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ORIGINAL PAPER

Behavioral responses of chinstrap and gentoo penguins to a stuffed skua and human nest intruders

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Abstract Breeding animals can increase the survival of their offspring by defending their offspring and perform a conspicuous display against nest predators and potential risks. Here, we recorded the behavioral responses of Antarctic penguins when a stuffed skua and a human approached their nests. We investigated (1) how sympatrically breeding chinstrap (*Pygoscelis antarcticus*) and gentoo (*Pygoscelis papua*) penguins responded to the approaching skua (a real nest predator) and human (a newly introduced intruder) and (2) how the penguin responses varied based on the degree of previous exposure to humans. Our results showed that chinstrap penguins mostly displayed strongly threatening behavior, with physical attacks on both the skua and human. However, gentoo penguins displayed a weaker threatening behavior toward the skua and responded differently to the presence of a human. Many gentoo individuals avoided the human rather than displaying threatening behavior. Furthermore, gentoo penguins near the pathway used by humans exhibited weak responses after 4 weeks of exposures to passers-by, whereas other individuals far from the pathway responded with threatening behavior. These results indicate that chinstrap and gentoo penguins may have different strategies for defending their offspring; gentoo penguins might discriminate between intruder types depending on the degree of danger, whereas chinstrap penguins consistently reacted to any intruders approaching to their nest sites. Our findings suggest that gentoo penguins may become habituated with humans following prior to short-term exposure.

Keywords Nest defense behavior · Human disturbance · *Pygoscelis antarcticus* · *Pygoscelis papua*

Won Young Lee and Jin-Woo Jung have contributed equally to this work.

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Introduction

Breeding animal parents can increase the survival of their offspring by defending them against predators with various forms of parental care by either or both parents in many taxa, including invertebrates (Tallamy 2000), fish, reptiles (Reynolds et al. 2002), birds (Cockburn 2006) and mammals (Clutton-Brock 1991). Parents carefully respond to predators and other potential risks to protect their offspring when they are young and vulnerable (Redondo 1989). It may be beneficial for parents to discriminate between predators on conspecific and harmless species and to then respond differently to approaching intruders. In many avian species, nest predation is one of the major causes of nesting failure (Nilsson 1984; Martin 1993; Caro 2005). Therefore, birds have evolved behaviors against predators, called 'nest defense behavior,' which is defined as "behavior that decreases the probability that a predator will harm the contents of the nest (eggs or chicks) while simultaneously increasing the probability of injury or death to the parent" (Montgomerie and Weatherhead 1988).

Nest defense behavior may vary among species, even between closely related species (Gochfeld 1984; Byrkjedal 1987), because there are several life history characteristics that determine this behavior, such as clutch/brood size, life expectancy, future breeding opportunity, offspring/parental quality and nest characteristics (reviewed in Montgomerie and Weatherhead 1988). Moreover, avian parents have been recently shown to use different strategies based on the type of predatory threat (Suzuki 2011, 2012; Suzuki and Ueda 2013). For Antarctic penguins, skuas (*Stercorarius* spp.) are the main nest predator, and they will prey on both penguin eggs and young chicks during the breeding season (Young 1994). Because penguins usually nest in large groups, with many thousands of nests packed together, skuas mostly attempt to access exposed eggs or chicks on the ground at the edge of the breeding colony. Therefore, breeding penguin parents in these locations must defend their offspring against approaching skuas and other potential predators. Accordingly, penguins respond defensively by displaying threatening behavior at offenders using bill and head movements (Jouventin 1982; Viñuela et al. 1995; Holmes et al. 2006). The degree of display varies among penguin species and among individuals within the same species (Young 1994; Holmes 2007).

Human disturbance has the potential to interrupt breeding penguins (Hockey and Hallinan 1981; Woehler et al. 1994; Ellenberg et al. 2006, 2007, 2012). Individuals of many penguin species are physiologically influenced by human activity (Fowler 1999; Villanueva et al. 2012, Magellanic Penguin *Spheniscus magellanicus*; Ellenberg et al. 2006, Humboldt Penguin *Spheniscus humboldti*; Ellenberg et al. 2007, Yellow-eyed Penguin *Megadyptes antipodes*; Ellenberg et al. 2012, Snares Penguin *Eudyptes robustus*; Viblanc et al. 2012, King Penguin *Aptenodytes patagonicus*), which can affect breeding success. The responses to humans vary among species and populations. At the species level, some species displayed more exaggerated behaviors than others against similar human disturbance. For example, Humboldt penguins are very sensitive to the presence of humans (Ellenberg et al. 2006) compared with other more tolerant species, such as Magellanic penguins (Yorio and Boersma 1992; Walker et al. 2006). Ellenberg et al. (2006) suggested that this difference between species might originate from different levels of hunting pressure on penguin species by humans. If there is a selection pressure by human hunting, reactions against humans can be selected for (Festa-Bianchet 2003). However, species-specific responses were observed even in the same area. For example, on Macquarie Island, gentoo penguins (*Pygoscelis papua*) were more sensitive to human visitation than king and royal (*Eudyptes schlegeli*) penguins (Holmes 2007). However, it is still unclear why there was such substantial variation to human disturbance among species. At the population level, previous reports showed behavioral differences (e.g., gentoo penguins in Holmes et al. 2006; Snares penguins in Ellenberg et al. 2012). To explain the differential responses among populations, the "habituation hypothesis" has been proposed. Habituation is defined as a 'reduced response to repeated stimulation not attributable to fatigue or sensory adaptation' (Domjan 2003). This hypothesis indicates that increased tolerance levels are acquired by frequent exposure to humans (Ellenberg et al. 2009). Many studies have shown that penguins are affected by human disturbance and have become habituated by repeated and predictable low-level disturbance, such as controlled tourist visits, i.e., "ecotourism" (Burger and Gochfeld 2007; Ellenberg et al. 2009; Viblanc et al. 2012). However, unregulated tourism can cause elevated hormonal response and eventually reduced reproductive output in yellow-eyed penguins (Ellenberg et al. 2007). This indicates that uncontrolled human disturbance can reduce breeding success.

