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African Penguin tolerance to humans depends on historical exposure at colony level

LORIEN PICHEGRU, TREVOR B. EDWARDS, BEN J. DILLEY, TOM P. FLOWER and PETER G. RYAN

Summary

Sustainable ecotourism requires careful management of human impacts on wildlife. Contrasting responses to the disturbance caused by ecotourism are observed across taxa and within species, because species and populations can differ in their tolerance to humans. However, the mechanisms by which tolerance develops remain unclear. Penguin colonies are popular tourist attractions. Although ecotourism increases public awareness and generates conservation income, it can also disturb penguins, raising concerns for threatened species such as the African Penguin *Spheniscus demersus*, whose populations are in rapid decline. We compared the tolerance of African Penguins to human disturbance across four colonies with contrasting histories of human exposure. Human approaches invoked the least response at colonies where human exposure was highest, suggesting increased human tolerance with increased exposure. The response to humans close to the nest also decreased more rapidly in highly exposed individuals within colonies. These results were consistent independent of breeding stage, and were repeated among colonies. Because the impacts of human disturbance, including temporary nest desertion, were greatest at the colony with least human exposure, human disturbance of breeding African Penguins potentially may be mitigated through increased levels of tolerance to humans, or displacement of shyer individuals, although this could not be assessed in the present study.

However, human exposure could significantly increase stress, impair reproduction and even reduce genetic diversity. Consequently, ecotourism must be managed carefully to minimize population level impacts, potentially by facilitating habituation in populations subject to non-threatening human disturbance, and maintaining some areas free of disturbance to allow shy individuals to breed.

Introduction

Humans profoundly alter ecosystems, modifying environmental landscapes and indirectly inducing wildlife responses to these changes through phenotypic plasticity or natural selection (Hendry *et al.* 2008). Human disturbance of wildlife can take many forms and responses by animals vary according to their life-history, breeding status or individual differences (Bejder *et al.* 2009). Behavioural responses to direct contact with humans can range from increased vigilance to desertion of the current breeding attempt or altered habitat selection (Tuomainen and Candolin 2011).

Reviews of the consequences of human disturbance on wildlife generally focus on negative impacts (e.g. Carney and Sydeman 1999), but some interactions with humans may be positive (Nisbet 2000), for example when human presence decreases predator abundance (Hemmings 1990) or provides additional food resources (Oro *et al.* 2014). Ecotourism includes visiting wild animals in their habitat (Higham and Lück 2001), and has to balance the impacts of disturbance with the revenue generated to support conservation efforts and enhanced public awareness (Emerton *et al.* 2006). Unfortunately, tourists desire close-up, unconstrained and prolonged interactions with wild animals for emotional satisfaction (Knight 2009), and the rapid development of the ecotourism industry, sometimes termed the "new mass tourism" (Burton 1998), raises concerns about the extent to which ecotourism is sustainable (Higham 2007).

Animal populations frequently exposed to non-threatening human activities, such as controlled ecotourism, may display tolerance to human approach (e.g. shorter flight distances, less aggressive responses) compared to conspecifics either less exposed or subject to more hazardous activities (e.g. hunting; Stankowich 2008). Bejder *et al.* (2009) identified four potential mechanisms by which tolerance to humans may originate: (1) behavioural habituation, where individuals learn not to respond to a given stimulus; (2) displacement of less tolerant individuals from the affected population; (3) physiological impairment by prolonged exposure to the stimulus; and/or (4) a lack of suitable alternative sites to which to move. The mechanisms by which tolerance develops are poorly known, yet they are likely to have important implications for sustainable management strategies.

Penguin colonies are particularly popular wildlife tourist destinations, mainly because of the penguins' anthropomorphic stance and gait (Seddon and Ellenberg 2008). Penguins are also among the most threatened of seabird groups (Croxall *et al.* 2012). Studies on impacts of human disturbance on penguins showed species- and even colony-specific responses to humans (Seddon and Ellenberg 2008). Human disturbance increases energy expenditure through physiological and behavioural responses (Ellenberg *et al.* 2012, Regel and Pütz 1997) or through deviation from paths by commuting birds (Burger and Gochfeld 2007, Culik and Wilson 1991). This can have significant adverse effects resulting in lower fledging weights and survival (McClung *et al.* 2004, Ellenberg *et al.* 2007), and potentially decreased adult survival (Culik *et al.* 1991). Some penguin species, like the Humboldt *Spheniscus humboldtii* or Yellow-eyed *Megadyptes antipodes*, are particularly sensitive to disturbance, showing increased physiological responses and low breeding success in areas visited by tourists (Ellenberg *et al.* 2006, 2007, Villanueva *et al.* 2012). In addition, previous encounters with humans can have long-lasting effect on the response of individuals to disturbance, as was shown in Snares Penguins *Eudyptes robustus* (Ellenberg *et al.* 2012). By contrast, other studies have found no decrease in breeding success due to human presence for Gentoo *Pygoscelis papua* (Cobley and Shears 1999, Holmes *et al.* 2006), Adélie *P. adeliae* (Carlini *et al.* 2007, but see Wilson *et al.* 1991) or Magellanic Penguins *S. magellanicus* (Yorio and Boersma 1992). However, few studies have considered how long-term exposure to humans at penguin colonies affects tolerance to humans (e.g. Villanueva *et al.* 2012).

