JZAR JOURNAL OF ZOO AND AQUARIUM RESEARCH
www.jzar.org

Research article

The effect of the zoo setting on the behavioural diversity of captive gentoo penguins and the implications for their educational potential

Courtney Collins[1,2], Thomas Quirke[3], Louise Overy[2], Kevin Flannery[2] and Ruth O'Riordan[1]

[1]School of Biological, Earth and Environmental Sciences, Distillery Fields, North Mall, University College Cork, Ireland
[2]Dingle Aquarium, Dingle, County Kerry, Ireland
[3]Reaseheath College, Nantwich Chesire, UK.
Correspondence: Courtney Collins; courtney.collins1@umail.ucc.ie

Keywords:
behaviour, education, enrichment, *Pygoscelis papua*, visitors, welfare

Article history:
Received: 30 July 2015
Accepted: 4 February 2016
Published online: 30 April 2016

Abstract
Investigations into the effect of the captive environment on zoo and aquarium-housed animals is now a well-established area of research, yet little attention is given to the effect of these animals on zoo visitors. It has been suggested that some animals have a greater ability to attract and thus educate visitors, but there is a dearth of information in this area. Furthermore, before a captive species' educational potential can be determined, its response to the zoo environment should be investigated to ensure its welfare. The current study first considered the effect of visitor presence and environmental enrichment on the behavioural diversity levels of aquarium-housed gentoo penguins (*Pygoscelis papua*), with particular attention given to pool-use and nesting behaviour. Then, based on the animals' response to the visitors and enrichment, we consider the educational potential of the penguin group. Data were obtained through scan samples taken throughout the breeding season. Results indicate that visitor number affects behavioural diversity levels, with higher numbers of visitors associated with greater behavioural diversity and pool use by penguins. However, neither visitor behaviour nor enrichment appeared to affect behavioural diversity. Nesting behaviour was not affected by any of the variables that were tested. Based on these results we conclude that the penguins at this aquarium have a high educational potential. The results of this study suggest that future research should consider the use of interactive enrichment and how captive penguins may further enhance visitor learning.

Introduction

The effect of the zoo environment on captive animals has generated considerable literature in recent years, with visitor presence and environmental enrichment recognised as two factors that affect a species' wellbeing in the zoo (Hosey 2008; Swaisgood and Shepherdson 2005). However, little attention has been given to the educational value of animals held in zoos, even though education is often one of the justifications for keeping animals in captivity (Moss and Esson 2010; Jensen 2014). Moss and Esson (2010) propose that zoos should consider which animals to display based on their educational value, and that those species that visitors are most interested in and spend the most time watching may offer the best learning potential. However, it is also essential to consider those animals' response to the zoo environment, including visitors, as it would be contrary to positive welfare to display animals that attract large crowds if these animals show an adverse response to visitors. The IUCN Red List categorises gentoo penguins as near threatened in the wild because of an overall decline in their population, which may be partially attributable to tourist disturbance during breeding (BirdLife 2012). Gentoo penguins are already a commonly held species by zoos and aquariums, which may become significant for the survival of this species.

Little is known about the relationship between captive penguins and zoo visitors. Ozella et al. (2014) report that captive African penguins in close proximity to human bathers used their pool less early in the season, especially when large numbers of bathers were present. However, they eventually habituated to the humans, and pool use was no longer affected. Hosey (2008) summarised a series of unpublished reports that investigated the effect of visitors on captive penguin behaviour and concluded that there were no consistent trends in the research. Limited research on other birds in captivity has found that cockatoos may either find visitors stimulating, or show no behavioural response to visitors (Nimon and Dalziel 1992; Collins and Marples 2015).

In wild populations of penguins, there is evidence that the birds are disturbed by the presence of humans (for reviews see Carney and Sydeman 1999; Seddon and Ellenberg 2008; Steven

Table 1. Ethogram for gentoo penguin behaviour at Dingle Aquarium.

