PNIE PROCEEDINGS OF NATIONAL INSTITUTE OF ECOLOGY

Review Article

Proceedings of NIE 2020;1(1):1-8
https://doi.org/10.22920/PNIE.2020.1.1.1
pISSN 2733-7243, eISSN 2734-1372

Individual Human Recognition of Wild Animals: A Review and a Case Study in the Arctic Environment

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ABSTRACT

Recent studies revealed that many animals identify individual humans. In this account, we review previous literatures on individual human recognition by wild or domestic animals and discuss the three hypotheses: “high cognitive abilities” hypothesis, “close human contact” and “pre-exposure to stimuli” hypothesis. The three hypotheses are not mutually exclusive. Close human contact hypothesis is an ultimate explanation for adaptive benefits whereas high cognitive abilities and pre-exposure to stimuli hypothesis are proximate explanations for mechanisms to perform such discriminatory behaviour. We report a case study of two bird species in a human-free habitat. Long-tailed skuas, which are known for having high cognitive abilities, exhibited the human discriminatory abilities whereas ruddy turnstones did not display such abilities toward approaching humans. This suggests that highly intelligent species may have this type of discriminatory ability so that they could learn to identify individual humans quickly by pre-exposure to stimuli, even in a human-free habitat. Here, we discuss that human recognition is more common in species with rapid learning ability and it could develop for a short period of time between an intelligent species and human.

Keywords: Close human contact hypothesis, High cognitive abilities hypothesis, Individual human recognition, Long-tailed skua, Pre-exposure to stimuli hypothesis, Ruddy turnstone

Individual Human Recognition by Animals

Many animal species have been reported to discriminate individual humans. In domestic animals, it was known that animals distinguished the specific humans who handled or feed them, based on experiences. It has been reported in dogs (*Canis familiaris*), sheep (*Ovis aries*), cows (*Bos taurus*), pigs (*Sus scrofa domesticus*) and horses (*Equus ferus caballus*) (Adachi *et al*., 2007; Huber *et al*., 2013; Knolle *et al*., 2017; Koba & Tanida, 2001; Munksgaard *et al*., 1999; Peirce *et al*., 2001; Rybarczyk *et al*., 2001; Sankey *et al*., 2011; Stone 2010; Tanida *et al*., 1995). Main cues were visual or vocal signals by feeders.

The discriminatory ability has mainly been observed in domestic mammals but recent studies have revealed that wild mammals are also able to distinguish humans at the individual level (Bates *et al*., 2007; Leroux *et al*., 2018; McComb *et al*., 2014; Sliwa *et al*., 2011; Taylor *et al*., 1998). In African elephant (*Loxodonta africana*) studies, free-living wild elephants recognized vocal sounds of Maasai men who can be threats (McComb *et al*., 2014).

Received October 15, 2020; **Accepted** October 20, 2020

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This implies that the discriminatory abilities are highly adaptive to increase survival against human predators. It may have additional costs to have sophisticated mechanisms to defend one species, but it may have greater benefits from distinguishing high risks of dangerous human individuals. Care in captivity provides opportunities to test the animals if they distinguish care givers and it was shown that the captive cheetahs (*Acinonyx jubatus*), monkeys (*Macaca mulatta*) and seals (*Phoca vitulina* and *Halichoerus grypus*) recognize the familiar human faces or voices (Leroux *et al*., 2018; Sliwa *et al*., 2011; Taylor *et al*., 1998). The previous studies were listed in Table 1.