African Penguins are one of the more accessible penguin species, with more than 500,000 people visiting their colonies annually in South Africa (Lewis *et al.* 2012). The penguins benefit from tourism, because funds generated by ecotourism are used to protect breeding colonies. However, the recent rapid decline in African Penguin numbers (Crawford *et al.* 2011) and their 'Endangered' status (BirdLife International 2010) raises the question of whether human presence may negatively impact populations through disruption of behaviour or breeding site use, and whether penguins can increase their tolerance levels to human exposure and potentially mitigate these costs.

We investigated tolerance levels of African Penguins at colonies with different histories of human exposure. We compared the penguins' disturbance response in response to a standard pedestrian approach to nests. Because responses to disturbance may depend on the physiological state of individuals (Ellenberg *et al.* 2009), which may differ between colonies because of e.g. varying prey availability, we performed similar comparisons within colonies with areas of high and low human exposure. We expected African Penguins breeding in colonies with high exposure to humans to be more tolerant of people, as a result of habituation and/or displacement of shy individuals.

Methods

Study sites

Observations and experiments were undertaken during March–July in 2010 and 2011 at four African Penguin colonies in South Africa. Colonies were selected to reflect different levels of human exposure: Boulders Beach (high), Bird Island (low but continuous), Robben Island (intermittent) and St Croix Island (rare).

Boulders Beach, a mainland colony near Simon's Town on the Cape peninsula, is the site with the greatest exposure to humans. It forms part of the Table Mountain National Park and is a major tourist attraction, with thousands of visitors daily (Lewis *et al.* 2012). The colony formed in 1985, at a time when penguins from nearby Dyer Island were searching for new breeding opportunities, and numbers initially grew exponentially (Crawford *et al.* 2011). The population peaked at around 1,200 pairs in 2005, but fell to < 1,000 pairs in 2010–2011 (Crawford *et al.* 2011). The colony has two parts: a recreational beach where people can move freely and where human exposure is consequently high, and a penguin reserve area where people are confined to elevated boardwalks and exposure is lower.

Bird Island is a small (19 ha) offshore island in Algoa Bay, off the south coast of South Africa, that supported 2,500 pairs of African Penguins in 2010 (Crawford *et al.* 2011). The island also lies within a National Park, the Greater Addo National Park, and has a lighthouse that has been manned since the 1800s. At the time of the study, two rangers were stationed on the island and up to 10 researchers and 40 contract workers visited at times. The rangers walk around the island daily and for at least two years prior to our study they also monitored penguin nests every week throughout the year to assess breeding success. Penguins breeding close to the rangers' accommodation have high human exposure, whereas those breeding > 300 m away on the other side of the island only experience ranger patrols.

Robben Island in Table Bay, off Cape Town, is South Africa's largest coastal island (574 ha). It has also long been inhabited by humans and is open to tourism, but direct interactions between penguins and tourists are limited. Penguins colonised the island in the early 1980s, and there were some 2,600 pairs in 2010 (Crawford *et al.* 2011). They breed among dense woody vegetation, which screens them from sight, but researchers and volunteers have monitored nests and breeding success for over 10 years (Ocean and Coasts unpubl. data).

Finally, St Croix Island, is a small (12 ha), rocky island in Algoa Bay that supported the largest African Penguin colony in 2010 (7,600 pairs; Crawford *et al.* 2011). It is seldom visited and in the last few decades, only 1–2 researchers have visited each year since 2009 for up to two weeks during the peak breeding season. Prior to that, the only regular visits were in the 1980s.

Human approach protocol

To investigate the effect of human exposures on the disturbance behaviour of breeding penguins at different colonies, we recorded the response of penguins to standardised human approaches to nests. Methods were adapted from Holmes *et al.* (2006). Attempts were made to record heart rates with electronic recorders (see Ropert-Coudert *et al.* 2009), but due to technical failures the data could not be included in this study. At all study sites, African Penguins nest loosely, with no clear demarcation of the colony edge, so test nests were selected where there was a clear path of approach. Nest density and the presence of non-breeders can affect the stress level of focal individuals, so we selected areas with < 3 nests and < 2 non-breeding individuals within a 1-m radius, which is typical for African Penguins (Hockey *et al.* 2005). We also selected single birds at their nest to avoid behavioural bias due to the presence of a partner.

Bird behaviours (Table 1) were recorded by an observer posted 20 m from the focal nest, before (pre-), during and after (post-) human approaches. With hindsight, the observer distance was probably too close to study nests at St Croix Island, where penguins were most sensitive to human disturbance. We calculated alertness as the time spent alert (vigilant and/or threatening) as a

Table 1. Behavioural categories of African Penguins use to assess their response to a pedestrian approach at four South African colonies.

