have their own individual feeding characteristics and habits, and these have remained the same throughout the two years of the study. None of the individuals across the whole bold-shy scale have become bolder or increased in feeding level, despite the potential for positive conditioning of this behaviour. The length of feeds (30 minutes) reduces the effect of a hierarchy on individual feeding amounts. This is because all birds have sufficient time to feed, each bird having the time to make multiple trips to aquarists throughout the half hour feed. If the feed time was shorter then this may have more impact as bolder individuals may have more influence and monopolise the food resource. Therefore, these factors were discounted when observing feeding amounts, but are both areas with potential for further study, for example, identifying the existence and structure of a hierarchy.

#### 5.4 Expression of Personality on Site Choice

Restricted space and lack of complexity is a common characteristic of captive environments (Mallapur & Chellam, 2002; Mallapur et al., 2002; Sherwen et al., 2015), with poorly designed enclosures being a source of stress to animals (Ross et al., 2009). For example, poor design may prevent animals retreating from stressors such as visitors (Hosey, 2008). It is, therefore, critical that zoos understand how animals use space within enclosures (Sherwen et al., 2015) to allow enclosure design to take into account the needs of the inhabitants (Ross et al., 2009). To date animal behaviour studies have been given little consideration in the design of enclosures (Ross et al., 2009). The penguins in this population distribute due to light levels, since this plays a large part in their visibility to visitors, with bolder individuals occupying brighter locations. This finding is supported by other studies with non-random dispersal by personality expected in both captive and wild animals (Sih & Bell, 2008; Wolf & Weissing, 2012). For example, chipmunks (*Tamias striatus*) are distributed dependent on human visitation and bolder individuals are found closer to the public (Fraser et al., 2001). Boldness is also linked to explorativeness (Sih & Bell, 2008). Explorativeness takes into account how readily individuals explore new areas, not just the use of a specific area, potentially exposing the individual to predation. This may further influence the ability or likelihood that animals will occupy certain locations (Martin & R  ale, 2008). This is seen in three-spined stickleback (*Gasterosteus aculeatus*) where bold individuals more actively explore environments (Bell, 2005). Further examples of this are found in a number of other fish species including sunfish (*Lepomis gibbosus*) and rainbow trout (*Oncorhynchus mykiss*) (R  ale et al., 2007; Biro & Post, 2008; Biro & Dingemanse, 2009). In addition, the relationship between boldness and explorativeness is also found in mammals and birds (Carter et al., 2012). Therefore, through both greater boldness towards stressors and increased explorativeness, different individuals

will occupy different parts of an enclosure dependant on their personality. These findings mirror the observations of this study and, therefore, show the requirement of taking personality into account during enclosure design to suit the needs of all individuals (Kuhar, 2008). This can be achieved through increased environmental complexity (Skibieli et al., 2007) providing shy individuals with darker places and bold animals with the opposite (Kuhar, 2008; Powell & Gartner, 2011). In enclosures where retreat spaces are made available they are used by animals, as shown by the studies on captive lion-tailed macaques (*Macaca silenus*) (Mallapur et al., 2005), goats (*Capra hircus*) and sheep (*Ovis aries*) (Anderson et al., 2002). These findings are further supported by the results of this study as shy individuals occupy darker spaces. Although this study found light levels to be the determining factor in site choice, there may be a number of related parameters that act together to produce more or less exposed areas preferred by shy and bold individuals respectively. These may be natural characteristics of the enclosure or specific design points implemented to create such areas. Examples of enclosure design improvements that can be made are one-way viewing glass windows and barriers for animals to hide behind (Chamove et al., 1988; Fernandez et al., 2009) such as plants, concealment screens and camouflage nets (Davey, 2007). Changes to enclosure design such as these allow animals to determine their level of exposure to stressors (Hosey, 2008). Increasing environmental complexity, as well as providing for all individuals, has the added advantages of reducing stress (Carlstead et al., 1993) along with increasing activity (Mallapur & Chellam, 2002) and cognitive use in the animals (Skibieli et al., 2007). In some cases, it has also been seen to influence and improve visitor behaviour towards animals (Fernandez et al., 2009). Therefore, personalities result in differences in site choice in captive conditions leading to welfare differences between individuals (Groothuis & Carere, 2005).

Optimising welfare is important for zoos and aquaria (Larsson, 2012) and understanding site choice and use of space in all individuals in a population is vital when designing enclosures.

