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Research article

Relationships between boldness and husbandry in captive gentoo penguins *Pygoscelis papua*

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Abstract
Personality traits have been identified in many species and the benefits of understanding animal personality for conservation and welfare are becoming increasingly apparent. Due to these potential benefits, we aimed to determine if the boldness personality trait is present in a population of captive gentoo penguins *Pygoscelis papua* by conducting two boldness tests. One test used quantitative behavioural coding to observe penguin interactions with the public, while the other used qualitative observer ratings carried out by keepers. We then investigated the relationship between boldness and three important aspects of animal behaviour: daily food consumption, site choice and reproductive attempts. The boldness trait was found to be present in this population, shown by the high repeatability of responses to the two tests (public interactions: R=0.695, 95% CI: 0.398-0.831; observer ratings: R=0.814, 95% CI: 0.561-0.920) and the significant correlation between tests (P=0.004, r^2=0.720). There were also relationships between the boldness of individuals and their food consumption and site choice, with bolder penguins consuming more food from keepers and occupying nests with higher light levels. However, there was no relationship between boldness and reproduction, with penguins across the whole boldness continuum completing reproductive attempts. There was also significant evidence for temporal changes in behaviour over the course of the study (2015-2023). Overall, the findings support literature showing that understanding personality traits can be used to inform animal welfare practices in captive environments.

Introduction

It is increasingly apparent that understanding animal personality can contribute to animal conservation and welfare (Arden et al. 2023; MacKinlay and Shaw 2023). Personality has become one of the fastest growing areas of animal behavioural research (Aplin et al. 2014) following the discovery that personality traits are common across the animal kingdom (Stamps and Groothuis 2010; Wolf et al. 2007). Personality in animals is characterised by consistent between-individual differences in behaviour over time and across contexts (Sih et al. 2004), and is comprised of traits, such as boldness, which lie along continuums (e.g., bold to shy; Sih and Bell 2008). Boldness is the most frequently studied trait (Kaiser and Müller 2021) and is often associated with risk taking behaviour (Šlipogor et al. 2016; Tan and Tan 2019). Bolder individuals are risk prone while shyer individuals are risk averse (Kaiser and Müller 2021). To date, there has been limited study on personality traits in wild (Colombelli-Négrel and Katsis 2021; Silverlake et al. 2024; Traisnel and Pichegru 2018; 2019a; 2019b) or captive (Pastorino et al. 2019) penguins and no study has investigated the potential consequences of these traits on penguins in a captive environment. Importantly, most previous research on captive animals, including penguins, has focused on differences between species and populations, not individuals (Goswami et al. 2020; Groothuis and Carere 2005; Mathot et al. 2012; Prentice et al. 2022).

There are numerous factors in captive environments that can influence animal welfare (i.e., Five Domains Model; Mellor et al. 2020). For example, space constraints can result in an inability to avoid stressful situations or carry out natural behaviours (Sherwen et al. 2015). Additionally, visitors may either be a stressor, be neutral or a source of enrichment (Ozella et al. 2015). The potential presence of individual differences, may therefore make visitors stressful to some individuals (Hosey

2000) whilst providing novel stimulation to others (Collins et al. 2016). This has been observed in wild penguins, where individuals differ in their response to human disturbance (Ellenberg et al. 2009). Furthermore, animal keepers can be enriching or stressful to captive animals (Claxton 2011). The observation of variations in reaction towards both non-familiar (visitors) and familiar (keepers) humans may therefore give an insight into an animal's personality (Stoinski et al. 2012).

Understanding the personality structure of a population can be used to help promote welfare (Réale et al. 2007; Vazire et al. 2007). Individuals' differing responses to keepers (Collins et al. 2016) may result in differing feeding levels, especially during close proximity hand feeding. This has not been investigated in captive penguins and, as an important aspect of animal husbandry is meeting an animal's energy demands (Worthy 2001), it is important to understand how personality influences feeding behaviour. Additionally, an individual's enclosure use may be influenced by personality if their ability to occupy different areas is determined by their response to visitor proximity (Martin and Réale 2008). This has potential welfare implications such as limiting resource acquisition if feeding is consistently carried out at a certain location and, therefore, necessitates enclosures suiting all individuals (Sherwen et al. 2015). Finally, stress from unsuitable environments can be a barrier to reproduction (Mason 2010) and there is evidence that boldness can increase reproductive success (Smith and Blumstein 2008). Therefore, it will be important to provide suitable breeding conditions for all individuals within a population (McDougall et al. 2006). However, it may also be important to breed 'resilient' individuals with a certain personality trait, which may improve animal reintroductions or relocations (Collins et al 2023).

There are two main methods for assessing personality traits in animals: behavioural coding and observer ratings (Carter et al. 2013). Behavioural coding is quantitative and reduces human bias by focusing on well-defined behaviours (Petelle and Blumstein 2014). In comparison, observer ratings are low cost and time efficient, utilising the experience of the people who know the animals best (Carter et al. 2013). Consequently, this more subjective method is common in captive animal studies (Ebenau et al. 2020; Pastorino et al. 2019; Powell and Svoke 2008; Torgerson-White 2014). Simultaneous use of both methods is recommended (Highfill et al. 2010) and scores from the two methods regularly correlate when investigating the same trait (Gosling 2008; Koski 2011).