Gentoo penguins in on-station areas with high human activity display weak responses to humans compared with populations in off-station areas (Holmes et al. 2006). However, only a few studies have tested this hypothesis in restricted areas, where the effects of human exposure can be identified (see Ellenberg et al. 2012). We studied sympatrically breeding chinstrap (*Pygoscelis antarcticus*) and gentoo penguins near the King Sejong Station on King George Island in Antarctica. Chang (1999) observed that chinstrap penguins were more aggressive to skuas or humans than gentoo penguins in this breeding area. Other studies have also demonstrated similar aggressiveness of chinstrap penguins compared with other penguins in the same breeding site while breeding (Crawford 1974; Conroy 1975; Trivelpiece and Volkman 1979; Macdonald et al. 2002). To explain the interspecific differences of degree of aggressiveness, Trivelpiece and Volkman (1979) and Macdonald et al. (2002) hypothesized that aggressiveness of chinstrap penguins may be related to nest-site competition and helps them invade the nest sites of other penguin species in mixed sites; they argued that aggressive chinstrap penguins expelled Adélie penguins (*Pygoscelis adeliae*) and took the nest sites near the shore even though chinstrap penguins arrived later than Adélie penguins. Another hypothesis, which is not mutually exclusive with the former hypothesis, is that intraspecific aggression could be linked with anti-predatory aggression (Huntingford 1976). This hypothesis implies that aggression toward predators could be correlated with intraspecific aggression. Huntingford (1976) suggested that the level of anti-predatory aggression and that of intraspecific aggression would be related through hormone effects. This hypothesis was supported by recent reports in a seabird (black-tailed gulls, *Larus crassirostris*), which found that individuals with high aggression levels as antipredator nest defense showed higher testosterone levels (Kazama et al. 2011) and had more frequent intraspecific aggression behaviors (Kazama et al. 2012).

In this study, we observed the nest defense behavior of breeding chinstrap and gentoo penguins using a human and a stuffed skua. For chinstrap and gentoo penguins, skuas are the main predator that will take eggs or chicks from nests, and humans are a recent intruder that may indirectly affect fitness by disturbance (Frid and Dill 2002). Here, we investigated how aggressiveness differed between gentoo and chinstrap penguins (chinstrap vs. gentoo) and whether the nest-defending response differs depending on the type of approaching intruders (skua vs. human). In addition, we evaluated whether penguin responses varied with the degree of previous exposure to humans. Among several sub-colonies of gentoo penguins, we investigated behavioral responses in the colonies with previous exposure where humans passed close by and less exposure to humans passing prior to the behavioral experiments (approximately 10 m vs. 50 m away).

Materials and methods

Study area and species

We performed this study on breeding chinstrap and gentoo penguins at Narębski Point (Fig. 1; 62°14.3′S, 58°46.5′W) on King George Island for two breeding seasons (December 2012–January 2013 and December 2013–January 2014). Migratory chinstrap penguins arrive at the rookery in early November and lay eggs in late November and early December (Trivelpiece and Trivelpiece 1990). Hatching of chinstraps is in late December and early January, and fledging is in late February (Trivelpiece et al. 1987). Semi-migratory gentoo penguins tend to remain near the rookery (Trivelpiece and Trivelpiece 1990). They lay eggs in mid-November (Trivelpiece and Trivelpiece 1990), hatch between mid- and late December, and fledge between late February and early March (Trivelpiece et al. 1987). In the 2012–2013 and 2013–2014 breeding seasons, penguin colony size and breeding nest locations were measured (Fig. 1) with a GPS unit (Geo7x handheld, Trimble GeoExplorer®, Sunnyvale, CA, USA) before fledging. The number of nests and the number of offspring were counted near the crèche. Locations of nest sites were recorded, and breeding areas of both species were plotted using ArcGIS Platform (version 10.0, ESRI Inc., Redlands, CA, USA). All measurements on colony size and nest locations were performed after the experiments. From our observations, 3332 chinstrap and 2496 gentoo breeding pairs were counted in the 2012–2013 season, and 3157 and 2378, respectively, were counted in 2013–2014. In the same area, we consistently observed breeding skuas (Brown Skua, *Stercorarius antarcticus*; four pairs in 2012–2013 and seven in 2013–2014). For calculating the densities of breeding nests (defined as the number of nests per given area), we excluded solitary nests over 5 m away from the nearest neighboring nests. Totally, 3 chinstrap and 41 gentoo penguin nests in the 2012–2013 season and 9 and 51, respectively, were excluded in 2013–2014 in the nest density estimation.

This breeding site is located in an Antarctic Specially Protected Area (ASPA; no. 171, for which a management plan was submitted by the Republic of Korea in 2009), where human activity such as ecotourism has been controlled. From the late 1980s to 2008, this area had occasionally been visited by a few scientists through the Korea Antarctic Research Program to study its fauna and geology (ASOC 2007, 2008). Thus, we cannot exclude the possibility that penguins had previously been exposed to humans. However, as far as we know, this area has not been visited by tourists compared with other places in King George Island. During the Antarctic summer (from early December until February) in 2012–2013 and 2013–2014, approximately 80–100 Korean researchers visited King Sejong station, which is 2 km away from the penguin breeding site, with permission from the Ministry of Foreign Affairs and Trade (Republic of Korea). Some of the researchers pass through the middle of the breeding site to get to their field site. There were 16–18 overwintering people annually at the station, but the ASPA area was not visited by these people because of the low accessibility from the station during the Antarctic winter.