Behaviour	Description
States*	
Rest	standing (on metatarsi with underside of tail in contact with ground) or sitting down motionless; sleeping, including comfort events as described below
Maintenance/Comfort	nest or body maintenance activities (e.g. preening or nest building) or preening and feeding of chick; stretching; shaking; yawning; head rubbing; rapid wing flap; scratching; defecating
Alertness	head up and watchful of environment and conspecifics; look around (stand with neck fully retracted, head held horizontal or slightly above horizontal with eyes half-closed or blinked and rotated slightly from side to side)
Threat	head turning; nest ownership vocalisations; point (basic threat in which aggressor points directly toward object of aggression while the head is fully retracted onto the shoulders or extended to a greater or lesser degree)
Events**	
Head turn	alternate stare (neck fully retracted or extended to varying degree while the head is rotated from side to side alternately and irregularly, sometimes held briefly on one side); single event was scored as turning the head from 0° to 180° from a forward facing position
Aggressive events	reaching or pecking (when recipient is within reach and especially where it is moving too close to the nest)
Fleeing	Movement away from the nest

*% of observed time; **# acts/observed time.

proportion of total observation time including when penguins were at rest and/or doing nest maintenance (Table 1). We also recorded the number of aggressive events (reaching/pecking movements), of head turns, i.e. alternate stares, when the head rotates from side to side (Hockey *et al.* 2005), indicative of a threatening behaviour (Eggleton and Siegfried 1979), and temporary nest desertions (movements away from the nest; Table 1). Due to the lack of cover at most sites and the surveyed nests being all surface nests, the observer was not hidden, but stood still during the pre- and post-approach observations. Pre- and post-approach observation periods (10 minutes) were undertaken to have consistent observation distances between colonies where lines of sight varied.

Direct approaches lasted c.25 seconds and were conducted by one person on foot at a speed of 1 step.s^{-1} (0.91 ± 0.02 m.s^{-1}) to 1 m of the nest. The person then spent 1 minute standing followed by 1 minute crouching (each divided into two 30-second subsets) 1 m from the nest, before retreating along the same path for another 15 s. When at the nest, the person remained still and quiet, other than shifting posture from standing to crouching. Any trial which resulted in temporary nest desertion was ceased immediately; all birds returned to their nests within 15 minutes and no nest was lost to predation. Approaches were conducted by people of similar stature, wearing dull-coloured clothing. Approaches were conducted in fair weather, when wind speeds did not exceed 20 km.h^{-1} and at air temperatures of 10–20°C.

Nest contents were recorded after completion of the trial to determine the breeding stage: incubating, rearing small chicks (from newly hatched to medium downy individuals) or large chicks (large downy to fledglings). Sample sizes for these stages were similar between breeding stages and across colonies (chi-square goodness-of-fit: $\chi^2 = 5.80$, $P = 0.446$).

Statistical analyses

We compared the response to an experimental human approach by African Penguins at colonies exposed to varying anthropogenic contacts using generalized linear models (GLMs) and mixed

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models (GLMMs) in R v2.15.2 (R Development Core Team 2012) using a binomial distribution with a logit link for the proportion data (levels of alertness) and a Poisson distribution with a log link for the count data (numbers of agonistic events and head turns).

To investigate whether behavioural responses to human approach differed among colonies, we used GLMMs with penguin disturbance behaviours, (i) proportion of time spent alert (binomial), and (ii) number of aggressive events (Poisson), set as the response variables. Explanatory variables included colony, period during the approach experiment (before, during, after), breeding stage (incubation, small chick, large chick) and the interactions between colony*approach, with individual as a random factor. Apart from one individual on Bird Island that continued performing head turns after the approach, no head turns were observed at any colony before or after the human approach (Table 2), therefore numbers of head turns were only compared during the approach using GLMs, with colony and breeding stage.

Tukey post-hoc tests were used for comparisons of levels of alertness and aggressive events between colonies before, during and after the approach. A matrix was used to remove the irrelevant comparisons (e.g. "Boulders before" compared to "St Croix after"). As there were no aggressive events observed on Robben Island before the approach and on St Croix Island after, these two categories were removed from the matrix for the analyses on aggression. Tukey tests were also used to compare numbers of head turns between colonies and breeding stages, and numbers of aggressions between breeding stages.

Temporary nest desertion occurred infrequently and almost invariably after human approach. Nest desertions were consequently pooled within colonies and comparisons between colonies were made separately with a chi-square goodness-of-fit test.

To control for environmental variability between colonies that may have influenced the penguins' behaviour, we compared responses to human disturbance between areas of high and low exposure within two colonies with different exposure levels, Boulders and Bird. We used similar GLMMs for alertness and aggression and GLMs for head turns to those used for between colony comparisons, adding level of human exposure within colony (i.e. high and low), and the interaction between human exposure*colony in the explanatory factors and between human exposure*approach. Again, a matrix of Tukey post-hoc tests was used for relevant comparisons of behaviour within colonies before, during and after the approach.