Behaviour	Definition
Pool behaviours	
Surface swimming	Swimming on the surface of the water
Underwater swimming	Entirely submerged and swimming under water
Preening in the Pool	Preening (see definition below) in the water
Porpoising	Jumping in an out of the water in typical penguin style
Out of pool behaviours	
Inactive	Individual is not in the pool and is sitting, sleeping, standing; the absence of any other behaviour
Preening	Feather maintenance, scratching, shaking
Locomotion	Movement on land; walking, hopping, running
Affiliative	Positive social behaviour with another penguin; allo-preening, bowing
Agonistic	Negative social behaviour with another penguin; staring, beaking, attacking
Attention to enrichment	Playing with, chasing or manipulating an enrichment device
Attention to visitors	Attempting to engage in some type of interaction with a visitor, such as tapping glass with beak, following in water, actively staring at a visitor through the glass wall
Nest behaviour	Engaged in any type of behaviour involving the nest, such as moving stones or sitting on the nest
Other	An unusual occurrence, any behaviour not listed above

et al. 2011), though there are conflicting results between studies. Culik and Wilson (1991) discovered that visits by tourists at Admiralty Bay were associated with a heart rate increase of 50% in Adélie penguins (*Pygoscelis adeliae*) during the breeding season, causing the authors to conclude that tourism negatively affects breeding colonies of penguins. Additionally, Wilson et al. (1991) suggested that human presence, in conjunction with aeroplane disturbance, is compromising the population growth of Adélie penguins, with some penguins abandoning nests or chicks when humans approach. In contrast, Cobley and Shears (1999) reported that visits by tourists to gentoo penguins at Port Lockroy, Goudier Island, Antarctica, were unlikely to interfere with breeding success or population growth. Similarly, Yorio and Dee Boersma (1992) found that Magellanic penguins (*Spheniscus magellanicus*) did not abandon their nests when humans approached.

Nimon et al. (1995) used an artificial egg to measure nesting penguin heart rate, thus limiting human handling. They reported that there was no difference in the heart rate of gentoo penguins in the absence or presence of one person from a distance of three metres (Nimon et al. 1995), but that a sudden movement from the same distance resulted in brief heart rate increases of 50%, leading the authors to conclude that penguins may be affected by the type of behaviour people engage in when observing penguins and not just their presence (Nimon et al. 1996). In addition, Nimon et al. (1995) concluded that the technique used by Culik and Wilson (1991) to tag penguins caused a learned response to fear humans, and thus penguins reacted with fear (i.e. increased heart rate) when humans were present. Culik and Wilson (1995) countered that inconsistent methodology, inter- and intra-specific differences and different stages of breeding were responsible for the contradictory results of these studies.

More recent studies suggest that tourists may disturb penguins in regard to breeding success, fledging weight, foraging access and energy expenditure in a variety of species (e.g. Burger and Gochfield 2007; Ellenburg et al. 2007; McClung et al. 2004); however, species type, age, health and breeding status, as well as previous history and exposure to tourists, are likely to be important components in penguins' responses (Seddon and Ellenberg 2008; Villanueva et al. 2012). These responses and limitations reflect those of animal–visitor studies in captivity, with the variables of the zoo setting, species type and previous experience with visitors often cited as contributing factors in visitor effect studies (Stoinski et al. 2012; Hosey 2008, 2013). Regardless, there is sufficient evidence that penguins in the wild are disturbed by tourists to warrant further investigation of the effect of zoo visitors on their captive counterparts.

Environmental enrichment is a practice used by zoos to improve the welfare of captive animals by providing environmental stimuli, with one of the major goals being to promote species-typical behaviour in captivity (Mellen and MacPhee 2001). It has even been suggested that visitors and staff can act as an enriching stimuli for animals in captivity (Morris 1964; Hosey 2000; Claxton 2011), though Hosey (2008, p.110) cautioned that visitor presence 'mostly supported the stressful hypothesis, with some support for the hypothesis that audiences could under some circumstances be enriching'. Carlstead and Shepherdson (2000) reported that enrichment may be useful in alleviating stress in captive animals, and some studies have used enrichment specifically to alleviate visitor induced stress. The majority of the latter studies focus on primates and results are variable, but tend to indicate that the provision of enrichment during periods of high visitor density was associated with a reduction of behaviours often correlated with visitor-induced stress (Birke 2002; Carder and Semple 2008; Clarke et al. 2012). Limited previous research on enrichment for captive penguins has produced contradictory results. Clarke (2003) found that enrichment devices did not have an effect on penguin pool use, while Larsson (2012) report that increased pool use in penguins was likely associated with the introduction of enrichment.

Yet increased animal activity is often a consequence of enrichment (Margulis et al. 2003), and previous studies confirm that zoo visitors show more interest in and learn more from active animals (Bitgood et al. 1988; Margulis et al. 2003). If there are no welfare implications, having animals engage with enrichment when visitors are present may increase the educational potential of that animal (Moss and Esson 2010). However, before employing this husbandry approach, the animals' reaction to visitors and enrichment should be evaluated. The objective of this research was to examine the behavioural diversity of a group of captive

Table 2. Sample sizes for categorical independent variables.