In birds, it has been widely tested on wild populations (Table 2). Many reports have been collected mainly in corvids (crows, magpies, and jackdaws) (Bogale *et al*., 2011; Cornell *et al*., 2012; Davidson *et al*., 2015; Lee *et al*., 2011; Marzluff *et al*., 2010; Wascher *et al*., 2012). Corvids are among the highly intelligent taxa in birds. In old Western stories, crows were suggested to have high levels of cognitive abilities including a famous story of the Aesop fable, 'The Crow and the Pitcher' (reviewed in Taylor, 2014). In a Korean proverb, it says that 'When a magpie calls, a welcome visitor comes'. Magpies have been regarded as a good sign for bringing us luck. This story is in accordance with the recent findings on human recognition of mapgies (*Pica pica*) (Lee *et al*., 2010). If magpies selectively scolded an unfamiliar human in their territories, it could imply that the visitors came to the town unless it would not necessarily mean a welcome visitor.

Corvids (Corvidae) and parrots (Psittacinae) were reported to have larger forebrain than most other taxa in birds and it was assumed to be responsible for the high cognitive behaviours (Emery, 2006). Brain imaging revealed that crows had activated brain regions to allow them to distinguish and recognize human visual stimuli and it is associated with brain activity for fear and escape behaviour (Marzluff *et al*., 2012). It appears that crows depend on visual systems to recognize humans and it is combined with emotional processes. The neural basis information allows us to understand how the bird brains work to recognize individual humans.

Human recognition by wild animals was first discovered in the Northern mockingbirds (Levey *et al*., 2009). House sparrows (*Passer domesticus*), pigeons (*Columba livia*), and robins (*Petroica longipes*) also recognize humans who threaten them by capturing or feeding them (Barnett *et al*., 2013; Stephan *et al*., 2012; Vincze *et al*., 2015). Recently, it was discovered that Antarctic skuas (*Stercorarius antarcticus lonnbergi*) also exhibited such discriminatory behaviour after a short period of exposure to nest intruders (Lee *et al*., 2016). While other studies focused on the animals near human habitat, this study reported the test result from a bird in human-free habitat. It demonstrated that the Antarctic birds could recognize humans despite a very short history of human settlement. The authors suggested that the high cognitive abilities of skuas enabled them to learn how to distinguish humans under the limited exposure condition. On the other hand, sheathbills (*Chionis albus*) and Antarctic terns (*Sterna vittata*) did not show such abilities even if they were also similarly exposed to humans (Lee *et al*., 2016). Discriminatory abilities do not appear to be acquired in all species under the

Table 1. Previous studies on human recognition in mammals

Species	Cue	Stimulus	Wild or domestic	Reference
African elephant	Odour and garment colour	Spearing	Wild	Bates *et al*., 2007
African elephant	Voice	Potential threat	Wild	McComb *et al*., 2014
Cheetah	Voice	Familiar person	Wild (in captivity)	Leroux *et al*., 2018
Rhesus monkey	Voice and face	Care	Wild (in captivity)	Sliwa *et al*., 2011
Harbor and gray seals	Face or body posture?	Familiar person (feeder)	Wild (in captivity)	Taylor *et al*., 1998
Dog	Voice	Owner/stranger	Domestic	Adachi *et al*., 2007
Dog	Face	Food reward	Domestic	Huber *et al*., 2013
Sheep	Face	Food reward	Domestic	Peirce *et al*., 2001
Sheep	Face (image)	Food reward	Domestic	Knolle *et al*., 2017
Holstein cow	Height and face	Food reward	Domestic	Rybarczyk *et al*., 2001
Pig	Face or body posture?	Handling	Domestic	Tanida *et al*., 1995
Miniature pig	Face and body size	Food reward	Domestic	Koba & Tanida, 2001
Dairy cow	Cloth colour	Handling	Domestic	Munksgaard *et al*., 1999
Horse	Voice	Food reward	Domestic	Sankey *et al*., 2011
Horse	Face	Food reward	Domestic	Stone, 2009