Experimental tests with an approaching skua in 2012–2013 and 2013–2014

We visited the gentoo and chinstrap penguin breeding site and recorded their responses to an approaching stuffed skua (South polar skua, *Stercorarius maccormicki*). In total, 74 chinstrap penguins (50 in four colonies in 2013 and 24 in three colonies in 2014) and 107 gentoo penguins (79 in nine colonies in 2013 and 28 in three colonies in 2014) were used. The tests were conducted for 2 days each year (1 and 4 January 2013; 4 and 7 January 2014). During a single test, 5–13 individuals were approached by the stuffed skua. Each colony was only visited once to avoid repeated sampling from one individual. The sex of the individuals was not determined in this study.

To estimate the behavioral responses of the chinstrap and gentoo penguins to the approaching nest predators, we operated a stuffed skua on a radio control car (R1 1/10 Rock Buggy ARTR, Gmade Co., Seoul, Korea; a picture in Online Resource 1) at a slow approach speed of

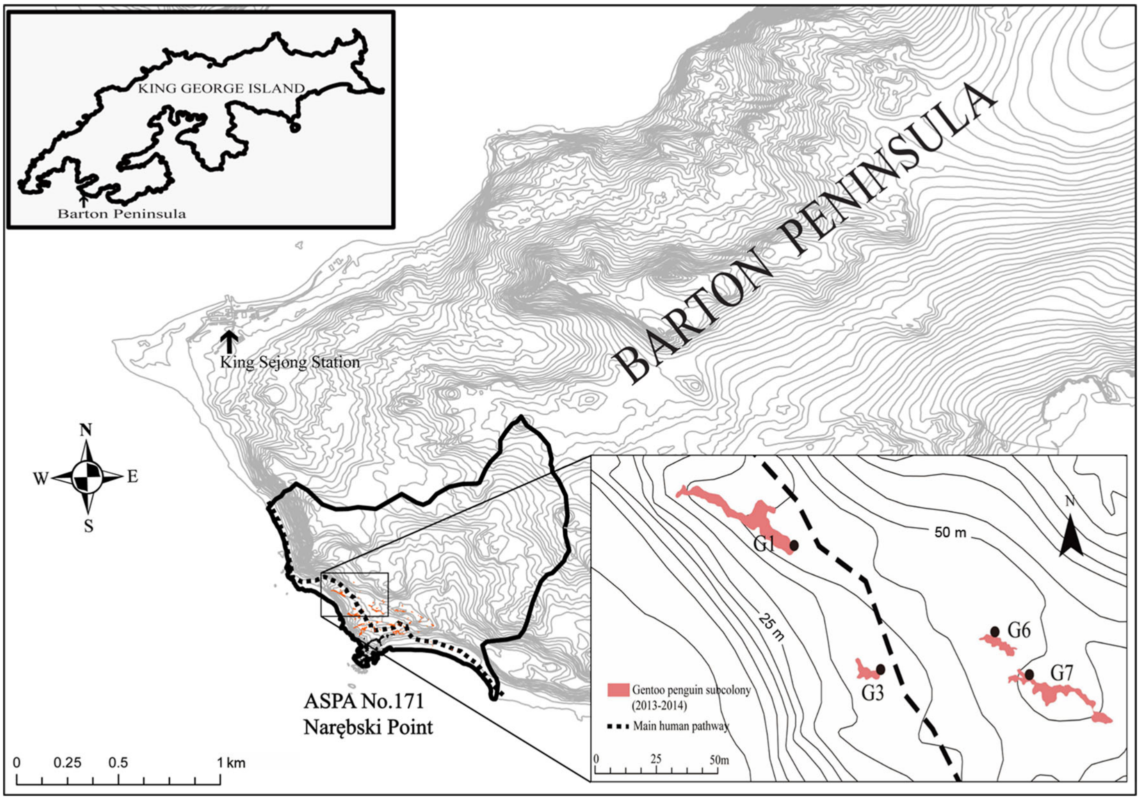

Fig. 1 Location of our study area at Narębski Point on King George Island. This breeding site is an Antarctic Specially Protected Area (ASPA, no. 171). The map of sub-colonies of chinstrap and gentoo penguins in the 2012–2013 and 2013–2014 breeding season. The edges of sub-colonies were measured with a GPS unit (Geo7x handheld, Trimble GeoExplorer®, Sunnyvale, CA, USA) before fledging. Four gentoo penguin colonies relative to the human pathway in 2014. Four gentoo penguin colonies were tested to determine the response of breeding penguins at their nest sites to an approaching human. Two gentoo penguin colonies were located near the human pathway, and the other two colonies were located farther away from the pathway. The distance of the closest colonies to the pathway was measured (*G1* 12.8 m, *G3* 8.5 m, *G6* 51.5 m, *G7* 48.5 m)

approximately 0.2 m/s. The car was operated with a remote radio at least 20–30 m away from the colonies. To reduce the possibility that penguins are affected by human presence, the human tried to hide himself and controlled the car. We mimicked the presence of a skua, which is known for hunting for penguin chicks on the ground by approaching the nest (Young 1994). We arbitrarily selected chick-guarding penguin adults that were sitting on their eggs or young hatchlings (0–7 days after hatching) in peripheral areas of the colonies. Because chinstrap and gentoo penguin breeding pairs alternate feeding trips by individual, either of the parents could have occupied the nest during testing. We did not conduct tests in the center of the colonies because penguins could be affected by the researcher walking into the colonies. To calculate the nest densities, we measured the nest distances between the nests in both penguin species. We randomly chose 652 chinstrap nests and 440 gentoo nests in the 2013–2014 season. Using a tape measure (in 0.1 cm unit), we measured the nest distances from a center of a nest to another center of a focal nest. To avoid the disturbance, the measurements were conducted after fledging. We recorded the behavioral responses of individual penguins when the stuffed skua entered the space between the nests, which is considered a defense zone (up to 0.5 m from the nest site), where active defensive behavior is displayed toward skuas on the ground (Young 1994). Based on the degree of responses, we categorized the penguin behavior to approaching intruders into three categories: "beak-bite," "head up" and "no response." "Beak-bite" is the physical action of biting the intruder with the beak and is regarded as a strong threat display. "Head up" is a defensive action whereby the head is moved upward while calling loudly, with no direct attack on the intruder. This behavior is assumed to be a weak threat, which is a less strong response. "No response" refers to when no apparent responses to the intruder were observed.