Independent variable	Category	Number of samples
Visitor behaviour	Compliant	58
	Non-compliant	9
Presence of enrichment	No	54
	Yes	42

gentoo penguins (*Pygoscelis papua*) during different visitor and enrichment conditions, and then to consider the educational potential of this group of penguins based on those results.

Methods

Study site, animals and enclosure

Data were collected on captive gentoo penguins in Dingle Aquarium, County Kerry, Ireland between March and August 2014. Dingle Aquarium has 12 gentoo penguins, eight females and four males, all born in captivity. During the study period, all penguins participated in nesting and breeding activity, resulting in the production of 13 eggs and one live chick (the first to be hatched at the aquarium). The penguin enclosure is a purpose-built indoor facility operational since 2011. It consists of a 120,000 litre pool with a land surface area of 35 m^2 and a water surface area of 30 m^2. There is a glass wall, interspersed with artificial rock structures, of approximately 15.6 m separating the penguins from the viewing public. The temperature of the enclosure is kept between 6 and 11° C, with a snow machine producing half a ton of snow and ice throughout the day. The penguins have no access to an outside area, and there is no 'off exhibit' area. The penguins are hand-fed at 1000 and 1400 daily. Penguins receive enrichment several times per week. During the study, enrichment varied from feeding devices in the water to mobiles (CDs hung from the ceiling) in the enclosure. These items have previously been determined to be successful at engaging penguins because of their natural interest in foraging and shiny objects that mimic fish scales (G. Meechan pers. comm.).

Data collection

In zoo-based studies increased behavioural diversity is generally considered a positive result of a treatment or condition, and we therefore used it as an overall indicator of welfare (Carlstead and Shepherdson 2000; Clark and Melfi 2012). However, particular attention was given to nesting behaviour and pool use, because it is essential to consider all possible effects of the zoo environment on breeding success and pool use is considered a positive behaviour for this pelagic bird (Larsson 2012).

To quantify the behavioural response of the penguins to their environment, instantaneous scan samples of the 12 penguins were taken throughout the study period (Altmann 1974). Observations were made several times a week during the study. Each scan took about three minutes to complete. The number of visitors was first noted, and then the behaviour of each penguin was recorded (see Table 1 for penguin ethogram), as well as the presence or absence of enrichment. Visitor behaviour was recorded during each scan and was categorised as: 0 = all visitors compliant with aquarium rules; or 1 = at least one visitor not compliant with aquarium rules and engaging in behaviour such as banging the glass, flash photography, or climbing structures overlooking the enclosure (see Table 2). Noise level was not a concern in this study, as it is in many visitor effect studies (Cooke and Schillaci 2007; Quadros et al. 2014), because the glass between the enclosure and the viewing area was soundproof.

All data were collected between1100 and 1600, which excluded the first hour after opening and the last hour before closing. Additionally, data were not collected half an hour before and after the 1400 feeding time. Aquarium staff participated in data collection, having been trained by the principal investigator. Observations were initiated based on staff availability and not by the current visitor or enrichment condition, resulting in a random, independent sample of 96 observations with and without enrichment and with visitors compliant or non-compliant with aquarium rules (see Table 2). Visitor number averaged 8.19 (SE = 1.01). Staff were never present within the enclosure when recordings occurred.

Data analysis

For each observation (n = 96, see Table 2), behavioural diversity for the penguin group was calculated using the Shannon-Weiner diversity index H (Shannon and Weaver 1949). The formula for the Shannon-Weiner index is:

$$H = - \sum (p_i \ln p_i)$$

where p_i is the proportion of time engaged in the *i*th behaviour. A higher value of H represents greater behavioural diversity, resulting from either a greater number of behaviours and/or a more even performance of different behaviours. Behavioural diversity can increase based on the number of different behaviours performed or the number of animals performing each behaviour, therefore the minimum and maximum values will vary for each study. Here behavioural diversity ranged from 0.28 to 1.74 (Table 3).

A histogram of the data and a quantile-quantile plot revealed that the data were approximately normally distributed. First a

Table 3. A random cross sample of observations to illustrate how frequency of behaviour, and the number of penguins performing the behaviours, relates to behavioural diversity, with varying levels of behavioural diversity (H) indicated in the last column.