Table 2. Previous studies on human recognition in birds

Species	Cue	Stimulus	Wild or domestic	Reference
Northern mockingbird	Face or body posture?	Nest intruder	Wild	Levey *et al*., 2009
American crow	Facial mask	Trapping	Wild	Marzluff *et al*., 2010
Black-billed magpie	Face or body posture?	Nest intruder	Wild	Lee *et al*., 2011
North Island Robin	Face or body posture?	Familiar person	Wild	Barnett *et al*., 2013
Jackdaw	Facial mask	Threaten	Wild	Davidson *et al*., 2015
House sparrow	Facial mask	Capturing	Wild	Vincze *et al*., 2015
Antarctic skua	Face or body posture?	Nest intruder	Wild	Lee *et al*., 2016
American crow	Facial mask	Trapping	Wild (in captivity)	Cornell *et al*., 2012
Jungle crow	Face	Food reward	Wild (in captivity)	Bogale *et al*., 2011
Carrion crow	Voice	Familiar person	Wild (in captivity)	Wascher *et al*., 2012
Pigeon	Face	Feed/capture	Wild (in captivity)	Stephan *et al*., 2012

Table 3. Previous studies on human recognition in insects, molluscs and fish

Species	Cue	Stimulus	Wild or domestic	Reference
Honeybee	Face (image)	Feed	Wild (in captivity)	Dyer *et al*., 2005
Giant Pacific octopus	Visual (not specified)	Feed/irritate	Wild (in captivity)	Anderson *et al*., 2010
Archerfish	Face (image)	Feed	Wild (in captivity)	Newport *et al*., 2016

similar levels of human exposures.

Then, how animals use discriminatory cues? Using visual signals on human faces (Davidson *et al*., 2015; Dyer *et al*., 2005; Marzluff *et al*., 2010) or auditory sounds (McComb *et al*., 2014; Wascher *et al*., 2012) or odours (Bates *et al*., 2007), animals selectively respond to the specific humans. In many studies, visual signals appeared to be a major factor for discrimination. African elephants and jungle crows were sensitive to colours (Bates *et al*., 2007; Bogale *et al*., 2011). In some experiments, researchers also used facial masks and posed threats (Cornell *et al*., 2012; Davidson *et al*., 2015; Marzluff *et al*., 2010; Vincze *et al*., 2015) and found that the animals use the masks as a signal to distinguish individuals. Voices are also important for recognition. Cheetahs (Leroux *et al*., 2018) and rhesus monkeys (Sliwa *et al*., 2011) were reported to use vocal signals for discrimination. While it is not expected to be common in birds due to their small olfactory bulbs, wild mammals such as elephants were discovered to use odours (Bates *et al*., 2007).

The human recognition abilities are not dominated by mammals and birds. It has also been reported in insects, molluscs and fish (Table 3). Bees (*Apis mellifera*) and fish (*Toxotes chatareus*) also showed the abilities to distinguish human face images (Dyer *et al*., 2005; Newport *et al*., 2016). Octopuses (*Enteroctopus dofleini*) showed selective responses to humans who conducted feeding or irritating behaviour (Anderson *et al*., 2010). The findings suggest that it is not necessary for animals to have complex brain system in order to distinguish individual humans. With no evolutionary backgrounds for adaptive functions, animals may exhibit the abilities using signals from human faces. If the animals can perform sophisticated visual discrimination, it may be possible to conduct accurate facial discrimination tasks by processing the visual interpretations.

Three Hypotheses to Explain the Human Discriminatory Abilities

Three hypotheses (”close human contact”, “high cognitive abilities”, and “pre-exposure to stimuli” hypothesis) have been suggested to explain the discriminatory ability of individual humans in wild animals. The three hypotheses are not mutually exclusive. The close human contact hypothesis is an ultimate explanation for evolutionary adaption whereas the high cognitive abilities and pre-exposure to stimuli hypothesis are proximate explanations for mechanisms to perform such discriminatory behaviour.