### 5.5 Expression of Personality on Mating Success

Contrary to expectation, breeding success is not related to personality in this population. This is shown by the similarity in breeding success with both bold and shy birds producing eggs in both years. This result is not supported by the literature, as personality traits have been linked to mating success (Martin-Wintle et al., 2017). These personality traits include boldness and aggressiveness (Smith & Blumstein, 2007; Koski, 2011). Bolder and more aggressive individuals have been shown to have higher mating success (Smith & Blumstein, 2007) and cases of this have been seen across a variety of species (Briffa & Weiss, 2010). Examples include bighorn sheep and black rhino (*Diceros bicornis*) with lower levels of stress behaviour observed in individuals that reproduced successfully (Carlstead & Brown, 2005). Non-breeding cheetahs are also more fearful (*Acinonyx jubatus*) (Wielebnowski, 1999) and shyness is correlated with poor sexual performance in giant pandas (*Ailuropoda melanoleuca*) (Powell et al., 2008). As stress is a barrier to reproduction (Mason, 2010) and poor enclosure design can cause stress (McDougall et al., 2006), breeding success may also be dependent on enclosure design, with effective design providing suitable reproductive conditions for all individuals (Sherwen et al., 2015). The lack of consideration of this may explain the low mating success in some personality types, demonstrated by the literature examples with enclosure conditions having a strong impact on stress levels (McDougall et al., 2006). Improving mating success through better enclosure design is supported by studies that have altered the captive environment and mating success has increased as a result (Wielebnowski, 1999; Powell et al., 2008; Powell & Svoke, 2008). Enclosure design and personality are therefore important

factors in captive animal breeding programs (Powell & Gartner, 2011). The complexity of the enclosure at The Deep, allowing choice of site among individuals, may therefore be the reason for the high breeding success in this population. This is the case despite the diverse range of personalities present, because suitable conditions are available for all personality types with shy animals needing more seclusion to breed successfully (Wielebnowski, 1999; Powell et al., 2008).

#### 5.5.1 Benefits of Understanding Personality for Captive Breeding

Increasing mating success to include all individuals, through better understanding of personality (Martin-Wintle et al., 2017) and enclosure design (McDougall et al., 2006), will have a number of advantages. First, the loss of genetic diversity that is hard or impossible to replace is limited by facilitating breeding in all individuals (Kleiman, 1989). This is an important issue because providing conditions for the population average without considering personality may result in the loss of important variation within a population. This in turn reduces the future adaptive ability of species (Bolnick et al., 2003; McDougall et al., 2006). Taking personality into account will aid the use of studbooks, artificial insemination and carefully structured breeding programs in optimising genetic output from breeding (McDougall et al., 2006). Second, the unique selective pressure of captive environments that produce tamer, more docile individuals (McDougall et al., 2006; Smith & Blumstein, 2007; Powell & Gartner, 2011) can be limited to maintain behavioural variation (Martin-Wintle et al., 2017). This selective pressure, caused by novel environments and husbandry practices, also causes divergence from wild populations of the same species (McDougall et al., 2006). An example of this selection can be seen in the reduction of anti-predator behaviour in captive oldfield mice (*Peromyscus polionotus*) (McPhee, 2004). Behavioural variation is an important

factor for the reintroduction of individuals to the wild (Smith & Blumstein, 2007). This is because animals that are going to be reintroduced require suitable anti-predator, foraging and social behaviour (McDougall et al., 2006; Martin-Wintle et al., 2017) and the loss of these behaviour variations may explain the high failure rate of previous reintroductions (Powell & Gartner, 2011). Finally, an understanding of the personality traits with the highest reproductive output will aid conservation of critically endangered species where maximum reproductive output is required (Frankham et al., 1986; McDougall et al., 2006). These advantages, therefore, have positive outcomes for conservation and reintroduction programs through the increased behavioural and genetic variation produced by greater mating success across a wider range of personalities within the population. Additionally, this understanding is of increased importance in conservation target species (Powell & Gartner, 2011).

## **6. Conclusion**

In summary, personality is present in the population of Gentoo penguins at The Deep shown by consistency and repeatability in response to staff and visitors. These consistent individual differences have consequences on feeding preference and choice of site but not mating success. The results highlight the value of including personality in husbandry practices, particularly with respect to creating feeding regimes and designing enclosures. This will assist husbandry staff in meeting the nutritional and spatial needs and provide enhanced enclosures that improve animal husbandry and welfare. Effective enclosure design can have a positive effects on individual mating success, with follow on advantages to conservation and reintroduction (Powell & Gartner, 2011). This study demonstrates that an understanding of personality can be used as a tool to increase animal welfare in captive populations through improved husbandry practice. Limited study has previously been carried out on the effects of



personality on reproduction and enclosure requirements so this study begins to address gaps in this research area (McDougall et al., 2006). The novel item aspect of the study could be improved as this was an unsuccessful aspect of the study, perhaps through better choice of items or when they are introduced. This would not only strengthen the identification of personality in the population but also provide knowledge of effective enrichment techniques. To further this research, a greater population size is required by including more collections (zoos/aquaria) to determine the presence and effects of personality in different Gentoo populations living in different captive environments. This is important as all enclosures are different, therefore understanding more collections will aid further the understanding of the effect of personality in different surroundings. The fact that animal personalities are also common throughout the animal kingdom means there is the potential for this research to be applied across species and animal groups living in a variety of conditions.

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