	Behaviours (number of times observed for different observations); 12 penguins													Behaviour diversity
Observation	Surface	Under	H_2O preen	Jump	Inactive	Preen	Loco	Affil	Agon	Vis Attn	Enrich	Nest	Other	calculation (H)
1	0	0	0	0	11	0	1	0	0	0	0	0	0	0.286836
2	0	1	0	0	0	0	0	0	0	1	0	10	0	0.566086
3	0	0	0	0	4	0	0	0	4	0	0	4	0	1.098612
4	2	2	0	0	2	0	0	1	2	0	0	3	0	1.748155

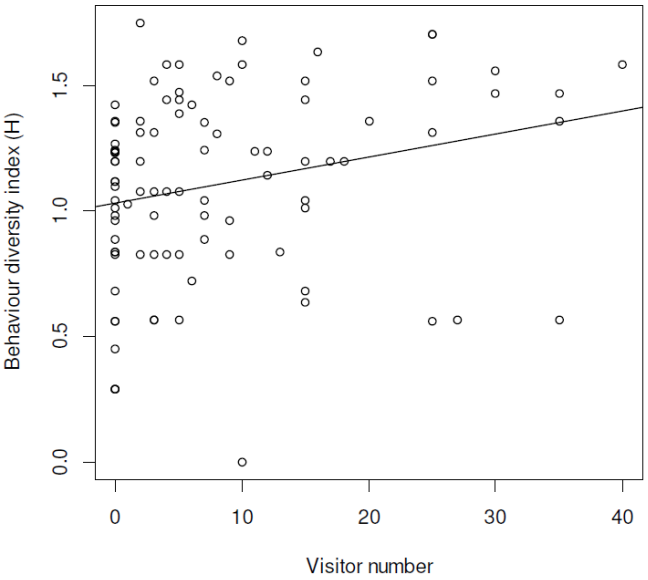

Figure 1. Behavioural diversity index (H) versus visitor number with regression line showing a positive relationship.

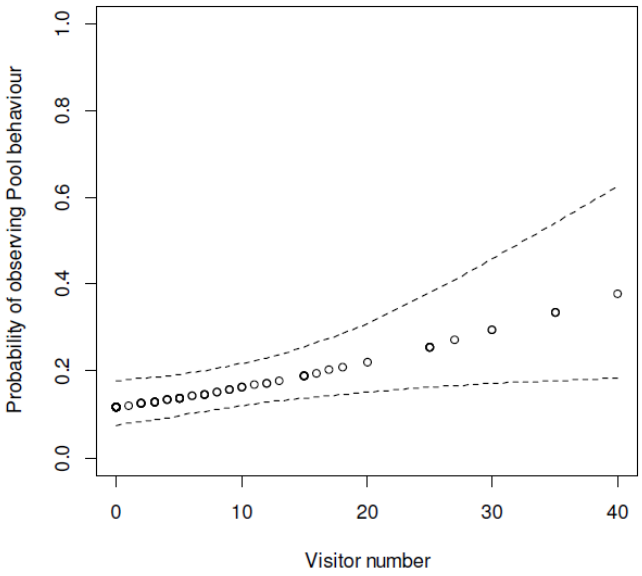

Figure 2. Fitted values and 95% confidence bands for the optimal GLM model for pool behaviour for the group of penguins at Dingle Aquarium.

general linear model (GLM) was conducted to test the significance of the three explanatory variables – visitor number (covariate), visitor behaviour and enrichment – on behavioural diversity, with enrichment and visitor number added as an interaction term. A backwards stepwise procedure was used to remove variables with the largest p-values from the model. Validation was conducted for each model by plotting a histogram of residuals, plotting the residuals against the fitted values and checking linearity of the models. Data analysis was conducted using SPSS version 22. The accepted alpha level for these analyses was $p<0.05$.

Second, for the behaviour categories of pool behaviour and nesting behaviour, the proportion of penguins performing each of these behaviours for each observation was used in further analysis. A generalised linear model (GLM) with a binomial distribution was conducted for each behaviour category to test the significance of the explanatory variables in addition to interactions between them. As over-dispersion was detected in the model, the standard errors were corrected using a quasi-GLM model. A backwards stepwise procedure was used to remove variables with the largest p-values from the model and model validation was conducted by plotting the deviance residuals against the fitted values and against each explanatory variable in the model. Data analysis for this section was conducted using R version 3.2. The alpha level for statistical significance was taken to be <0.05.