To investigate whether penguins decrease their levels of response to a human at their nest and whether this decrease differed between colonies, we used a GLMM with a Poisson distribution and log link distribution, with number of head turns as the explanatory variable, and colony, disturbance type (standing and crouching), observation period (first [I] and second [II] 30-second period), breeding stages and the interactions colony*period and disturbance type*period (as the disturbance type was not random, with crouching always following standing) as explanatory factors, and individual as a random factor. Subsequently, we quantified the decrease in intensity of the behavioural response of African Penguins during the close-up period by estimating the proportion of decrease in number of head turns between the first and second 30-second bin for each of the standing and the crouching observation periods. As there was no difference in decrease in head turns when a human was either standing or crouching (Wilcoxon tests: $W = 3801.0$, $P = 0.289$), we averaged the decrease between the two periods. We then tested the difference in the proportion of decrease in the number of head turns between colonies with a Kruskal-Wallis test, and used post-hoc Tukey-type tests to make inter-colony comparisons. To compensate for multiple tests, we used $P < 0.01$ for significance levels.

Results

A total of 167 African Penguin nests were approached: 45 at Boulders Beach (high disturbance levels), 41 at Bird Island (low but continuous), 38 at Robben Island (intermittent) and 43 at St Croix Island (rare).

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Table 2. Results of statistical analyses (GLMMs for proportion of time spent alert and/or threatening, and for number of agonistic events; and GLMs for head turns) comparing behavioural responses of breeding African Penguins between colonies exposed to different human exposures and between breeding stages (incubating, rearing small chicks and large chicks) before, during and after a single pedestrian approach (except for head turns only compared between colonies during the approach, see methods). Levels of significance were $P < 0.01$. Significant relations are shown in bold.

Factors		Alertness/Threat			Aggressive events			Head turns		
		Estimate	*Z*	*P*	Estimate	*Z*	*P*	Estimate	*Z*	*P*
	Intercept	**-1.06**	**-2.84**	**0.005**	**-3.36**	**-5.70**	**<0.001**	**2.64**	**93.23**	**< 0.001**
	Boulders	**-3.10**	**-2.68**	**0.007**	**-0.70**	**-3.70**	**<0.001**	**0.79**	**13.63**	**< 0.001**
	Robben	1.13	2.38	0.017	**-3.71**	**-5.17**	**<0.001**	**2.50**	**80.47**	**< 0.001**
Colony	St Croix	**2.83**	**4.86**	**<0.001**	-18.10	-0.02	0.982	**2.86**	**102.94**	**< 0.001**
	Large chicks	0.42	1.41	0.158	**0.76**	**6.71**	**<0.001**	**0.11**	**3.59**	**< 0.001**
Stage	Small chicks	0.27	0.97	0.334	**0.97**	**8.60**	**<0.001**	0.06	1.94	0.052
	Before	-0.97	-1.71	0.088	-0.41	-0.44	0.658			
Approach	During	**2.37**	**4.49**	**<0.001**	**3.95**	**6.76**	**<0.001**			
	Boulders:Before	1.22	0.77	0.441	0.81	0.87	0.387			
	Robben:Before	-0.06	-0.08	0.936	-13.92	-0.02	0.987			
	St Croix:Before	-0.52	-0.65	0.517	14.92	0.02	0.985			
	Boulders:During	0.66	0.52	0.603	**-2.70**	**-4.41**	**<0.001**			
	Robben:During	-0.92	-1.20	0.231	-0.50	-0.54	0.589			
Colony*Approach	St Croix:During	-2.11	-3.39	0.017	15.06	0.02	0.985			

Does variation in human exposure between colonies affect penguin disturbance behaviour?

Before human approach, time spent alert by penguins already followed the distribution gradient of historical human exposure, presumably because of the presence of an observer 20 m from a nest (Figure 1a). Penguins at the colonies most exposed to humans, Boulders and Bird Island, were alert for < 20% of the observation period (Boulders 2 ± 3%, Bird Island 13 ± 14%), while penguins from the least exposed colony (St Croix) spent most of the time alert (62 ± 31%) (Figure 1a, Table 2; Table S1 in the online supplementary material). Penguins from Robben fell between these extremes, and were alert for 32 ± 28% of the pre-approach period. Although aggressive displays were infrequent before human approach, Boulders penguins showed more aggression towards conspecifics than at other colonies (Figure 1a, Table 2, Table S1).

During human approach, penguins at all colonies increased their time spent alert. However, this increase was significant neither at the most exposed colony Boulders, where levels of alertness remained low overall, nor at the least exposed colony St Croix, where they were already high (possibly as a result of the observer being too close to the nest). Penguins also systematically increased their number of aggressive displays directed at the human approaching during the experiment (Figure 1a, Table 2).

After the approach, penguins at Bird and Robben Islands reduced their alertness to near pre-approach levels (Figure 1a, Table 2, Table S1). Alertness also decreased after the approach for penguins at Boulders, but remained low overall before, during and after the approach (Figure 1a, Table 2). However, at St Croix, where human exposure was least, alertness remained high throughout the experiment, even after human approach ceased (Figure 1a, Table 2). The number of aggressive events and head turns by penguins after human approach returned to levels similar to that before approach at all colonies (Figure 1a, Table 2).

Most nest desertions occurred on St Croix Island during the post-approach observation period, where 21% of approached birds (9 of 43) temporarily left their nests ($\chi^2 = 12.82$, df = 3, $P < 0.01$). None of the Boulders penguins left their nest during the experiment. Most nests where the parent fled contained large chicks (13 of 15), the other two contained small chicks (one on Robben and one on Bird Island). However, parents with chicks displayed significantly larger numbers of aggressive responses and head turns than incubating birds (Tukey post-hoc: aggressions of parents with large chicks versus incubating birds: $Z = 6.67$, $P < 0.001$; with small chicks versus incubating: $Z = 8.52$, $P < 0.001$; head turns of parents with large chicks versus incubating birds: $Z = 3.59$, $P < 0.001$).