Close human contact hypothesis

It has been hypothesized that urban animals may benefit from recognizing individual humans who can harm them (Sol *et al*., 2013). According to this hypothesis, some animal species could adapt better to human habitats with the discriminatory ability acquired throughout their evolutionary history. In this context, such a discriminatory ability is an adaptive strategy to avoid dangerous humans and/or choose beneficial humans. Urban species exhibited the abilities to distinguish and remember human individuals (mockingbirds on campus in Levey *et al*., 2009, American crows on campus in Marzluff *et al*., 2010, magpies on campus in Lee *et al*., 2011, captive pigeons in Stephan *et al*., 2012). Previous studies on individual human recognition of wild animals have mostly been conducted on species that evolved near human habitats, such as crows and magpies (Lee *et al*., 2011; Marzluff *et al*., 2010). Under the urban environments, animals quickly learn to recognize individual predators (Marzluff 2017).

High cognitive abilities hypothesis

The close human contact hypothesis does not explain the behaviour of species that live in habitats with no or very little human presence. A recent study in the Antarctica showed that brown skuas distinguished individual humans who had visited their nest sites (Lee *et al*., 2016). The authors hypothesized that the high cognitive abilities of Antarctic skuas enabled them to perform such behaviour even in a human-free habitat with little human contact (Lee *et al*., 2011, 2016). Skuas often steal food from other birds and mammals (Booth & Reynolds, 1984; Furness, 1978; Spear *et al*., 1999). Such “kleptoparasitism” (Barnard 1984; Brockmann & Barnard 1979) reflects high cognitive abilities with a relatively large residual brain size (Morand-Ferron *et al*., 2007). The high cognitive level of skuas is likely related to the ability to discriminate individual humans within a short period of interaction.

Pre-exposure to stimuli hypothesis

If the same humans are pre-exposed to animals, the animals may acquire abilities to distinguish the repeated human stimuli (Davis, 2002; Lee *et al*., 2011). It does not necessarily require high cognitive abilities to discriminate individual humans. This hypothesis predicts that various animals are able to show the abilities if the stimuli are given repeatedly. The highly cognitive animals are expected to have accelerated learning skills aided by the pre-exposure.

A Case Study in a Human-Free Habitat

As a case study, we examined the discriminatory abilities of individual humans by two Arctic bird species in North Greenland: the long-tailed skua (*Stercorarius longicaudus*) and ruddy turnstone (*Arenaria interpres*). One human researcher walked to the nest and posed a threat to the bird parents and hatchlings for four consecutive days and another human approached the nest in a similar manner on the fifth day. We assumed that if the birds were able to distinguish individual humans, then the flush distances would increase in response to repeated approaches by the same human for four consecutive days but decrease in response to the approach on the fifth day by a new human and their response should be similar to that to the previous human on the first day. Based on the close human contact hypothesis, we expected that none of the two species have such discriminatory abilities in the human-free habitat. In accordance with the high cognitive abilities hypothesis, however, we predicted that long-tailed skuas would exhibit a higher level of discriminatory behaviour as another skua species (e.g. brown skuas) did in the Antarctica and that turnstones would not distinguish humans if their cognitive levels were not high enough to allow them to have such a ability. According to the pre-exposure hypothesis, we predicted that both species would acquire the abilities with the repeated stimuli.

Study site and behavioural responses to nest intruders

From 25 July to 13 August in 2016 and from 30 June to 21 July in 2017, we visited the east shore of the J. P. Koch Fjord in North Greenland, a northern Arctic area (latitude 82°47.6′N, longitude 42°13.7′W; see Lee 2018). The study site was located in a human-free habitat where no human residents had been recorded to dates. We determined the breeding status of the bird species by surveying daily within a study area of approximately 5 km^2 (Lee, 2018). We observed 8 pairs of territorial long-tailed skuas in 2016 (no breeding attempts were observed in 2017). Our study periods were late for checking the breeding season of ruddy turnstones in 2016. So we monitored 7 ruddy turnstone nests incubating eggs in 2017.