Results

Behavioural diversity

Graphs of standardised residuals revealed that assumptions of normality were maintained throughout the analysis. For behavioural diversity, model selection resulted in the final model with visitor number as the only remaining explanatory variable. In this case, the variable visitor number was statistically significant ($F = 5.769$; $p = 0.018$) with higher levels of behavioural diversity associated with higher visitor numbers (Figure 1).

Table 4. Remaining explanatory variable after backwards selection, estimate, standard error, p value residual deviance and degrees of freedom information for binomial GLM models.

Behaviour	Variable remaining in model	Estimate	Standard error	P value	Residual deviance, df
Nest	Visitor number	-0.01514	0.00952	0.1155	257.76, 94
Pool	Visitor number	0.03843	0.01625	0.0201*	403.32, 94

Pool and nest behaviour

For nest behaviour, model selection resulted in a final model with visitor number as the only remaining explanatory variable. This explanatory variable was not statistically significant, thus none of the explanatory variables or combinations of their interactions significantly influenced penguin nest behaviour during this study (Table 4). For pool behaviour, model selection also resulted in a final model with visitor number as the only remaining explanatory variable. In this case, the variable visitor number was statistically significant ($p<0.05$) with higher levels of pool behaviour being associated with higher visitor numbers (Table 4; Figure 2).

Discussion

In contrast to wild populations of penguins, the gentoo penguin group at Dingle Aquarium showed a behavioural response to the presence of visitors, indicated by a positive association between visitor number and behavioural diversity. Pool use was associated with higher numbers of visitors. This may indicate that penguins are not negatively affected by visitors, but they may respond positively to visitors by becoming more active, thus supporting the hypothesis that in some circumstances visitors may be stimulating to captive animals (Morris 1964; Hosey 2000). In the current study, pool use is considered a positive outcome since penguins are pelagic birds that naturally spend large amounts of time foraging at sea, and this contributes to the overall level of behavioural diversity (Larsson 2012). Condon et al. (2003) also reported that Humboldt penguins swam and specifically dived more when visitors interacted with penguins through an underwater viewing window. Of course, in visitor–animal interaction studies directionality must be considered (Hosey 2008; Margulis et al. 2003), since it is known that visitors are attracted to active animals (Bitgood el al. 1988; Margulis, et al. 2003). The current study supports that hypothesis; when penguins were swimming in the pool, a larger group of visitors was present. However, without further investigation, it is difficult to disentangle directionality in this situation, and this could be an area for further research.

There was no indication that the penguins changed their nesting behaviour during any of the conditions of the study. This is in contrast to the report by Wilson et al. (1991) that wild Adélie penguins may abandon their nests when tourists approach. It is likely that the captive-born penguins in this study have habituated to the zoo environment so that their nesting behaviour is not affected, in a similar way to the descriptions by Yorio and Dee Boersma (1992), Walker et al. (2006) and Villanueva et al. (2014) of behaviour in wild populations of Magellanic penguins exposed to tourists during the breeding season. However, it should be noted that at the time of the study the penguins at Dingle Aquarium had only produced one live chick. The reason for this is unknown (staff at the aquarium suggest it may be due to the penguins' relatively recent arrival at the aquarium and the necessary adjustment time to the change in photoperiod; L. Overy, pers. comm.), but given the results of this study, visitor disturbance seems an unlikely cause. However, until further investigation is carried out, all possibilities should be considered. Blay and Côté (2001) recommend that penguin population and pool size, as well as enclosure substrate and nesting material, should be considered when assessing breeding success. Additionally, future work should consider if behavioural diversity varies outside the breeding season, as nesting and breeding may affect behavioural responses.

There was a low rate of visitor non-compliance with aquarium rules; therefore, the sample size when visitors were behaving inappropriately was low. Regardless, no difference in behavioural diversity was detected when visitors did or did not comply with the aquarium rules. However, it may be premature to state that penguins are not affected by banging, climbing and flash photography. An important consideration in interpreting our results is that the glass separating the visitors and penguins at Dingle Aquarium is virtually soundproof. Some previous studies have shown that it is noise, in particular, that may disturb captive animals (Birke 2002; Cooke and Schillaci 2007; Quadros et al. 2014). In addition, Nimon et al. (1996) found that wild penguins may be adversely affected by specific negative behaviours of visiting humans and not just their presence; they further report that 'the presence of a well-behaved visitor' may barely affect nesting penguins (Nimon et al. 1995, p. 415). Furthermore, Carney and Sydeman (1999) suggest that wild penguins show little behavioural response to humans, but may react with a physiological response such as increased heart rate, which may be too subtle to be detected by changes in their behaviour. However, Ozella et al. (2015) did investigate adrenocortical activity in captive African penguins (*Spheniscus demersus*) by measuring faecal glucocorticoid metabolites (FGM) and found no association between visitor number and adrenocortical activity. Physiological monitoring of captive penguins was out of the scope of the current study, but simultaneous monitoring of behavioural and physiological responses could be an area for further investigation. It is essential to consider that if penguins were continuously exposed to higher degrees of negative visitor behaviour and noise the results may be significantly different, as previous studies have shown that captive birds may have a threshold of tolerance for visitors (Nimon and Dalziel 1992; Collins and Marples 2015).