Does variation in human exposure within colonies affect penguin response behaviour?

Within-colony comparisons of penguin behaviour showed that penguins more exposed to humans were significantly less alert but more aggressive before and after the approach, compared to penguins in areas of low human exposure, regardless of their colony of origin (Figure 1b, Table 3, Table S2). Comparisons of behaviour before, during and after human approach in areas of high and low human exposure present similar patterns to comparisons of behaviour between colonies. All individuals increased their responses to humans during the approach, but this increase was higher for less exposed penguins (Figure 1b, Table 3, Table S2).

Do penguins decrease their response to humans during a temporary close approach?

Even though the frequency of head turns varied between colonies, all individuals rapidly decreased their response to a human at their nests by decreasing their frequency of head turns during the 2-minutes of exposure (Figure 2, Table 4). The shift from standing to crouching positions typically increased head turning responses and then once again penguins decreased

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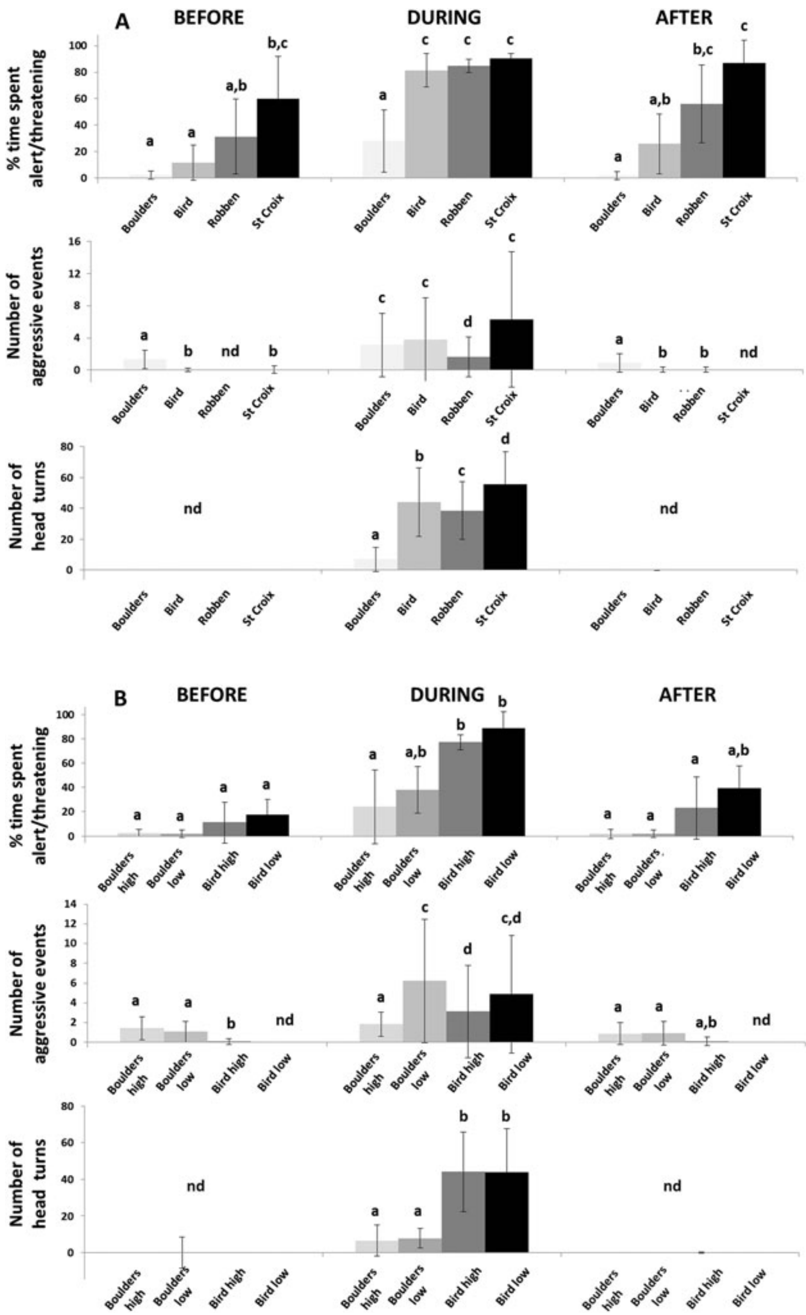

Figure 1. Behavioural responses (average ± SD of proportion of time spent alert and/or threatening, number of aggressive events and number of head turns) before, during and after a human approach by African Penguins breeding at (A) four South African colonies and (B) in areas of low and high levels of human exposure at Boulders and Bird Island colonies. Different letters above histogram bars denote significant differences among colonies from Tukey post-hoc tests (see Table S1), nd = not determined.