Experimental tests with an approaching human in 2013–2014

To examine the responses of penguins to human approaching, we measured the behavioral responses in a similar manner to that of the stuffed skua. We used different penguin nests for the stuffed skua experiment in 2012–2013 and 2013–2014 and for the human experiment in 2013–2014. Before the behavioral tests, we recorded the number of human subjects who passed across the penguin breeding site. For 16 days, from 6 December 2013 until 4 January 2014, 28 human individuals used the pathway between 09:00 and 10:30 h when departing from the station to the field sites and between 16:00 and 17:00 h when returning to the station. Researchers were supposed to record the time and the number of groups when departing and arriving at the station. During the period, an average of 9.12 (±3.90 SD) people per day was recorded. Moreover, we gave a GPS (GPS850, AscenKorea Inc., Seoul, Korea) to each researcher who went through this site, and, from the GPS data, human pathways were recorded. For safety, a solitary human was not allowed to move out in the field. Based on the records, 2–9 members (average 3.74, ±2.01 SD) made groups, and an average of 2.47 groups (±1.30 SD) per day used the pathway. After the human visits for 4 weeks, we had a human subject who had not previously visited the breeding site. The human slowly approached the nest site and move into the defense zone. The response of the penguins was recorded by a researcher located 30–40 m away from the nesting penguins. These tests were conducted on two clear days on 5 and 9 January 2014 between 09:00 and 11:00 h.

We compared the responses to the approach of a human between penguins that were previously exposed to humans and those that were less exposed to humans. We conducted the human approach experiments in different sub-colonies where we did the skua experiments. We arbitrarily selected 116 chinstrap penguins from six colonies and 72 gentoo penguins from four colonies. During a single test, 8–40 individuals were approached by a human who did not stare at the penguins. Each colony was visited one time, and the same individual was not evaluated multiple times. The human approached the nests with a similar speed as the stuffed skua did (approximately 0.2 m/s). Consequently, the human was in the defense zone (up to 0.5 m from the nest) for approximately 2–3 s during a single approach.

In addition to the three types of behavioral response observed with skuas (“beak-bite,” “head up” and “no response”), “desertion” behavior was included as a response to humans. “Desertion” is a form of escape behavior, whereby the parent bird leaves the nest and takes up a position approximately 1 or 2 m away, then returning to the nest when the intruder has passed by. During this behavior, no aggressive or threatening displays toward humans were observed, and we therefore concluded that this is not a threat display. Desertion behavior was not observed in the skua experiments in 2012–2013 and 2013–2014, so this behavior was not included in analyses of the skua experiments.

To determine the effect of the degree of previous human disturbance (i.e., distance from the human pathway) on the penguins’ response to an approaching human, we used gentoo sub-colonies that were different distances from the human pathway. A previous test on heart rate response in king penguins to human approaches revealed that the penguins did not react until the human was within 30 m, increased heart rates occurred at around 20–25 m, and behavioral responses occurred at 10 m (Viblanc et al. 2012). Preliminary data indicated that gentoo penguins in our population also showed behavioral responses toward approaching humans at approximately 10 m away (Jung, unpublished data), so we think there was a similar behavioral threshold in our penguins. Four colonies were arbitrarily selected for gentoo penguins: two colonies were near the human pathway (less than 10–15 m), and two were far from the pathway (over 40–50 m). Thus, we selected two sub-colonies that were close to one another and approximately 10 m from the human pathway (G1: 12.8 m, $n = 24$; G3: 8.5 m, $n = 36$) and two sub-colonies that were far from one another and approximately 50 m away from the human pathway (G6: 51.5 m, $n = 24$; G7: 48.5 m, $n = 39$) (see Fig. 1). In addition, G6 and G7 were located beyond an approximately 10-m-high hill (Fig. 1), which could interrupt the visions of incubating penguins. Therefore, we expected that the researchers were less visible in the far sub-colonies, compared to those in the close sub-colonies.

Statistics

We used t tests in SPSS, version 21.0, to compare the densities of breeding nests between 13 chinstrap and 17 gentoo sub-colonies in 2012–2013 and 13 chinstrap and 33 gentoo sub-colonies 2013–2014.

We used multinomial analyses (Lee et al. 2013) with generalized linear mixed models (GLMMs) using the lme4 package in R software, version 3.0.1 (Bates et al. 2015), to examine the behavioral differences of the two species (chinstrap and gentoo) to different intruder types (skua and human). Statistical significances of the fixed effects were acquired using the likelihood ratio test with log-likelihood of the two models (one model with fixed effects and the other without fixed effects) in the lme4 package. To compare the behavioral responses between the two species in 2013 and 2014 experiments toward the stuffed skua, behavioral response (“beak-bite,” “head up,” “desertion” or “no response”) was included as a dependent variable with multinomial distribution. Species (chinstrap and gentoo) and year (2013 and 2014) were included as fixed effects, and sub-colony identity was treated as a random effect in the model. The effect of year was initially tested, and then it was removed from the actual models because the year effect was not statistically significant in either species ($\chi^2 = 0.75$, $P = 0.39$ in chinstrap penguins and $\chi^2 = 0.01$, $P = 0.99$ in gentoo penguins). To compare the behavioral responses between the two different intruder types (skua and human) in 2014 experiment, behavioral response ("beak-bite," "head up" or "no response") was included as a dependent variable with multinomial distribution, and intruder type was a fixed effect. Sub-colony identity was included as a random effect.