Gentoo penguins *Pygoscelis papua* are colonial seabirds with a circumpolar sub-Antarctic distribution (Martinez et al. 2020) and are commonly held in zoos and aquariums (Collins et al. 2016). The number of captive populations has grown in Europe in recent years, and this is largely due to the charismatic nature of penguins which attracts large crowds (Sherwen et al. 2015). Gentoos are socially monogamous and reach sexual maturity after two years (Martinez et al. 2020). They respond with curiosity to novel objects and can live for 15-25 years (Martinez et al. 2020), making them an ideal species for this study as their personality traits can be assessed over long periods.

There are two aims of this study. First, to identify whether the boldness personality trait is present in a captive population of gentoo penguins using two assessments of boldness: quantitative observation of interactions with the public and qualitative observer ratings by keepers. Second, to investigate relationships between boldness and behaviour: daily food consumption, site choice and reproductive attempts. An additional element to the second objective is to determine if there are temporal changes in the relationships between boldness and behaviour. We hypothesised that gentoo penguins would exhibit the boldness trait and that there would be relationships between boldness and behaviour. Therefore, we predicted that individuals would exhibit repeatable responses to boldness tests, and that bolder individuals would have higher daily food consumption, occupy sites more visible to visitors and have higher rates of reproductive attempts. Finally, we also predicted that the relationships between boldness and behaviour would diminish over time, as familiarity with the environment increased. Overall, this study builds on research in the field of animal personality and aims to improve the welfare of captive animals by linking understanding of individual differences to feeding techniques, enclosure design and reproductive strategies.

Methods

Study Animals and Enclosure

The Deep (Hull, UK) is home to a colony of gentoo penguins in a climate controlled enclosure with 70m² of land space, a 60,000-litre pool and four viewing windows (for further details see Supplementary Material). The population size increased over the course of the study: starting at 11 in 2015 (6 males and 5 females), increasing by two in 2016 (1 male and 1 female) and by one in 2019 (1 male). The original population arrived at The Deep in 2014/2015 and the additions all hatched at The Deep. Husbandry practices follow a consistent routine, with two daily feeds (11:30h and 15:30h). Feeding is carried out by hand and the diet is predominantly herring *Clupea harengus*, sprat *Sprattus sprattus* or capelin *Mallotus villosus*. All individuals were of known age (5 to 14 years in 2023) and each was identifiable by their coloured wing bands.

Assessment of the Boldness Trait.

Two methods were used to determine whether the boldness trait is present in this population: assessments of boldness towards visitors (i.e., behavioural coding) and keepers (i.e., observer ratings). Carrying out two different tests allowed cross context assessment of boldness.

Boldness towards visitors was determined by quantifying interactions with visitors at the main pool viewing window in a standardised manner to facilitate repeatability analysis (Sánchez-Tójar et al. 2022). Observations were carried out by the author (MJL) during the two daily feeds between 11:30-12:00h and 15:30-16:00h (see Figure S1 for observation location). The number of interactions with visitors longer than one second that each penguin carried out was noted (i.e., all occurrence sampling). An interaction was defined as a penguin moving to the window (within 50 cm of glass) on the water surface and holding position in front of a visitor(s). This behaviour is associated with boldness because bolder individuals are expected to demonstrate interest when faced with challenging (e.g., large number of visitors) or novel (e.g., visitors are constantly changing) situations while shyer individuals will show avoidance (Rose and Croft 2020). The number of visitors that were stationary within 2 m of the viewing window were counted at 5 min intervals during the observation period and summed to give a total over the observation period. 110 observations were carried out with an equal number of observations in both low (<100 people) and high (>100 people) visitor periods. The data were collected from November 2015 to March 2017. The two chicks that hatched in 2016 are included in the second half of the study. Individual months with greater than ten observation periods were used to generate a mean number of monthly interactions in 30 mins by each of the penguins for repeatability analysis.

The keepers who worked with the penguins regularly (3-5 days per week for at least one year) completed a questionnaire ranking the penguins sequentially from low to high boldness (ordinal scale) based on four questions considering behaviour over the preceding

Table 1. The four questions presented to keepers and the responses to consider when completing the observer rating and subsequent ranking of boldness.

Behavioural question	Response
What is the bird's general approachability?	Greater levels of approachability equate to higher boldness.
What is the bird's general aversiveness when approached?	Greater levels of aversiveness equate to lower boldness.
To what extent does the bird interact with you?	Greater levels of uninitiated interaction equate to higher boldness.
How easy is it to carry out routine work on (e.g., feeding) or around (e.g., cleaning) this bird?	Greater levels of ease equate to higher boldness.

year (Table 1). The questions were constructed by considering the definition of boldness (i.e., risk taking; Kaiser and Müller 2021) with a higher boldness ranking being associated with riskier behaviour (e.g., lower response to keeper approach) and a lower boldness ranking being associated with more cautious behaviour (e.g., avoidance of close contact with keepers). Measuring responses to approach by humans has previously been used as an assessment of boldness in wild seabird species (Grace and Anderson 2014; Patrick et al. 2013, 2017) including penguins (Traisnel and Pichegru 2018; 2019a; 2019b). The rankings were completed without discussion between the keepers to meet the fundamental requirement that the observer ratings are independent (Pastorino et al. 2019). Five keepers ranked the penguins in both 2015 and 2016 and of those five, three ranked the penguins in 2023. As the population size increased throughout the study, the ranking scale also increased (11 birds were ranked in 2015, 13 in 2016 and 14 in 2023). Over the study, observer rankings were averaged for each penguin in each year to generate a single rating for repeatability analysis.