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Table 3. Results of statistical analyses (GLMMs for proportion of time spent alert and/or threatening, and number of agonistic events; and GLMs for head turns) comparing behavioural responses of breeding African Penguins within colonies between areas of high and low exposure to human disturbance and between breeding stages (incubating, rearing small chicks and large chicks) before, during and after a single pedestrian approach (except for head turns only compared between colonies during the approach, see methods). Levels of significance were $P < 0.01$. Significant relations are shown in bold.

Factors		Alertness/Threat			Aggressive events			Head turns		
		Estimate	*Z*	*P*	Estimate	*Z*	*P*	Estimate	*Z*	*P*
Exposure	Intercept	**-1.38**	**-2.72**	**0.007**	**-1.12**	**-4.60**	**< 0.001**	**2.59**	**62.30**	**< 0.001**
	Low	-0.57	-1.08	0.280	**-1.58**	**-4.65**	**< 0.001**	**2.59**	**57.58**	**< 0.001**
Colony	Boulders	**-2.33**	**-4.39**	**<0.001**	0.09	0.57	0.572	**-1.90**	**-25.13**	**<0.001**
	Large chicks	0.22	0.45	0.651	**0.47**	**2.81**	**0.005**	**0.16**	**2.78**	**0.006**
Stage	Small chicks	0.16	0.36	0.718	0.31	1.81	0.071	**0.17**	**3.37**	**<0.001**
Exposure*Colony	Low:Boulders	-0.35	-0.37	0.713	0.66	2.46	0.014	0.23	1.74	0.08
	Before	-0.67	-0.94	0.347	0.44	1.88	0.060			
Approach	During	**2.47**	4.24	**<0.001**	**1.49**	**7.41**	**<0.001**			
	Low:Before	-0.34	-0.32	0.747	-0.28	-0.62	0.537			
Exposure*Approach	Low:During	0.20	0.20	0.842	**1.10**	**3.04**	**0.002**			

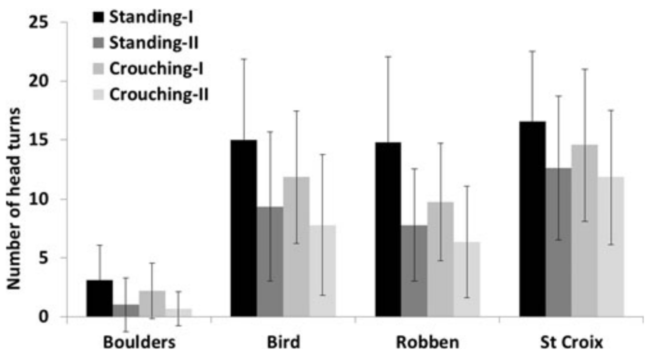

Figure 2. Average (± SD) number of head turns displayed by African penguins while a human was standing for one minute and then crouching for one minute at 1 m from their nest. Periods were divided into two subsets of 30 seconds each (I and II).

their threatening behaviour (Figure 2, Table 4). As a result, the intensity of penguin responses was systematically lower during the second 30-second period during both standing and crouching (Table 4). Standing provoked consistently more head turns by penguins than crouching (Table 4), independent of the fact that crouching always followed standing during our experiment, as shown by the non-significance of the interaction period*disturbance (Table 4).

The decrease in number of head turns between the first and second 30-s periods varied between colonies (H_3 = 61.23, P < 0.001). Penguins at St Croix Island, which exhibited the greatest number of head turns at the start of the close-up period (Figure 3), showed the lowest decrease (20.6 ± 23.2%, Tukey tests: P < 0.001 compared to all other colonies, Figure 3). By comparison, most Boulders birds soon stopped their alternating stares during the 2-minute approach (63.1 ± 36.7%, Tukey tests: P < 0.001 compared to all other colonies). Penguins at Bird and Robben islands reacted similarly (Tukey tests: P = 0.882, Figure 3), decreasing their levels of alertness by 40.9 ± 26.5 and 46.3 ± 24.9%, respectively.

Table 4. Results of GLMMs analyses comparing behavioural responses (number of head turns) of breeding African Penguins between colonies exposed to different human exposures during a two-minutes close-up, constituted of one minute standing followed by one minute crouching, by a human within one meter of the nest. Both minutes are divided into two 30s-periods (I and II). See methods for details. Levels of significance were P < 0.01. Significant relations are shown in bold.

		Head turns		
		Estimate	*Z*	*P*
	Bird	**2.37**	**34.83**	**<0.001**
	Boulders	**0.67**	**7.62**	**<0.001**
	Robben	**2.29**	**32.91**	**<0.001**
Colony	St Croix	**2.51**	**37.12**	**<0.001**
Period	II	**-0.39**	**-6.92**	**<0.001**
Disturbance Type	Standing	**0.25**	**7.44**	**<0.001**
	Large	0.10	2.51	0.012
Stage	Small	0.05	1.29	0.197
	Boulders:PeriodII	**-0.69**	**-4.89**	**<0.001**
	Robben:PeriodII	-0.10	-1.42	0.156
Colony*Period	St Croix:PeriodII	**0.21**	**3.26**	**0.001**
Period*Disturbance Type	PeriodII:Standing	-0.11	-2.02	0.043