Similar to the findings of Clarke (2003), the penguins in this study showed no change in behavioural diversity levels when enrichment was absent or present. This may have been due to the type of enrichment used. Distinguishing between pool-based and non-pool-based enrichment devices may have clarified the penguins' preferred type of enrichment. It would be ideal to use a specific type of enrichment consistently; however, this was not possible in the present study due to husbandry routines. Future work could focus on the penguins' response to different types of enrichment, in a randomised design, to isolate any effects of different enrichment devices (Quirke and O'Riordan 2011).

Finally, we considered the educational potential of the gentoo penguins at Dingle Aquarium. The penguins are amongst the visitors' favourite animals at Dingle Aquarium (M. O'Shea, personal communication, November 6 2014), and recently, penguins in general have received much attention in the media, which may also contribute to visitor interest (Wagoner and Jensen 2010). Although, Moss and Esson (2010) found that birds were amongst the least exciting animals to zoo visitors, they suggest that in the absence of mammals, as at Dingle Aquarium, bird species may become more interesting to visitors. The results of this study appear to support previous research that visitors are attracted to more active animals (Bitgood et al. 1988; Moss and Esson 2010). However, we do not know if the visitors actually learned more by observing the birds when they were active, which could be an area of further research. It does, though, appear that visitors are attracted to the swimming penguins and that the penguins do not show an adverse behavioural reaction to the visitors, indicating that their educational potential is high.

Zoos must balance their goals of conservation, education, entertainment and welfare, yet these goals can appear contradictory. By attracting large crowds of visitors, who offer financial support for conservation and participate in education programmes, there is also the possibility of diminished animal welfare (Fernandez et al. 2009; Hosey 2013). However, here we offer evidence that large numbers of visitors at the penguin enclosure do not appear to interfere with the animals' welfare and may be enriching. This finding supports the idea that zoos may be able to use husbandry routines to their advantage, to encourage animals to be more active (taking careful consideration of animal welfare) when visitors are present, perhaps through the use of enrichment, which would benefit both captive animals and visitors alike (Margulis et al. 2003; Moss and Esson 2010). Although, in the current study, penguin behavioural diversity level did not change when enrichment was present, perhaps a different type of enrichment, or an interactive device that visitors could use, may benefit both visitors' learning and penguins' welfare. This should be investigated further. We suggest that penguins (especially at aquariums) may prove to be the ideal 'educational' animal. Though the current study investigated gentoo penguins, it is possible that other species would present different behaviour towards visitors, as seen in different species of wild penguins, and thus comparative research is being carried out on Humboldt penguins at Fota Wildlife Park, Ireland. This research is part of a project investigating animal–visitor interactions, education and enrichment in the zoo setting.

Conclusions

As visitor numbers increased, gentoo penguin behavioural diversity increased. Pool use was affected by visitors, but nesting behaviour was not. As visitor numbers increased, the number of penguins using the pool increased. It is not possible at this point to determine the directionality of this association. Behavioural diversity was not affected by enrichment or by visitors not complying with aquarium rules, but the sample size is small and further research would be beneficial. Penguins at Dingle aquarium have high educational potential.

Acknowledgements

The authors would like to acknowledge the staff of Dingle Aquarium for giving their time and support to this research. We would also like to thank the Irish Federation of University Teachers and The School of Biological, Earth and Environmental Sciences at UCC for financial assistance and support of the project.

References

Altmann J. (1974) Observational study of behavior: sampling methods.