Relationships Between Boldness and Behaviour

The daily amount of food consumed (g) by each bird during hand feeds was recorded for 2016 and 2022 (calculated using a mean weight of each food type, see Table S1 for details). The two chicks that hatched in 2016 were removed from the 2016 data set as feeding data were only present for the later part of the year and include changes in feeding rates during development to adult body size. The penguins were regularly weighed (kg) and the weights used in this study were all taken in early 2017 (all birds January 2nd) and late 2022/early 2023 (between 7 September and 7 February). Supplementary tray feeds were also carried out with a tray (65 cm x 53 cm, allowing multiple penguins to eat simultaneously) containing 50 sprat/capelin placed in the enclosure at 13:45h and left unattended for 30 min. The number of fish taken by each bird was then observed over the 30 min using footage taken with a GoPro Hero4/Hero8 camera (2016/2023). Four of these feeds were carried out at weekly intervals over one month in both late 2016 and late 2023.

GoPro Hero4 cameras set to 5 min time lapse were used to observe site choice in December 2016. The observations were carried out during daylight hours when no keepers were present (10:00-11:30h, 12:30-15:30h and 16:00-18:00h). The enclosure was split into 14 sites (Figure S1) and the location of each individual was noted every 5 min. This was completed over 5 days to generate a percentage use of each site and, therefore, the site predominantly used by each bird. The light intensity at each site was then determined using a light meter (lux). Light measurements were taken at 09:30h over the 5 days (10 cm above the ground), but were found to be identical due to artificial lighting. As the site predominantly used by each individual was found to be identical to that individual's nesting location in the preceding breeding season, the site choice of birds was determined in 2023 by noting the locations during the corresponding breeding period (summer 2022). Only birds that formed pairs plus built and maintained nests were incorporated in the data set (10/13 in 2016 and 12/14 in 2023).

Finally, the reproductive attempts of individuals were determined (2016-2023, no data for 2020). A reproductive attempt being defined as an attempt to breed by building and maintaining a nest in each year. Management considerations (e.g., enclosure size) in some years prevented completion of the reproductive cycle by replacing eggs with dummy eggs after laying. The birds that attempted to reproduce were noted and individual reproductive attempts calculated as a percentage across all years.

Statistical Analysis

All data analysis was carried out in R version 4.3.0 (R Core Team 2023). As it is important to investigate the inter-rater reliability of observer ratings (Petelle and Blumstein 2014), the consistency of penguin boldness ratings between each keeper in each year was determined using Kendall's coefficient of concordance (Kendall's W) using the package irr (Gamer et al. 2019). This metric assesses agreement among observers (Legendre 2005) and values range between 0 (no agreement) and 1 (complete agreement), with > 0.6 considered high agreement (Gearhart et al. 2013).

A generalized linear mixed model (GLMM) was used to calculate adjusted repeatability and therefore determine the temporal consistency of interactions with visitors (monthly mean) and observer ratings (yearly mean). This was achieved with the rpt function in the rptR package (Stoffel et al. 2017). Repeatability shows how much variation in the data is due to within-individual variation (Bell et al. 2009) by dividing the variance across individuals by the addition of the residual within-individual variance and the variance across individuals (Biro and Stamps 2015). Adjusted repeatability allows for the incorporation of fixed effects and for these factors to be accounted for in the analysis (Stoffel et al. 2017). Time (observation month for interactions, rating year for observer ratings) and sex were added as fixed effects and analysis was completed using a Gaussian distribution. Parametric bootstrapping (n=1000) was used to generate 95% confidence intervals. The high repeatability of interactions with visitors and observer ratings were used to justify the averaging of each behavioural measure for each penguin across the whole study period for further analysis.

The relationships between boldness and behaviour were analysed using GLMMs. Averaged observer ratings were selected as the boldness measure to assess these relationships for several reasons: the significant relationship between observer ratings and visitor interactions, the high repeatability of this boldness measure and the fact that these ratings represented the longest

running assessment of boldness (2015-2023). Data sets for daily food consumption and site choice were combined, while keeping the corresponding individual boldness ratings for each year. Therefore, individual was added as a random factor to account for pseudoreplication along with sex to account for potential sex differences. Year was included as a fixed factor in all models to investigate temporal changes but was added as an interaction with boldness when investigating the relationship with hand feeding. Also, when investigating hand feeding, penguin weight was added to incorporate the effects of body size on feeding rates and month was added as a random factor to account for seasonal variations in feeding rate (e.g., pre breeding/pre moult). The mean yearly feeding (g) of each penguin was included in the model investigating supplementary feeds to determine if there was a relationship between hand and supplementary feeding. Additionally, pairwise correlations between boldness and light intensity were assessed using Pearson's Correlation tests in each year (2016/2023) independently. A generalised linear model (GLM) was used to analyse the relationship between boldness and reproductive attempts. As the response variable was a percentage, the data were arcsine square root transformed prior to analysis. Sex was again added as a fixed factor along with the number of possible attempts (years since arrival/reaching maturity). In all cases, models were run with a Gaussian distribution and assumptions were verified by plotting residuals against each predictor in the model and against fitted values (Zuur and Ieno 2016).