To examine the behavioural responses of birds to individual humans, we followed similar procedures as those described in Levey *et al*. (2009). Over four consecutive days, one researcher visited the same site while parents were present and checked the breeding status of the birds. The survey lasted for 5-10 min per visit. When approached by humans, parental birds flushed and often exhibited aggressive defensive behaviours with flushing (Fig. 1; examples of responses of long-tailed skuas to approaching humans). In long-tailed skuas, both parents were sitting on the same ground during the tests. Ruddy turnstones were being incubated by females and males came soon to the nest sites when females started to respond to approaching humans.

To record when the birds responded to approaching humans, we measured the flush distances of the parents. When the researcher first visited a site, small stones were placed to roughly measure the distances every 5 m (from 0 to 40 m). The researcher used the same pathway when the bird parents started to flush, holding a red tent pack with 20 cm in length and placing the pack when the birds responded. In the approaching trials, two humans (WYL and MJ) acted as nest intruders and seven (WYL, MJ, AN,

Fig. 1. Flush responses of long-tailed skuas (in black circles) to approaching humans.

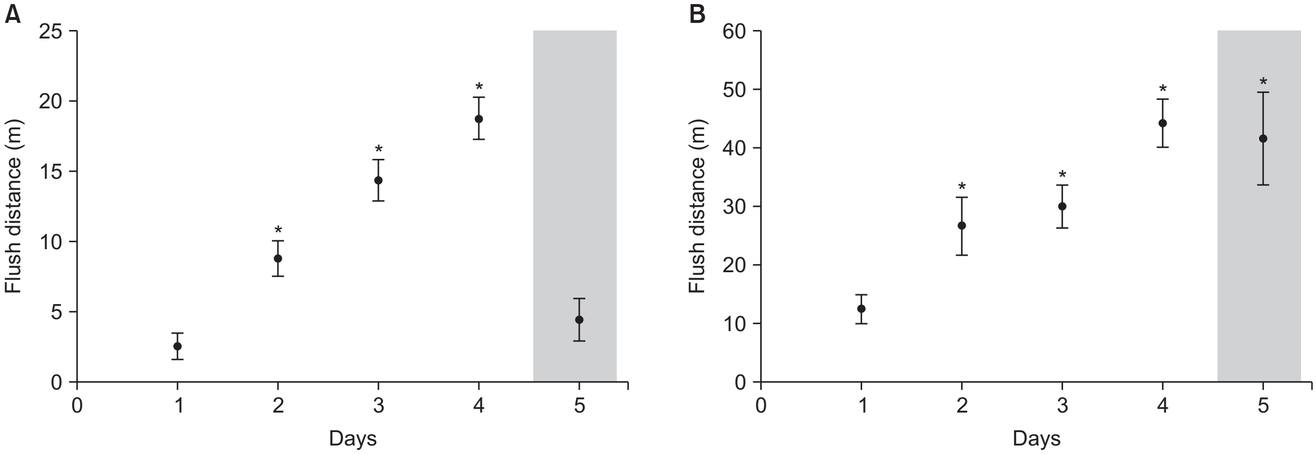

Fig. 2. Flush distances (m) of the two bird species to humans approaching their nest sites: (A) long-tailed skuas; (B) ruddy turnstones.

TYP, JW, JHK, and JV) participated as control humans on the fifth day. The human participants did not wear the same clothes during the approaches, and they were of varying age, hair style and colour.

We evaluated the responses of birds against nest intruders for five consecutive days. For each species, we analysed the flush distances to approaching humans by using linear mixed models with lme function in nmle package with maximum likelihood (ML) coefficient estimation. Statistical analyses were conducted in R version 3.3.2. The residuals of the flush distance data for the long-tailed skuas did not follow the null distribution in the Shapiro-Wilkinson test for normality. Thus, we used the square-root of the data to satisfy the assumption of the null distribution and used the transformed data in the linear mixed model. For ruddy turnstones, the residuals met the assumption of the null distribution. The flush distance was included as a response variable, and the bird individual identity was treated as a random variable.