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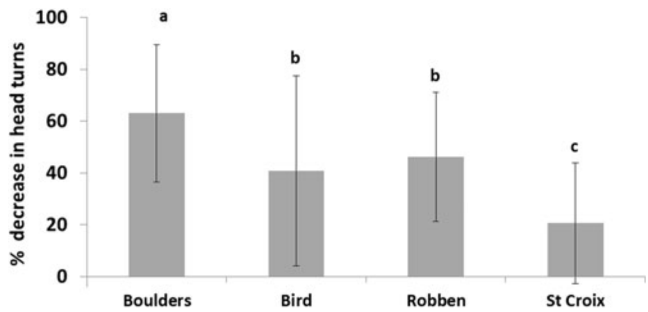

Figure 3. Average percentage decrease in number of head turns displayed by African penguins within two minutes of human approach (see methods for details). Different letters above histogram bars denote significant differences among sites.

Discussion

African Penguins from the colony where human exposure was highest had greater levels of tolerance, with least response to human approach and a rapid decrease in response during the two minutes of close proximity with a human. Because behavioural responses to disturbance are likely correlated with energetic and physiological costs to penguins that may impact survival and reproductive success, increased tolerance may mitigate these costs. These results remain to be interpreted with caution, as we did not measure physiological responses such as elevated heart rates that may reveal more accurately the stress experienced by individuals (e.g. Ellenberg *et al.* 2006, Wilson *et al.* 1991). Some studies indeed suggested that although behavioural tolerance may be observed, physiological responses may continue to be unaltered (Walker *et al.* 2006, Ellenberg *et al.* 2012). However, the frequency of head turns in *Spheniscus* penguins has been shown to be correlated with levels of stress hormones (Fowler 1999, Walker *et al.* 2006) and may thus be used as a proxy for internal state. Increased levels of alertness are also generally associated with elevated heart rates in penguins (e.g. Holmes *et al.* 2006), representing increased metabolism and energy expenditure compared to resting behaviour (Weimerskirch *et al.* 2002). Although short-term peaks in hormonal stress can be advantageous in enabling individuals to respond appropriately to a potential threat, sustained alertness can be translated in chronic stress (Warm *et al.* 2008), which can decrease individual performance (Dukas and Clark 1995), and in turn compromise fitness (McEwen and Stellar 1993, Cyr and Romero 2007).

The proportion of adult penguins remaining alert during the 10-minute observation period after the approach followed the gradient of human exposure, both among and within colonies. Thus we may predict that the penguins least exposed to humans carried the greatest metabolic costs from this short-term exposure. Penguins at St Croix Island were consistently more alert than birds at other colonies and also had the highest frequency of nest desertion. Most chicks deserted were large, so parents might have left the nest more easily because their chicks were better able to fend for themselves (Côté 2000), but such desertion is still likely to carry an additional cost, for example in intra-specific aggression. By contrast, parents with chicks were more aggressive towards the person approaching than incubating birds, which may reflect the increase in parental investment linked to brood age (Montgomerie and Weatherhead 1988).

Even though penguins at Robben and Bird islands showed some degree of tolerance, with levels of vigilance lower than those at St Croix, they reacted equally strongly to a direct human approach. A direct approach is most threatening to animals, which apparently perceive it as a predation attempt (Beale and Monaghan 2004, Ellenberg *et al.* 2006, Frid and Dill 2002). Such threats are an

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acute stress (Wingfield *et al.* 1995) that generally elevate corticosterone levels and may result in individual's decision to favour survival over reproduction, hence increase nest desertion (Ellenberg *et al.* 2007). By contrast, Boulders birds reacted least to the approach and stopped threatening within two minutes of close approach, with none deserting their nests. Their high tolerance to humans potentially offset the short-term costs of human disturbance.

Increased tolerance levels and decreased aggressive reactions can be beneficial for animals when facing regular stressors with limited predatory risks (Nisbet 2000). Animals need to balance the risks of being captured against the costs of predator avoidance to maximise fitness (Lima and Dill 1990). Decreased response to limited threat can improve the body condition of individuals (Rodríguez-Prieto *et al.* 2010) and even allow them to utilise higher-quality habitat occupied by humans (Jiménez *et al.* 2011). However, we were unable to evaluate the long-term costs of tourism at Boulders, in terms of fledging survival or recruitment, as no such data are available. Chronic human disturbance can reduce penguin breeding success (Ellenberg *et al.* 2006, 2007) and may often go unnoticed (all temporary nest desertions occurred after the approach experiment). Low breeding success may result not only from nest desertion, but also be an indirect effect of human-induced stress, through increased energy expenditure of adults defending their nest and subsequent lower chick condition and survival (McClung *et al.* 2004). Nevertheless, African Penguins at Boulders have a higher breeding success (0.7 fledglings per attempt in 2006; Hampton *et al.* 2009) than penguins breeding at the three other colonies studied (0.3–0.35; Pichegru *et al.* 2012, Sherley *et al.* 2012). Even though comparisons in breeding success between areas of high and low exposure at Boulders could not be made, it seems unlikely that ecotourism significantly decreases the breeding success of African Penguins at Boulders, since food availability around the colonies probably plays a greater role in their breeding success (Pichegru *et al.* 2012).