Behaviour 49: 227–266.
BirdLife International (2012) *Pygoscelis papua*. The IUCN Red List of Threatened Species 2012: e.T22697755A40173793 (accessed 1 November 2014).
Birke L. (2002) Effects of browse, human visitors and noise on the behaviour of captive orang-utans. *Animal Welfare* 11: 189–202.
Bitgood S., Paterson D., Benefield A. (1988) Exhibit design and visitor behaviour: empirical relationships. *Environmental Behavior* 20: 474–491.
Blay N., Côté I.M. (2001) Optimal conditions for breeding of captive Humboldt penguins (*Spheniscus humboldti*): a survey of British zoos. *Zoo Biology* 20: 545–555.
Burger J., Gochfeld M. (2007) Responses of emperor penguins (*Aptenodytes forsteri*) to encounters with ecotourists while commuting to and from their breeding colony. *Polar Biology* 30: 1303–1313.
Carder G., Semple S. (2008) Visitor effects on anxiety in two captive groups of western lowland gorillas. *Applied Animal Behaviour Science* 115: 211–220.
Carlstead K., Shepherdson D. (2000) Alleviating stress in zoo animals with environmental enrichment. In: Moberg G.P., Mench J.A. (eds). *The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare*. Wallingord: CABI, 337–354.
Carney K.M., Sydeman W.J. (1999) A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22: 68–79.
Clarke A.G. (2003) Factors affecting pool use by captive Humboldt penguins (*Spheniscus humboldti*). In: *Proceedings of the 5th Annual Symposium on Zoo Research, Marwell Zoological Park, Winchester, UK, 7–8th July 2003.* London: Federation of Zoological Gardens of Great Britain and Ireland, 190–204.
Clark F.E., Fitzpatrick M., Hartley A., King A.J., Lee T., Routh A., George K. (2012) Relationship between behavior, adrenal activity, and environment in zoo-housed western lowland gorillas (*Gorilla gorilla*). *Zoo Biology* 31: 306–321.
Clark F.E., Melfi V.A. (2012) Environmental enrichment for a mixed-species nocturnal mammal exhibit. *Zoo Biology* 31: 397–413.
Claxton A.M. (2011) The potential of the human–animal relationship as an environmental enrichment for the welfare of zoo-housed animals. *Applied Animal Behaviour Science* 133: 1–10.
Cobley N.D., Shears J.R. (1999) Breeding performance of gentoo penguins (*Pygoscelis papua*) at a colony exposed to high levels of human disturbance. *Polar Biology* 21: 355–360.
Collins C.K., Marples N.M. (2015) Zoo playgrounds: a source of enrichment or stress for a group of nearby cockatoos? A case study. *Journal of Applied Animal Welfare Science* 18: 375–387.
Condon E., Wehnelt S., Turner Z. (2003) The effect of visitors on the behavior of Humboldt's penguins at Chester Zoo. *Federation Research Newsletter* 4(2): 3.
Cooke C.M.. Schillaci M.A. (2007) Behavioural responses to the zoo environment by white-handed gibbons. *Applied Animal Behaviour Science* 106: 125–133.
Culik B., Wilson R. (1991) Penguins crowded out? *Nature* 351: 340–340.
Culik B., Wilson R. (1995) Penguins disturbed by tourists. *Nature* 376: 301–302.
Ellenberg U., Setiawan A.N., Cree A., Houston D.M., Seddon P.J. (2007) Elevated hormonal stress response and reduced reproductive output in yellow-eyed penguins exposed to unregulated tourism. *General and Comparative Endocrinology* 152: 54–63.
Fernandez E.J., Tamborski M.A., Pickens S.R., Timberlake W. (2009) Animal–visitor interactions in the modern zoo: conflicts and interventions. *Applied Animal Behaviour Science* 120: 1–8.
Hosey G. (2000) Zoo animals and their human audiences: what is the visitor effect? *Animal Welfare* 9: 343–357.
Hosey G. (2008) A preliminary model of human–animal relationships in the zoo. *Applied Animal Behaviour Science* 109: 105–127.
Hosey G. (2013). Hediger revisited: how do zoo animals see us? *Journal of Applied Animal Welfare Science* 16: 338–359.
Jensen E. (2014). Evaluating children's conservation biology learning at the zoo. *Conservation Biology* 28: 1004–1011.
Larsson A. (2012) *Development and Evaluation of Environmental Enrichment for Captive Humboldt Penguins.* Student Report 443.Uppsala: Swedish University of Agricultural Sciences.
Margulis S.W., Hoyos C., Anderson M. (2003) Effect of felid activity on zoo visitor interest. *Zoo Biology* 22: 587–599.