To determine the effect of the degree of human disturbance (i.e., distance from the human pathway) on the penguins' response to an approaching human, we also used a GLMM with the lme4 package in R software. As a dependent variable, we included binary data for the presence (*Y*) or absence (*N*) of threat displays, such as "beak-bite" or "head up," with the binary distribution. As a fixed effect, we used the binary coded distance data ("near," which was less than 13 m, or "far," which was more than 48 m). We treated each colony as a random effect in the analysis.

Results

Densities of breeding nests of chinstrap and gentoo in 2012–2013 and 2013–2014

Our GPS data indicated that a 4705.7 m^2 area was occupied by 3329 breeding chinstrap nests (0.71 nests/m^2) in 13 sub-colonies in 2012–2013 and 4187.8 m^2 by 3148 nests (0.75 nests/m^2) in 13 sub-colonies in 2013–2014. In gentoo penguins, a 6111.0 m^2 area was used by 2455 nests (0.40 nests/m^2) in 17 sub-colonies in 2012–2013 and 3916.4 m^2 by 2327 nests (0.59 nests/m^2) in 33 sub-colonies in 2013–2014. The nest density of chinstrap penguins was marginally higher than that of gentoo in 2012–2013 (*t* test, $F = 0.17$, $t = -0.1.87$, $df = 28$, $P = 0.07$) and significantly higher than that of gentoo in 2013–2014 (*t* test, $F = 1.20$, $t = -2.66$, $df = 44$, $P = 0.01$).

The mean distance between the chinstrap nests was 65.3 cm (±18.0 SD) in 444 nests in 2012–2013 and 82.2 cm (±15.5 SD) in 652 nests in 2013–2014. In gentoo nests, the mean distance was 84.0 cm (±19.3 SD) in 1022 nests in 2012–2013 and 90.3 cm (±14.5 SD) in 440 nests in 2013–2014.

Responses to approaching nest intruders

The responses of chinstrap penguins did not differ between the skua and human (for pictures, see Fig. 2b to the skua and Fig. 2d to the human; multinomial GLMM, $\chi^2 = 0.81$, $P = 0.37$; Fig. 3a); they predominantly displayed strongly threatening behavior to both the approaching skua and human. However, gentoo penguins displayed different responses to different approaching intruders; they displayed weakly threatening behavior (mainly the "head up" display; Fig. 2a) to the skua, but displayed "head up," "no response" or "desertion" (Fig. 2c) to the approaching human (multinomial GLMM, $\chi^2 = 102.64$, $P < 0.001$; Fig. 3b). The responses of chinstrap and gentoo penguins to an approaching stuffed skua and human were different (multinomial GLMM, $\chi^2 = 18.25$, $P < 0.001$; Fig. 3a, b).

Responses of gentoo penguins to an approaching human based on pathway proximity

In gentoo penguins, the responses to the approaching human were different between individuals in the colonies near the pathway and colonies far from the pathway (binomial GLMM; $\chi^2 = 5.91$, $P = 0.02$; Fig. 4). Gentoo penguins in two colonies near the human pathway (G1 and G3) displayed no threatening behavior, but the individuals in the other two colonies far from the pathway (G6 and G7) responded aggressively to an approaching human by displaying "beak-bite" and "head up" behaviors.

Discussion

Our results indicated that chinstrap and gentoo penguins displayed different defensive behaviors to approaching intruders. Chinstrap penguins consistently displayed threatening behavior and strongly attacked the approaching intruders, both the skua and human, with their beaks. However, gentoo penguins displayed weaker responses to both the skua and human, compared with chinstrap penguins.

Although many factors are related to their aggressiveness, one possible explanation about the interspecific aggression differences is that chinstrap penguins invade the colonies of other species at mixed sites, which could indicate nest-site competition among different species (Trivelpiece and Volkman 1979; Trivelpiece et al. 1987; Macdonald et al. 2002). In our study populations, Chang (1999) described that gentoo adults arrived earlier (around September) than chinstrap adults (late October). Although chinstrap breeders came to the breeding sites later than gentoo, chinstrap occupied the nesting places near the seashore, and gentoo penguin colonies were located inland and far behind the chinstrap colonies (Fig. 1). We suspect that the aggressive characteristics of chinstrap penguins potentially enabled them to assume a higher nesting rank than the gentoo penguins by interspecific competition. However, it is still unclear whether the two species have conflicts in a limited space and compete for the nesting places.

Fig. 2 Examples of behavioral responses to an approaching stuffed skua and a human in gentoo (**a**, **c**) and chinstrap (**b**, **d**) penguins. Gentoo penguins displayed weakly threatening behavior to an approaching skua by moving their heads upward and calling loudly. We termed this "head up" (**a**). Chinstrap penguins displayed strongly threatening behavior with actual physical attacks, such as pecking the stuffed skua with their beaks. We termed this "beak-bite" (**b**). When a human approached, many gentoo penguins moved 1–2 m away from the nest sites and returned after the human had passed by. We termed this "desertion" behavior (**c**). In chinstrap penguins, the responses to humans were similar to the responses to the stuffed skua, with strongly threatening behavior, including "beak-bites" (**d**)

In addition to interspecific competition for breeding territory, intraspecific competition in chinstrap penguins can also explain anti-predatory aggression. Chinstrap penguins were more likely to compete for breeding territory, compared with gentoo penguins; in both breeding seasons, chinstrap penguins were in more densely populated areas (1.8 and 1.3 times as dense as those of gentoo penguins; 0.71 in 2012–2013 and 0.75 nests/m^2 in 2013–2014 in chinstrap penguins; 0.40 and 0.59 nests/m^2, respectively in gentoo penguins). Thus, we hypothesize that, if the chinstrap penguins in a densely populated breeding territory had more chances to interact with each other for nesting competition, this could induce more intraspecific competitions and high levels of hormonal secretion, such as testosterone, and consequently affect aggressiveness.