The observed rapid decrease in the number of head turns during the 2-minute close-approach was consistent across colonies, which suggests that African Penguins may be able to rapidly decrease their behavioural response to the presence of non-threatening humans. It is important to note that, while the closely related Humboldt Penguins decreased their behavioural response to humans during a similar experiment, their stress levels, measured with heart rates, remained elevated (Ellenberg *et al.* 2006). If the observed decrease in behavioural response in African Penguins could be corroborated in future experiments with a concomitant decrease in heart rates, this response may then be a sign of potential for habituation in African Penguins. Repeated approaches to the same nests would also be necessary to confirm this potential (e.g. Walker *et al.* 2006). The observed gradient of tolerance to humans from a single visit to nests across colonies with varying degrees of historical exposure to humans might, however, confirm this potential for habituation in African Penguins. Habituation in individual animals exposed to human disturbance has been observed in many species, from marine iguanas *Amblyrhynchus cristatus* (Romero and Wikelski 2002) to primates (Lloyd and Ajarova 2005). Several penguin species have also shown habituation (decreased behavioural and/or hormonal responses) to repeated approaches and captures or to chronic disturbance, such as Magellanic (Walker *et al.* 2006), Gentoo (Holmes *et al.* 2006) or King Penguins *Aptenodytes patagonicus* (Viblanc *et al.* 2012). On the other hand, species such as Yellow-eyed or Snares Penguins become more sensitive to disturbance with increased exposure (Ellenberg *et al.* 2009, 2012). Generally, however, responses vary among individuals, and within species some individuals remained more sensitive to human disturbance than others (Ellenberg *et al.* 2009). Previous studies showed potential habituation in non-breeding African Penguins (van Heezik and Seddon 1990), where beach groups of penguins were approached regularly over several weeks and their response diminished.

The potential for habituation in African Penguins does not, however, preclude other parallel mechanisms increasing tolerance to humans at a population level, such as physiological condition, a lack of suitable alternative sites to which to move to, or displacement of less tolerant individuals (Nisbet 2000), although the experimental design of this study does not allow us to distinguish between these mechanisms. In African Penguins, neither the condition of individuals (Pichegru, Steinfurth, Robinson unpubl. data) nor the availability of alternative nest sites could explain differences in response to humans at the studied sites. However, displacement of shy individuals may have contributed to the high tolerance levels observed in penguins from highly frequented colonies, such as Boulders. Similarly, Fowler (1999) reported decreased nest density and lower variability in Magellanic Penguins behavioural responses when breeding in a tourist area compared to more isolated colonies, and suggested that the habituation he observed was due to the elimination of shy individuals. In our experiment, penguins in areas more exposed to humans tended to be more aggressive towards their conspecifics than penguins less exposed, regardless of their colony. This result might indicate that these areas are occupied by more aggressive birds, suggesting the potential displacement of shy individuals. However, exposure to human may also have increased aggression in African Penguins (e.g. Self *et al.* 2013) and additional research would be necessary to disentangle the two effects. Urban colonisation and ecotourism could potentially be an important driver of directional phenotype selection and may favour certain "bold" phenotypes through selective desertion of the more stress-sensitive phenotypes in specific populations (Møller and Garamszegi 2012), potentially leading to a loss in phenotypic plasticity and/or genetic diversity (Hendry *et al.* 2008).

In order to assess more accurately the impact of human disturbance on African Penguins, future research should include measurements of heart rates, with for example the use of non-invasive egg dummies (see Ellenberg *et al.* 2012), which would reveal physiological stress levels. Repeated approaches of the same nests (e.g. Walker *et al.* 2006) would also help confirming the potential for habituation in African Penguin. Finally, comparisons of baseline levels of stress hormones and fledgling weights across colonies of different human pressure could reveal the existence or absence of chronic stress on colonies largely exposed to human visitation and the potential longer-term effect of human disturbance. The latter measurements should, however, be controlled for differences in environmental conditions between colonies.

Conclusions

Ecotourism can have positive effects for wildlife (e.g. Tisdell and Wilson 2002), but it requires careful management with appropriate site-specific visitor guidelines (Seddon and Ellenberg 2008, Bertellotti *et al.* 2013). Managing African Penguin colonies to ensure a disturbance gradient would perhaps facilitate habituation, thus allowing secondary movement from less disturbed to disturbed areas within a colony. However, it is also essential to maintain an undisturbed area to allow settlement of shy individuals, and to control for the potential impacts of ecotourism. The present results suggest that it should be preferable to increase visitation of already accessible, frequently visited colonies, if necessary, rather than opening up new colonies for visitation. Generally, ecotourism projects should account for and manage levels of human tolerance in populations of animals frequently exposed to tourists, in order to allow wildlife to behave naturally.

Supplementary Material

The supplementary materials for this article can be found at journals.cambridge.org/bci

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LORIEN PICHEGRU*
Institute for Coastal and Marine Research, Nelson Mandela Metropolitan University, University Way, Port Elizabeth 6031, South Africa.

TREVOR B. EDWARDS, BEN J. DILLEY, TOM P. FLOWER, PETER G. RYAN
Percy FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence University of Cape Town, South Africa.

**Author for correspondence; email: lorienp@hotmail.com*

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