Behavioural responses: Long-tailed skuas vs. Ruddy turnstones

Long-tailed skuas significantly increased their flush distances as the same intruder repeated the nest visits (t=3.8 at day 2, 5.6 at day 3, and 6.8 at day 4, respectively; all P<0.01); however, with a new intruder at day 5, the flush distance decreased to a level similar to that of the previous intruder at day 1 (t_{28}=1.1; P=0.28) (Fig. 2A).

Turnstones increased their flush distances to the same approaching human from the second day onwards (t=2.5 at day 2, t=3.1 at day 3 and 5.5 at day 4, respectively; all P<0.01) and maintained the increased distance with a new intruder at day 5 (t_{24}=5.1; P<0. 01) (Fig. 2B).

Discussion on the case study

Our case study in the Arctic showed that two species increased their flush distances very rapidly with repeated human visits. The increased responses were regarded as a result of learning from repeated stimuli (human visit). Only the long-tailed skua distinguished individual humans, whereas the turnstone and sanderling did not exhibit such behaviour. Long-tailed skuas increased their aggression towards the same human that acted as a nest intruder over repeated visits and decreased their aggression towards the control human with no prior visit. This result indicates that skuas are able to discriminate humans and show selective responses toward approaching humans.

How do long-tailed skuas recognize humans? In Arctic environments with strong winds, where it may snow in July and August, we do not think that olfactory or auditory signals played an important role. As revealed for crows (see Marzluff *et al*., 2010) and magpies (Lee *et al*., 2011), visual signals, such as human faces and body postures, might provide clues to the birds. Our study area was a wide open habitat, but the breeding density (1.6 pairs per km^2) was similar with the one at Zackenberg in East Greenland, which turned out to be among the highest (1.4-1.6 pairs per km^2) in recent surveys (Meltofe & Høye, 2007). Although we did not record other neighbouring skuas during the human approach trials, breeding birds could be very sensitive to neighbours at close distances. Thus, we do not exclude the possibility of skuas learning from the reactions of neighbouring birds (Cornell *et al*., 2012). It was quite surprising that long-tailed skuas increased their flush distances more quickly compared with urban mockingbirds, which responded from the third visit onwards (Levey *et al*., 2009). Antarctic brown skuas responded from the fourth visit (Lee *et al*., 2016). We think that the neighbouring skuas' reactions could accelerate their learning to distinguish humans.

Our results in a case study are in accordance with the predictions of the high cognitive abilities hypothesis that long-tailed skuas, which have high cognitive abilities, would selectively respond to individual humans who could harm them among others whereas the other two bird species would not show selective responses. Comparative studies revealed that avian intelligence varies among taxa (Emery, 2006; Emery and Clayton, 2004). In this study, we did not measure the cognitive levels of the two bird species. Considering that long-tailed skuas engage in kleptoparasitism (Paterson, 1986), however, a behaviour that is correlated with high cognition (Morand-Ferron *et al*., 2007), we expected that they would have higher cognitive levels than turnstones and sanderlings. Similar to the result of a previous study on brown skuas in the Antarctica (Lee *et al*., 2016), Arctic skuas also had the ability to distinguish individual humans. When Lee *et al*., (2016) found that brown skuas recognized individual humans in the Antarctica, the authors suspected if other Antarctic birds also had discriminatory abilities in the same study area. The results of this case study generally support the high cognitive abilities hypothesis.

It is surprising, though, that wild birds subject to rare human visits throughout a long evolutionary history have discriminatory abilities like other urban birds. Since breeding birds at our study site are unlikely to have close relationships with humans, the close human contact hypothesis does not explain our results. However, we do not exclude the possibility that the birds could have been exposed to humans at wintering places. Tracking studies have revealed that long-tailed skuas in North-East Greenland migrate to and stay along the coasts of South Africa (Gilg *et al*., 2013). Although the skuas may not encounter humans frequently, we can not entirely dismiss the possibility of close human contact.