To explain the different levels of intensity of nest defense behaviors, body size difference between the two species can be also considered. Body mass of gentoo penguins is 20 % higher than that of chinstrap penguins at King George Islands (Volkman et al. 1980). Because body size differences may affect their vulnerability to the same predator (Montgomerie and Weatherhead 1988), chinstrap penguin, which is smaller than gentoo penguin, could have stronger aggression toward nest intruders as a defensive strategy.

Notably, many gentoo penguin adults displayed desertion behavior to the human subject rather than aggression. In our study area, humans were controlled so as not to disturb the penguins and have become "predation-free predators" (Beale and Monaghan 2004). When an unfamiliar species approaches a nest, perceiving the degree of danger they impose and responding accordingly are important. Discrimination between approaching intruders (i.e., dangerous or harmless) is beneficial by allowing the birds to expend energy defending against dangerous predators and ignoring harmless intruders (McLean and Rhodes 1991). Gentoo penguins may be able to adjust their anti-predatory behavior based on the type of intruder. Considering that gentoo penguin habitats are located in sub-Antarctic areas from 46° to 65°S (Bost and Jouventin 1990), which overlap with human habitats, they therefore are likely to be exposed to humans. Previous studies revealed that wild birds that adapt to human areas quickly learn to identify dangerous humans (Levey et al. 2009; Marzluff et al. 2010; Lee et al. 2011). Gentoo penguins likely did not develop the ability to discriminate between humans. Rather, we hypothesize that gentoo penguins may have the ability to distinguish between heterospecific intruders and react differently depending on the degree of danger.

Gentoo penguins that were near to the human pathway displayed a weaker threatening behavior, whereas individuals far from the pathway displayed strongly threatening behavior. Our results support the habituation hypothesis, because gentoo penguins became familiar with humans through repeated exposure. Holmes et al. (2006) showed that penguin colonies located close to research

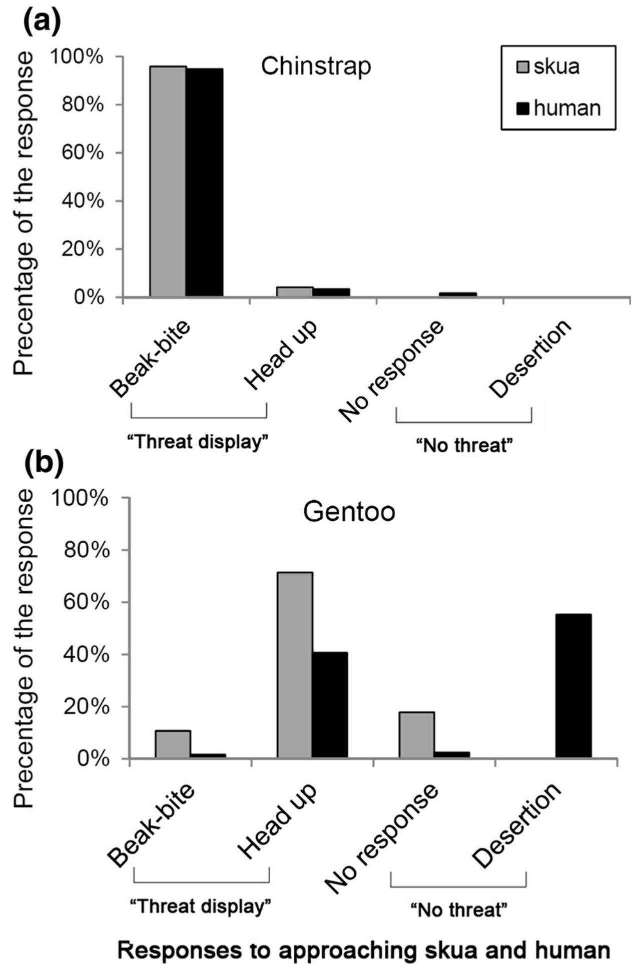

Fig. 3 Responses of chinstrap (**a**) and gentoo penguins (**b**) to approaching skua and human. All experiments were performed in 2012–2013 with skua ($n = 50$, chinstrap; $n = 79$, gentoo) and 2013–2014 with skua ($n = 24$, chinstrap; $n = 28$, gentoo) and with human ($n = 116$, chinstrap; $n = 72$, gentoo)

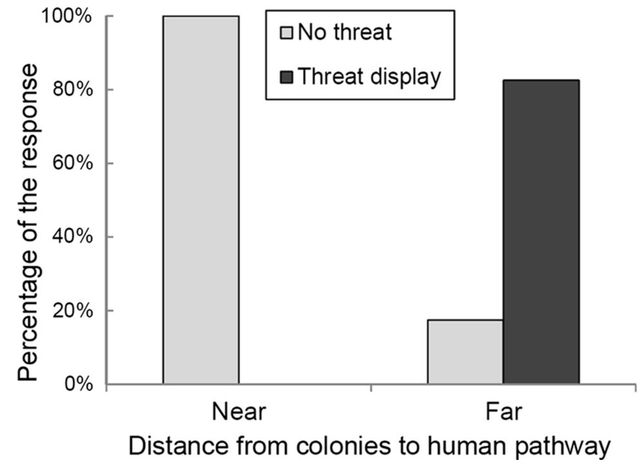

Fig. 4 Responses of gentoo penguins to an approaching human based on the distance from the colonies to the human pathway. Two colonies were near the pathway (*G1* 12.8 m and *G3* 8.5 m), and the other two colonies were far from the pathway (*G6* 51.5 m and *G7* 48.5 m)

stations that had previously been exposed to human stimuli weakly responded to human approach compared with penguins breeding far from the stations.