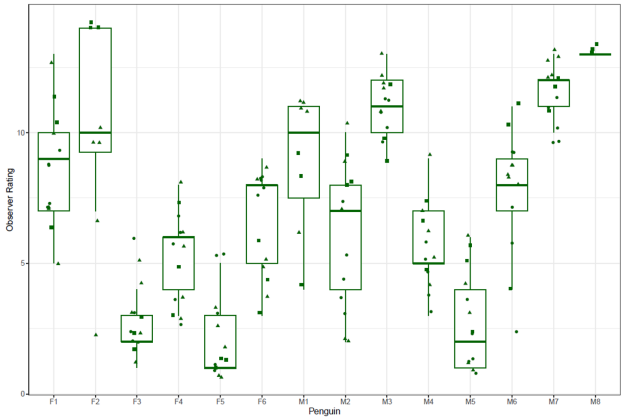

Figure 1. Observer ratings of the boldness personality trait for each penguin (M=male, F=female) in the three years these were carried out (2015-circle, 2016 – triangle, and 2023-square). Note that some variation between years is explained by changes in rating scale as population size increased.

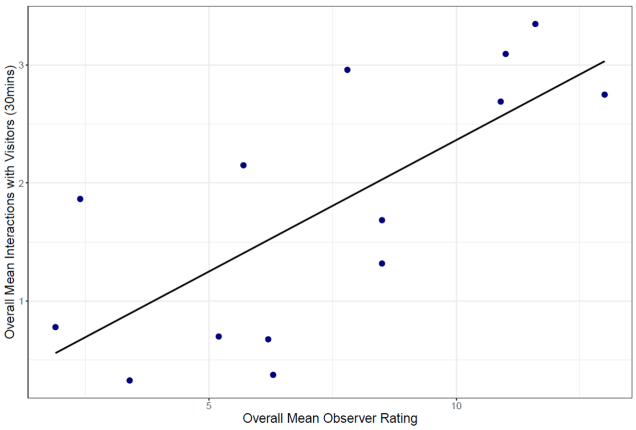

Figure 2. Correlation between overall mean observer ratings of boldness by keepers and overall mean interactions with visitors for each penguin.

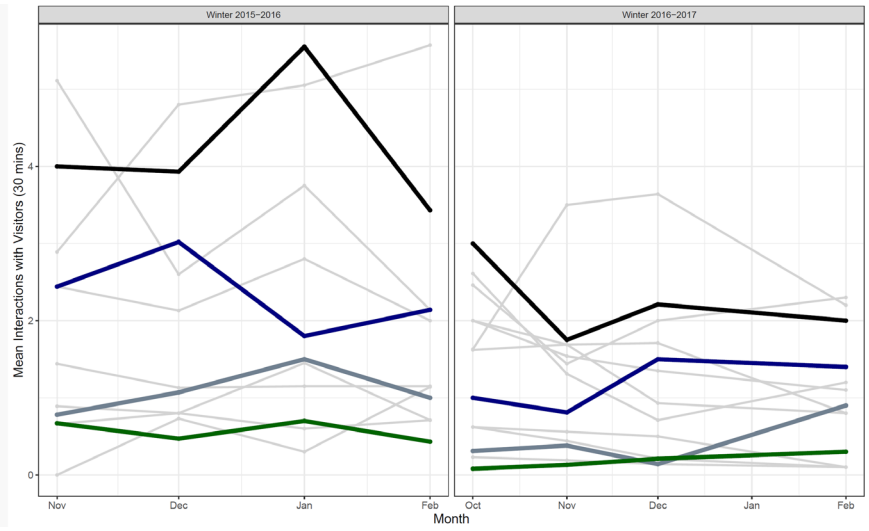

Figure 3. Mean visitor interactions for each of the thirteen birds in the eight months of the study with ten or more repeat observations, split into two four-month sections due to the eight-month gap between observation month 4 (Feb 2016) and observation month 5 (Oct 2016). The same four penguins are highlighted (black, blue, green and grey lines) in both to show examples of the consistent differences between individuals throughout the whole study period.

Table 2. GLMM results for the relationships between boldness and daily hand feeding (A), supplementary feeding (B) and site choice (C). Estimate ± standard error, degrees of freedom (df), t and P values shown for each fixed factor. Significant P values shown with *.