McClung M.R., Seddon P.J., Massaro M., Setiawan A.N. (2004). Nature-based tourism impacts on yellow-eyed penguins *Megadyptes antipodes*: does unregulated visitor access affect fledging weight and juvenile survival? *Biological Conservation* 119: 279–285.
Mellen J., MacPhee M.S. (2001) Philosophy of environmental enrichment: past, present, and future. *Zoo Biology* 20: 211–226.
Morris D. (1964) The response of animals to a restricted environment. *Symposia of the Zoological Society of London* 13: 99–118.
Moss A., Esson M. (2010) Visitor interest in zoo animals and the implications for collection planning and zoo education programmes. *Zoo Biology* 29: 715–731.
Nimon A.J., Dalziel F.R. (1992) Cross-species interaction and communication: a study method applied to captive siamang (*Hylobates syndactylus*) and long-billed corella (*Cacatua tenuirostris*) contacts with humans. *Applied Animal Behaviour Science* 33: 261–272.
Nimon A.J., Schroter R.C., Stonehouse B. (1995) Heart rate of disturbed penguins. *Nature* 374: 415.
Nimon A.J., Schroter R.C., Oxenham R.K. (1996). Artificial eggs: measuring heart rate and effects of disturbance in nesting penguins. *Physiology and Behavior* 60: 1019–1022.
Ozella L., Favaro L., Carnovale I., Pessani D. (2015). Pond use by captive African penguins (*Spheniscus demersus*) in an immersive exhibit adjacent to human bathers. *Journal of Applied Animal Welfare Science* 18: 303–309.
Ozella L., Anfossi L., Di Nardo F., Pessani D. (2015). Effect of weather conditions and presence of visitors on adrenocortical activity in captive African penguins (*Spheniscus demersus*). *General and Comparative Endocrinology* (in press).
Quadros S., Goulart V.D., Passos L., Vecci M.A., Young R.J. (2014). Zoo visitor effect on mammal behaviour: Does noise matter? *Applied Animal Behaviour Science* 156: 78–84.
Quirke T., O'Riordan R.M. (2011). The effect of a randomised enrichment treatment schedule on the behaviour of cheetahs (*Acinonyx jubatus*). *Applied Animal Behaviour Science* 135: 103–109.
Seddon P.J., Ellenberg U. (2008). Effects of human disturbance on penguins: the need for site and species specific visitor management guidelines. In: Higham J., Luck M. (eds). *Marine Wildlife and Tourism Management: Insights from the Natural and Social Sciences*. Wallingford: CAB International, 163–181.
Shannon C.E., Weaver W. (1949) *The Mathematical Theory of Information.* Urbana: University of Illinois Press.
Shepherdson D.J., Mellen J.D., Hutchins M. (1998) *Second Nature: Environmental Enrichment for Captive Animals*. Washington DC: Smithsonian Institution Press.
Steven R., Pickering C., Castley J.G. (2011) A review of the impacts of nature based recreation on birds. *Journal of Environmental Management* 92: 2287–2294.
Stoinski T.S., Jaicks H.F., Drayton L.A. (2012) Visitor effects on the behavior of captive western lowland gorillas: the importance of individual differences in examining welfare. *Zoo Biology* 31: 586–599.
Swaisgood R.R., Shepherdson D.J. (2005) Scientific approaches to enrichment and stereotypies in zoo animals: what's been done and where should we go next? *Zoo Biology* 24: 499–518.
Villanueva C., Walker B.G., Bertellotti M. (2012) A matter of history: effects of tourism on physiology, behaviour and breeding parameters in Magellanic penguins (*Spheniscus magellanicus*) at two colonies in Argentina. *Journal of Ornithology* 153: 219–228.
Villanueva C., Walker B.G., Bertellotti M. (2014) Seasonal variation in the physiological and behavioral responses to tourist visitation in Magellanic penguins. *The Journal of Wildlife Management* 78: 1466–1476.
Wagoner B., Jensen E. (2010) Science learning at the zoo: evaluating children's developing understanding of animals and their habitats. *Psychology and Society* 3: 65–76.
Walker B.G., Dee Boersma P., Wingfield J.C. (2006) Habituation of adult Magellanic penguins to human visitation as expressed through behavior and corticosterone secretion. *Conservation Biology* 20: 146–154.
Wilson R.P., Culik B., Danfeld R., Adelung D. (1991) People in Antarctica – how much do Adélie penguins (*Pygoscelis adeliae)* care? *Polar Biology* 11: 363–370.
Yorio P., Dee Boersma P. (1992) The effects of human disturbance on Magellanic penguin (*Spheniscus magellanicus*) behaviour and breeding success. *Bird Conservation International* 2: 161–173.