In our study, we focused on behaviors at species and sub-colony levels. Gentoo penguins displayed weaker responses to an approaching human when they were closer to the human pathway. Our findings indicate that, even within the same population, penguins may have different responses to an intruder depending on their degree of exposure to human disturbance. Although during the 30 days of exposure to 2.47 human groups (mean ± 1.30 SD) per day, which were composed of 2–9 members, passing along the pathway, with no intention to interrupt the colony, this experience enabled the penguins to respond differently.

In addition to the penguins' behavior in response to approaching humans, we also observed that brown skuas seemed to exploit humans to predate penguin chicks. In one instance, we watched that a brown skua pair took a gentoo penguin nestling very quickly while we were conducting the human approach experiments. We did not video-record the situation, but it appeared that the skuas were waiting for us to approach the nest sites and rapidly hunted the nestling on purpose. Although it needs more evidence, we think that skuas might take advantage of approaching humans. It will be very interesting to test whether the skuas recognize penguins' responses to humans and learn to predate penguin chicks while the chicks are uncovered because of human visitation. Overall, chinstrap penguins displayed strongly threatening behavior toward approaching intruders, but gentoo penguins displayed relatively weak threatening behavior and responded differently depending on the types of intruder. Although chinstrap and gentoo penguins breed at the same site under similar levels of predation pressure, the two species may have evolved different strategies against predation. From our results, we think it is possible that even researchers not directly involved in penguin surveys could affect their behavior because of their frequent visits to the area around the breeding ground. Therefore, we suggest that researchers in Antarctic regions take care to consider the presence of these birds when they are approaching breeding sites.

Although we used a radio control car with a stuffed skua to mimic skua approaching, it may still be distant from the real situation. In Adélie penguin and skua studies, there were two different attack approaches of skua to penguins: one is 'opportunistic attacks' in which skuas attempt to predate by a quick move mostly at visible eggs or chicks and the other is 'sustained attacks' in which skuas attempt to steal defended eggs and chicks from alert parents

(Young 1994). Here, we could mimic the slow approach from a distance so that it may be close to the sustained attack. Thus, it is hard to exclude the possibility that we only observed penguins' responses to the sustained attacks of skuas. Moreover, we did not mimic skuas' searching behaviors, such as hunting flights and observation of penguins, before the actual predation events. In future works, it would be interesting to mimic the two different approaches of skuas and investigate the penguin responses to opportunistic attacks and sustained attacks.

In our study, the sex of each individual was not determined, although the responses could potentially differ between sexes (Villanueva et al. 2012). Because other individual variables, such as age (Müllner et al. 2004), social hierarchy (Creel 2001) and personality (Ellenberg et al. 2009), may potentially affect behavioral responses, it will be interesting to investigate individual variation in response to intruders. Future studies with detailed experiments at the individual level could clarify the effects of nest intruders on the defensive behavior of penguins.

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References

Antarctic and Southern Ocean Coalition (ASOC) (2007) Implementing the Madrid Protocol: a case study of Fildes Peninsula, King George Island. XXX ATCM/IP136

Antarctic and Southern Ocean Coalition (ASOC) (2008) Some land-based facilities used to support/manage Antarctic tourism in King George Island. XXXI ATCM/IP41

Bates D, Maechler M, Bolker B, Walker S (2015) lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-8. http://CRAN.R-project.org/package=lme4

Beale CM, Monaghan P (2004) Human disturbance: people as predation-free predators? J Appl Ecol 41:335–343

Bost CA, Jouventin P (1990) Evolutionary ecology of the gentoo penguin (*Pygoscelis papua*). In: Davis L, Darby J (eds) Penguin biology. Academic Press, San Diego, pp 85–112

Burger J, Gochfeld M (2007) Responses of emperor penguins (*Aptenodytes forsteri*) to encounters with ecotourists while commuting to and from their breeding colony. Polar Biol 30:1303–1313

Byrkjedal I (1987) Antipredator behavior and breeding success in Greater Golden plover and Eurasian Dotterel. Condor 89:40–47

Caro TM (2005) Antipredator defenses in birds and mammals. Chicago University Press, Chicago

Chang SK (1999) The species of penguins and penguins occurring in the vicinity of King Sejong Station. Ocean Res 21:137–147 **written in Korean with English abstract**

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton

Cockburn A (2006) Prevalence of different modes of parental care in birds. Proc R Soc Lond B Biol Sci 273:1375–1383

Conroy JWH (1975) Recent increases in penguin populations in Antarctica and the Subantarctic. In: Stonehouse B (ed) The biology of penguins. Macmillan, London, pp 321–336

Crawford RD (1974) Chinstrap penguin at Cape Hallett. Notornis 21:264–265

Creel S (2001) Social dominance and stress hormones. Trends Ecol Evol 16:491–497

Domjan M (2003) The principles of learning and behavior, 5th edn. Wadsworth/Thomson Learning, Belmont

Ellenberg U, Mattern T, Seddon PJ, Luna-Jorquera G (2006) Physiological and reproductive consequences of human disturbance in Humboldt penguins: the need for species-specific visitor management. Biol Conserv 133:95–106

Ellenberg U, Setiawan AN, Cree A, Houston DM, Seddon PJ (2007) Elevated hormonal stress response and reduced reproductive output in yellow-eyed penguins exposed to unregulated tourism. Gen Comp Endocr 152:54–63

Ellenberg U, Mattern T, Seddon PJ (2009) Habituation potential of yellow-eyed penguins depends on sex, character and previous experience with humans. Anim Behav 77:289–296

Ellenberg U, Mattern T, Houston DM, Davis LD, Seddon PJ (2012) Previous experiences with humans affect responses of Snares penguins to experimental disturbance. J Ornithol 153:621–631

Festa-Bianchet M (2003) Exploitative wildlife management as a selective pressure for the life history evolution of large mammals. In: Festa-Bianchet M, Apollonio M (eds) Animal behaviour and wildlife conservation. Island Press, Washington, pp 191–207