Fixed effects	Fixed effects	Estimate±SE	df	t value	P value
A	Intercept	30.544±3712.091	4110.315	8.228	<0.001*
	Boldness	2684.353±556.430	1923.276	4.824	<0.001*
	Year	-14.910±1.847	3960.286	-8.074	<0.001*
	Boldness:Year	-1.326±9.181	304.153	-4.816	<0.001*
	Weight	-24.623±9.181	1928.823	-2.682	0.008*
B	Intercept	792.278±182.739	15.666	4.336	<0.001*
	Boldness	0.035±0.086	15.617	0.411	0.685
	Year	-0.390±0.090	22.083	-4.327	<0.001*
	Mean Hand Feeding	-0.008±0.003	18.715	-2.615	0.017*
C	Intercept	0.016±0.058	3.110	-0.283	0.795
	Boldness	0.013±0.006	11.946	2.093	0.058
	Year	0.029±0.025	9.588	1.165	0.272

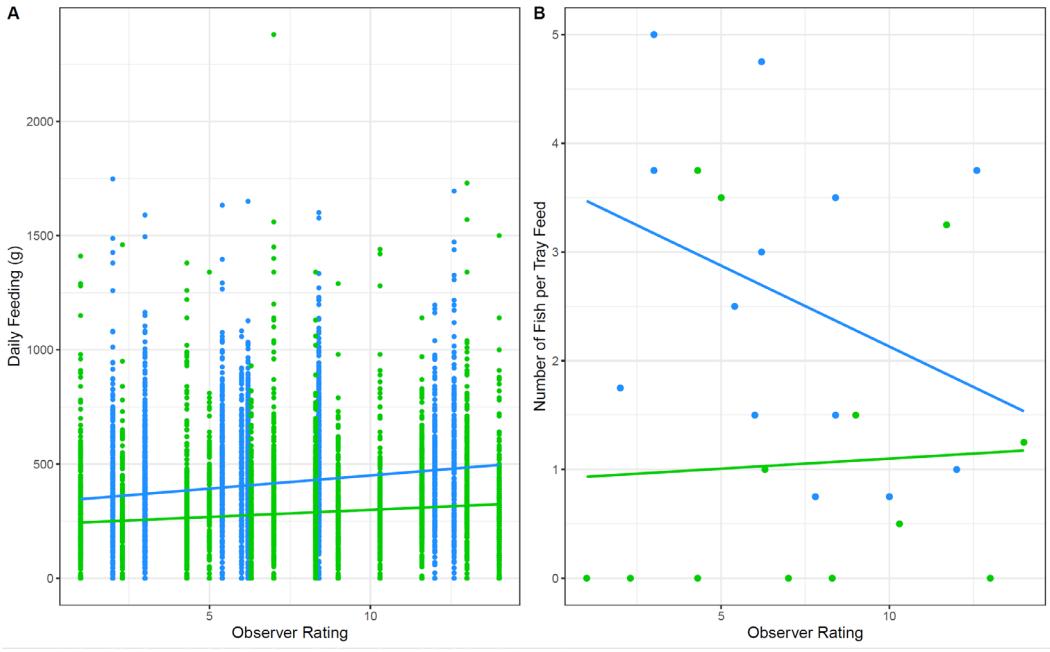

Figure 4. The boldness relationship with daily feeding from keepers (A) and mean number of supplementary food items consumed (B). Year is shown by colour, blue representing data collected early in the study (2016) and green the later period (2022/2023). The best fit line for each year is shown for both relationships.