We report in this case study that long-tailed skuas in a human-free habitat are able to distinguish individual humans while turnstones and sanderlings did not. This is the first study to simultaneously test the discriminatory abilities of different bird species in the same breeding area. We hypothesize that the high cognitive abilities of long-tailed skuas enabled them to recognize individual humans within a short period.

General Discussion and Suggestions for Future Studies

Here we reviewed previous literatures on individual human recognition by wild or domestic animals. Domestic animals have shared evolutionary histories with humans and developed appropriate social skills in the inter-specific interaction (Adachi *et al*., 2007; Huber *et al*., 2013). Familiar human faces or voices were accurately distinguished in the tests. Wild animals were also reported to recognize humans. There were mostly anecdotes and rarely developed to scientific researches. Since Levey *et al*. (2009), however, a number of studies have been reported on wild animal populations in urban and remote polar regions.

To explain the individual human recognition behaviour by animals, three hypotheses were discussed: high cognitive abilities, close human contact and pre-exposure to stimuli hypothesis. The high cognitive abilities hypothesis predicts that species with high intelligence have acquired discriminatory abilities. Animals that have evolved in human-free habitats are also able to discriminate individual humans, as long as they have high enough intelligence. The close human contact hypothesis predicts that animals having evolved near humans follow beneficial humans or avoid dangerous humans. Selective responses to beneficial or dangerous humans could incur greater survival advantage. When a predatory species has highly varied behaviours among individuals, prey animals can benefit from identifying the degrees of possible danger.

Since the three hypotheses are complementary and mutually non-exclusive, researchers need to conduct comparative studies with multiple species or populations of the same species. For instance, it requires a comparison between urban and rural areas to examine the human influences on animals' discriminatory abilities (Davidson *et al*., 2016; Vincze *et al*., 2015). Vincze *et al*., (2015) conducted experiments in multiple populations along the varied human population densities and compared the responses of house sparrows (*Passer domesticus*). This approach enabled them to examine the effects of urbanization on recognition behaviour and test the close human contact hypothesis. Our case study provided an example of testing the high cognitive abilities hypothesis with comparisons among multiple species (different levels of cognition) in the same habitat.

In the future, various taxa should be tested to compare the cognitive abilities. It will also be worth testing the discriminatory mechanisms in various environments. We still do not know much about mechanisms how animals discriminate individual conspecifics. Although it should be dependent on the senses in each species, multiple cues, such as visual and olfactory signals, can be used. In an African elephant study, the animals distinguished the smells of clothes of dangerous humans as well as the colours in separate tests (Bates *et al*., 2007). It appeared that colours and odours worked independently for elephants, but it is still unclear how animals integrate multiple signals into a cue. Birds seem to distinguish humans based on the appearance, i.e., visual signals (mockingbirds in Levey *et al*., 2009 and magpies in Lee *et al*., 2011). Carefully designed experimental approaches would be needed in the further studies.

We expect that the human recognition behaviour could be a specific example of the general discrimination for hetero-specific individuals. It may be more widespread and common behaviours among many animals that have high cognitive abilities. As it was suggested in the American crow studies (Cornell *et al*., 2012; Marzluff *et al*., 2010), it will be interesting to test how the learned knowledge lasts and the information spreads to others in social animals.

Acknowledgements

We specially thank to Mr. Man Jung, Arne Nielsen, Tae-Yoon Park, Jusun Woo, and Jakob Vinther for their help in the field and Dr. Changku Kang for statistical advice. We also thank to Mr. Ik-Ho Kim for the literature survey. This research was supported by Korea Polar Research Institute (PE17160, PE20220). Data collection adhered to the ASAB/ABS guidelines. All field research was conducted under permission from the Government of Greenland (License number: G16-074).

Conflict of Interest

The authors declare that they have no competing interests.

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