Fowler G (1999) Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. Biol Conserv 90:143–149

Frid A, Dill LM (2002) Human caused disturbance stimuli as a form of predation risk. Conserv Ecol 6:11

Gochfeld M (1984) Antipredator behavior: aggressive and distraction displays of shorebirds. In: Burger J, Olla BL (eds) Shorebird breeding biology and populations. Plenum Press, New York, pp 289–377

Hockey PAR, Hallinan J (1981) Effect of human disturbance on the breeding behaviour of Jackass penguins *Spheniscus demersus*. S Afr J Wildl Res 11:59–62

Holmes N (2007) Comparing king, gentoo, and royal penguin responses to pedestrian visitation. J Wildl Manag 71:2575–2582

Holmes ND, Giese M, Achurch H, Robinson S, Kriwoken LK (2006) Behavior and breeding success of gentoo penguins *Pygoscelis papua* in areas of low and high human activity. Polar Biol 29:399–412

Huntingford FA (1976) The relationship between anti-predator behavior and aggression among conspecifics in three-spined stickleback. Anim Behav 24:245–260

Jouventin P (1982) Visual and vocal signals in penguins, their evolution and adaptive characters. Verlag Paul Parey, Berlin

Kazama K, Niizuma Y, Sakamoto QK, Watanuki Y (2011) Factors affecting individual variation in nest defense intensity in colonially breeding Black-tailed Gulls. Can J Zool 89:938–944

Kazama K, Niizuma Y, Watanuki Y (2012) Consistent individual variations in aggressiveness and a behavioral syndrome across breeding contexts in different environments in the Black-tailed Gull. J Ethol 30:279–288

Lee WY, Lee SI, Choe JC, Jablonski PG (2011) Wild birds recognize individual humans: experiments on magpies, *Pica pica*. Anim Cogn 14:817–825

Lee SI, Hwang S, Joe YE, Cha HK, Joo GH, Lee HJ, Kim JW, Jablonski PG (2013) Direct look from a predator shortens the risk-assessment time by prey. PLoS ONE 8:e64977

Levey DJ, Londoño GA, Ungvari-Martin J, Hiersoux MR, Jankowski JE, Poulsen JR, Stracey CM, Robinson SK (2009) Urban mockingbirds quickly learn to identify individual humans. Proc Natl Acad Sci USA 106:8959–8962

Macdonald JA, Barton KJ, Metcalf P (2002) Chinstrap penguins (*Pygoscelis antarctica*) nesting on Sabrina Islet, Balleny Island, Antarctica. Polar Biol 25:442–447

Martin TE (1993) Nest predation among vegetation layers and habitat types: revising the dogmas. Am Nat 141:897–913

Marzluff JM, Walls J, Cornell HN, Withey JC, Craig DP (2010) Lasting recognition of threatening people by wild American crows. Anim Behav 79:699–707

McLean IG, Rhodes G (1991) Enemy recognition and response in birds. In: Power DM (ed) Current Ornithology, vol 8. Plenum, New York, pp 173–211

Montgomerie RD, Weatherhead PJ (1988) Risks and rewards of nest defence by parent birds. Q Rev Biol 63:167–187

Müllner A, Linsenmair KE, Wikelski W (2004) Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). Biol Conserv 118:549–558

Nilsson (1984) The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand 15:167–175

Redondo T (1989) Avian nest defence: theoretical models and evidence. Behaviour 111:161–195

Reynolds JD, Goodwin NB, Freckleton RP (2002) Evolutionary transitions in parental care and live bearing in vertebrates. Philos Trans R Soc Lond B 357:269–281

Suzuki TN (2011) Parental alarm calls warn nestlings about different predatory threats. Curr Biol 21:R15–R16

Suzuki TN (2012) Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. Anim Behav 84:53–57

Suzuki TN, Ueda K (2013) Mobbing calls of Japanese tits signal predator type: field observations of natural predator encounters. Wilson J Ornithol 125:412–415

Tallamy DW (2000) Sexual selection and the evolution of exclusive paternal care in arthropods. Anim Behav 60:559–567

Trivelpiece WZ, Trivelpiece SG (1990) Courtship period of Adélie, Gentoo, and Chinstrap Penguins. In: Davis LS, Darby JT (eds) Penguin biology. Academic Press, San Diego, pp 113–127

Trivelpiece W, Volkman NJ (1979) Nest site competition between Adélie and chinstrap penguins: an ecological interpretation. Auk 96:675–681

Trivelpiece WZ, Trivelpiece SG, Volkman NJ (1987) Ecological segregation of Adélie, gentoo, and chinstrap penguins at King George Island, Antarctica. Ecology 68:351–361

Viblanc VA, Smith AD, Gineste B, Groscolas R (2012) Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors. BMC Ecol 12:10

Villanueva C, Walker BG, 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. J Ornithol 153:219–228

Viñuela J, Amat JA, Ferrer M (1995) Nest defence of nesting chinstrap penguins (*Pygoscelis antarctica*) against intruders. Ethology 99:323–331

Volkman NJ, Presler P, Trivelpiece WZ (1980) Diets of Pygoscelid penguins at King George Island, Antarctica. Condor 82:373–378

Walker BG, Boersma PD, Wingfield JC (2006) Habituation of adult Magellanic penguins to human visitation as expressed through behavior and corticosterone secretion. Conserv Biol 20:146–154

Woehler EJ, Penney RL, Creet SM, Burton HR (1994) Impacts of human visitors on breeding success and long-term population trends in Adélie penguins at Casey, Antarctica. Polar Biol 14:269–274

Yorio P, Boersma PD (1992) The effects of human disturbance on Magellanic Penguin *Spheniscus magellanicus* behaviour and breeding success. Bird Conserv Int 2:161–173

Young EC (1994) Skua and penguin: predator and prey. Cambridge University Press, Cambridge