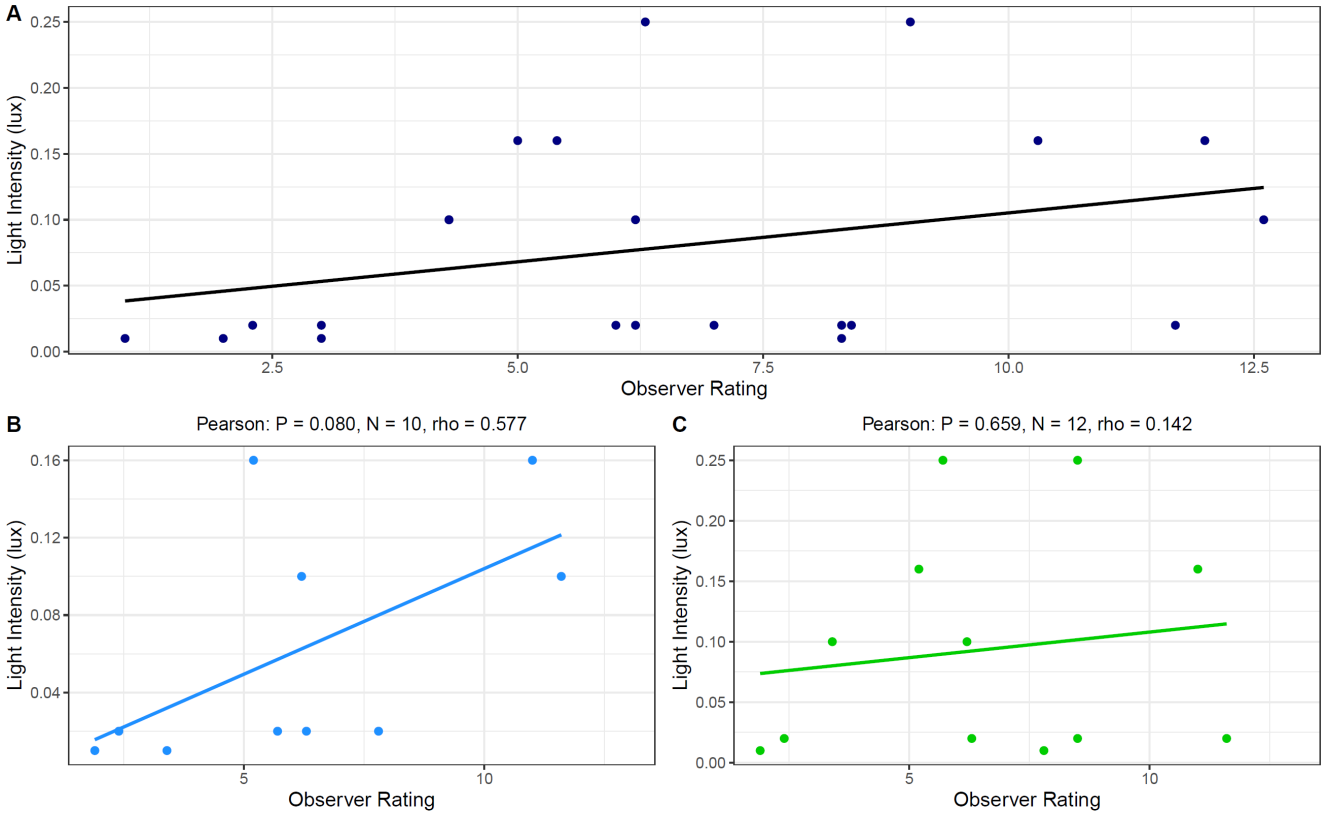

Figure 5. Correlation between mean boldness rating and light intensity across both years (A). The boldness relationship with light split by year (B, blue: 2016; C, green: 2023). The Pearson's r and P values are indicated for each pairwise correlation.

Table 3. The number of successful reproductive attempts out of the total number possible (% also shown) for each individual (M= male, F= female) along with the corresponding mean boldness rating. The output of the Generalised Linear Model (GLM) analysing the relationship between reproductive attempts (response variable) and boldness, sex and number of possible attempts (fixed effects) is also presented: estimate±standard error, degrees of freedom (df), t and P values shown for each fixed factor. Significant P values shown with a *.

Penguin	Completed reproductive attempts	%	Mean observer rating
M8	0 of 2	0	13.0
M7	7 of 7	100	11.6
M3	7 of 7	100	11.0
F2	1 of 5	20	10.9
M2	6 of 7	86	8.5
M1	3 of 5	60	8.5
M6	7 of 7	100	7.8
M2	7 of 7	100	6.3
F6	7 of 7	100	6.2
M4	5 of 7	71	5.7
F4	7 of 7	100	5.2
M5	7 of 7	100	3.4
F3	7 of 7	100	2.4
F5	7 of 7	100	1.9

Fixed effects	Estimate±SE	df	t value	P value
Intercept	-0.588±0.450	13.000	-1.307	0.220
Boldness	-0.017±0.023	11.000	-0.737	0.478
Sex	0.102±0.131	10.000	0.785	0.451
Attempts	0.302±0.053	12.000	5.731	<0.001*

Results

Boldness

There was high agreement (Kendall's W> 0.6) between observers across all years (W: 2015=0.817, 2016=0.724, 2023=0.872; Figure 1). The means of observer ratings of boldness by keepers and interactions with visitors were significantly correlated (P=0.004, N=13, r=0.720; Figure 2).

The high and significant adjusted repeatability values for interactions with visitors (R=0.695, CI=[0.398-0.831], P<0.001) and observer ratings (R=0.814, CI=[0.561-0.920], P<0.001) show that there was high temporal consistency in these measures of boldness providing evidence for personality traits in gentoo penguins. Sex ($t_{11.690}$=1.324, P=0.211) and rating year ($t_{23.180}$=0.826, P=0.417) had no significant impact on observer ratings by keepers. Sex ($t_{10.880}$=1.015, P=0.332) also had no significant effect on interactions with visitors but there was a significant relationship between time (interaction month, $t_{82.980}$=-6.518, P<0.001) and visitor interactions. This is visible in the evident changes in the interaction mean over time within the population, with a decrease in mean interactions as the study progressed (Figure 3). Despite this, the high repeatability in interactions with visitors is visualised by highlighting individuals that remained consistently different throughout the whole study period (Figure 3).

Relationships Between Boldness and Behaviour

Boldness had a significant relationship with daily hand feeding but only in the first year, as shown by the significant interaction between year and boldness ($t_{304.153}$=-4.816, P<0.001; Table 2A, Figure 4A). Additionally, penguin weight also influenced daily hand feeding ($t_{1928.923}$=-2.682, P=0.008). Year also had a significant effect on supplementary feeding ($t_{22.083}$=-4.327, P<0.001), along with mean hand feeding rates ($t_{18.715}$=-2.615, P=0.017) but there was no effect of boldness (Table 2B, Figure 4B). The effect of year on both feeding methods is evident in the reduced feeding levels in the later study period (Figure 4).

There was also a strong trend between boldness and the site choice of penguins ($t_{11.946}$=2.093, P=0.058, Table 2C, Figure 5A). While year had no significant effect on site choice the relationship between boldness and light was stronger in 2016 than 2023 (Figure 5B, 5C).

Boldness had no effect on reproductive attempts (Table 3) as high rates of attempts were present across the boldness continuum. The factor that had the greatest effect on reproductive attempts was the number of years it was possible to make an attempt, with birds that had more opportunities having greater rates of attempts ($t_{12.000}$=5.731, P<0.001). Nine penguins attempted to reproduce in all years and two penguins attempted to reproduce in more than 70% of observed years. For these two individuals there were a couple of years with no available members to pair with due to the odd number of individuals in the population (11 until 2018 and 13 from 2018 to 2021). The three chicks that were raised at The Deep have the lowest rates of attempts (<65%).

Discussion

Gentoo penguins at The Deep exhibit the boldness personality trait, aligning with our prediction. This is demonstrated by repeatable between-individual differences in behaviour towards both visitors and keepers. Therefore, our results contribute to the growing evidence that animal personality traits are widespread throughout the animal kingdom (Weiss 2018; Wolf and Weissing 2012). Also in line with our predictions, there were relationships between penguin boldness and daily food consumption plus site choice, with bolder birds feeding more from keepers and occupying nest sites with higher light intensity. Furthermore, there were temporal changes in penguin behaviour over time, with the relationships between behaviour and boldness weakening over time. In contrast to our prediction, boldness had no influence on reproductive attempts in this population.

The Boldness Trait in Gentoo Penguins

For a personality trait to be present there must be observable between-individual differences in behaviour that are both consistent over time and across contexts (Kaiser and Müller 2021). The population at The Deep satisfies these requirements. First, the penguins exhibit a continuum of responses to the boldness tests, shown by a range of responses to visitors at the viewing window. Second, these differences are consistent over long time periods, 16 months for interactions with the public and eight years for observer ratings, with the repeatability of responses to both tests being greater than the average repeatability in animal behaviour (R=0.37; Bell et al. 2009). Repeatability has been shown to reduce with larger durations between tests (e.g., great tits, *Parus major*; Dingemanse et al. 2002) because the chance of developmental change is greater (Sánchez-Tójar et al. 2022). The high repeatability values are therefore especially notable in the case of the observer ratings due to the large duration between them (2015-2023). The drop in interactions over time is evidence of habituation to visitors, especially as the penguins were relatively new to The Deep when the first observations were carried out in 2015. Animals in captivity may eventually ignore visitors (Rose et al. 2020) and behaviours are not fixed (Biro and Stamps 2008) but if a personality trait is present individual differences will persist (Adriaenssens and Johnsson 2013; Mathot et al. 2012). Finally, behavioural responses are the same across contexts, with bolder behaviour towards keepers correlating with increased interactions with visitors. Overall, this study complements those showing personality to be present in penguins (e.g., Pastorino et al. 2019) and common in birds (Bell et al. 2009) in both wild and captive settings (Pogány et al. 2018).

This study supports the use of observer ratings and tests measuring responses to visitors to assess boldness in captive animals. As boldness impacts how animals react to challenging situations (Réale et al. 2000) such as enriching or stressful visitor presence (Hosey 2008), and as visitors make up a significant part of a captive animal's life (Hosey 2013) it is possible to observe and collect behavioural coding data (Stoinski et al. 2012) for repeatability analysis. Furthermore, personality traits influence human—animal relationships (Hosey 2008), for example the way tigers *Panthera tigris tigris* interact with keepers is influenced by their personality (Phillips and Peck 2007). This study provides further evidence that utilizing the knowledge and experience of keepers, who have regularly been shown to rate animals with high reliability (McDougall et al. 2006; Pastorino et al. 2019; Powell and Svoke 2008; Wielebnowski et al. 2002), can be a valuable method of personality trait assessment. There are, however, important considerations when interpreting observer ratings. Ratings are usually most accurate at the extreme ends of the continuum (Torgerson-White 2014) and they can be influenced by knowledge of the sex of individuals (Uher and Visalberghi 2016).

Relationships Between Boldness and Behaviour

Bolder penguins fed more by keeper hand feeding than shyer individuals but only in the first year. Additionally, although not significant, the relationship between boldness and supplementary feeding was opposite to this in the first year (Figure 4). Therefore, there is potential evidence that different personalities display different feeding strategies, but the sample size for supplementary feeding is low and warrants further study to form a proper conclusion. Across the animal kingdom there is significant evidence that feeding strategies are dependent on personality

(Sih and Watters 2005). For example, shyer great tits flock, trading greater competition for safety while bolder individuals forage alone but face greater predation risk (Aplin et al. 2014). The same distribution in feeding strategies has also been noted in other bird species (e.g., Kurvers et al. 2012). In addition to this, shy individuals take longer to feed in a captive environment than bold individuals (Herborn et al. 2010). In this population bolder individuals may be more comfortable feeding from keepers in this potentially risky situation and shyer individuals may spend less time feeding, resulting in the differences in feeding rates between personality types. Furthermore, bolder individuals, due to potentially being more active (Sih and Bell 2008) may have greater energy expenditure and subsequently greater food requirements (Careau et al. 2003).

As feeding levels dropped across both methods over time there is evidence for adjustment to the captive environment. In birds, differences in stress (corticosterone level) influence foraging behaviour (Wingfield 2003), with greater food intake associated with increased stress (Crossin et al. 2012). As the penguins had recently arrived at The Deep at the start of the study, increased feeding levels may be due to individuals adjusting to the uncertainty of the new environment by maintaining extra energy stores and utilising additional feeding options (e.g., tray feeds, Dall 2010). Therefore, the decrease in feeding may be explained by a reduction in uncertainty over time (e.g., learning enclosure routines). Overall, the variation in food intake during keeper feeds, and the potential difference in feeding strategies in this population related to boldness, highlight the need for further investigation to ensure the relationships between personality traits, captivity and food consumption are understood. This will allow feeding techniques that suit all individuals to be implemented, therefore, helping to meet the nutrition component of the Five Domains Model (Mellor et al. 2020).

Restricted space and lack of complexity can be a common characteristic of captive environments (Sherwen et al. 2015) and poorly designed enclosures are a source of stress (Ross et al. 2009). An example of this is when animals cannot retreat from stressors such as visitors (Hosey 2008). It is therefore important that enclosure design considers the needs of the inhabitants (Ross et al. 2009). There is evidence that the penguins in this study distributed based on light levels. Light may play a role in visibility to visitors, with darker areas offering a level of retreat, and shyer individuals tended to occupy these darker locations. This finding is supported by other studies showing non-random dispersal linked to personality (Sih and Bell 2008; Wolf and Weissing 2012). For example, chipmunks *Tamias striatus* are distributed dependent on human visitation, with bolder individuals being found closer to the public (Fraser et al. 2001). However, during the latter part of the current study this relationship is much weaker, showing that penguins that had greater avoidance of visibility to visitors may have habituated to this potential stressor. Whilst this again demonstrates that captive species may habituate to their enclosure and environment (Fernandez et al. 2009), the requirement of taking personality into account during the design phase of enclosures to cater for the needs of all individuals is important (Kuhar 2008). This can be achieved through environmental complexity (Skibiel et al. 2007), providing shy individuals with places to hide and bold animals with places to explore (Kuhar 2008). In enclosures where retreat spaces are available, they are used by animals (Mallapur et al. 2005) and this is supported by the results of this study as shyer individuals did initially occupy less exposed spaces. Increasing environmental complexity also has the advantages of increasing activity (Mallapur et al. 2002) and cognitive use (Skibiel et al. 2007) in captive animals.

Although animal personalities may influence the success of captive breeding and reintroduction programs (Merrick and Koprowski 2017), the link between reproductive success and personality remains relatively unstudied (Kelleher et al. 2018). In this population reproductive attempts are not related to personality, with individuals across the boldness continuum carrying out attempts in all years. However, it is important to note that because this study only investigated reproductive attempts, there may be relationships between boldness and other components of the reproductive cycle (e.g., hatching success). Consideration of the personality composition of a breeding pair when assessing the relationships between personality and reproductive success is also warranted (McCully et al. 2023), although this was not necessary in this study due to the high rates of attempts by all individuals. Interestingly, the results of this study are contrary to others showing personality traits to be linked to reproductive success (Martin-Wintle et al. 2017). Bolder individuals have been shown to have higher reproductive success (Smith and Blumstein 2008) in bighorn sheep *Ovis canadensis* (Carere and Eens 2005), black rhino *Diceros bicornis* (Carlstead and Brown 2005) and giant pandas *Ailuropoda melanoleuca* (Powell and Svoke 2008). As stress is a barrier to reproduction (Mason 2010) and poor enclosure design can cause stress (McDougall et al. 2006), breeding success may be dependent on enclosure design that provides for all individuals (Sherwen et al. 2015). This is supported by studies that show increased reproductive success after enclosure alterations (Powell and Svoke 2008). Enclosure design and personality are therefore important factors in captive animal breeding programs (Powell and Gartner 2011). The heterogeneity (e.g., variety of light levels) of the enclosure at The Deep, allowing choice of nesting conditions among individuals, may therefore contribute to the high rate of breeding attempts in the population as suitable conditions are available for all personality types. Increasing reproductive success to include all individuals through better enclosure design (McDougall et al. 2006) will have several advantages. For example, reducing loss of genetic diversity (Kleiman 1989) and limiting the unique selective pressures of captive environments that produce tamer, more docile individuals (Dugatkin and Trut 2017), hence maintaining behavioural variation (Martin-Wintle et al. 2017). Importantly, population management is complex, and it may also be necessary to select for individuals with a particular personality trait. For example, considering animal personality can increase the likelihood that a reintroduction or relocation project is successful (Collins et al. 2023).

Conclusion

In conclusion, gentoo penguins at The Deep exhibit the boldness trait and there are relationships between boldness and some behaviours (daily food consumption and choice of nesting site) but not reproductive attempts. The penguins showed temporal changes in behaviour, suggesting habituation to the captive environment. These results highlight the need for personality to be considered in husbandry practices when creating feeding regimes and designing enclosures. Therefore, understanding the personalities of captive animals can provide a low cost, non-invasive way of improving the welfare needs of animals (Goswami et al. 2020). Further investigation into the relationships between boldness and feeding, for example the individual requirements of supplementary feeding, is however recommended to form stronger conclusions in this area. Overall, understanding personality can be used as a tool to increase animal welfare in captive populations alongside providing important conservation benefits through maintenance of genetic and behavioural diversity.

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