



Cues to individuality in Greylag Goose faces: algorithmic discrimination and behavioral field tests

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Abstract

Cues to individuality, and the corresponding capacity for individual-level discrimination, can allow individually specific investment by conspecifics into offspring, partners, neighbors or competitors. Here we investigated possible cues to individuality via faces in an ancient avian lineage, the Greylag Goose (*Anser anser*). Konrad Lorenz could famously name each Greylag Goose in ‘his’ flock from a photograph. Confirming this anecdotal observation, we developed facial recognition software that can reliably (~97% accuracy) assign a goose face to a goose ID within a database, using bill morphology normalized during photo preparation. To explore conspecific detection of individuality cues, we erected life-size photos of geese and measured subjects’ responses to photos of themselves (unfamiliar goose), their partner, and another flock mate. Geese displayed significantly greater affiliative response to photos of their partners, providing evidence that geese can use two-dimensional images as cues to determine social category (partner/non-partner) and/or individual-level recognition. Our methods provide novel approaches to automatically detect and monitor geese and to test avian cognition. Our approach may also create new opportunities for species monitoring approaches more generally using photographic images and citizen-science engagement.

Keywords Facial recognition software · Photograph · Anatidae · Individuality signaling · Communication · Discrimination

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This article is a contribution to the Topical Collection 50 years anniversary of the Nobel Prize in Physiology or Medicine to Karl von Frisch, Konrad Lorenz and Niko Tinbergen in 1973.

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Zusammenfassung

Indizien für Individualität in Gesichtern der Graugans: algorithmische Diskrimination und Verhaltenstests im Freiland

Indizien für Individualität und die entsprechende Fähigkeit zur Unterscheidung zwischen Individuen könnten spezifische Investitionen in Nachkommen, Partner, Nachbarn oder Konkurrenten begünstigen. Hier untersuchten wir anhand von Gesichtern mögliche Hinweise auf Individualität bei einem alten Vogelstamm, der Graugans (*Anser anser*). Konrad Lorenz konnte bekanntlich jede Graugans in „seiner“ Schar anhand eines Fotos erkennen. Um diese anekdotische Beobachtung zu bestätigen, haben wir eine Gesichtserkennungssoftware entwickelt, die ein Gänsegesicht zuverlässig (~97% Genauigkeit) innerhalb einer Datenbank zuordnen kann, und zwar anhand der Schnabelmorphologie, die bei der Fotovorbereitung normalisiert wurde. Zur Untersuchung der Erkennung von Individualitätsmerkmalen durch Artgenossen stellten wir lebensgroße Fotos von Gänsen auf und maßen die Reaktionen der Probanden auf Fotos von sich selbst (unbekannte Gans), ihrem Partner und einem anderen Artgenossen der Schar. Die Gänse reagierten signifikant stärker auf Fotos ihrer Partner. Dies belegt, dass Gänse zweidimensionale Bilder als Anhaltspunkte nutzen können, um die soziale Kategorie (Partner/Nicht-Partner) und/oder die Erkennung auf individueller Ebene zu bestimmen. Unsere Methoden bieten neuartige Ansätze zur automatischen Erkennung und Überwachung von Tieren und zur Untersuchung der Kognition von Vögeln. Unser Ansatz kann auch neue Möglichkeiten für die Überwachung von Arten im Allgemeinen schaffen, indem fotografische Bilder und die Beteiligung von Bürgerwissenschaftlern eingesetzt werden.

Introduction

Across multiple taxa, many studies have shown that receivers can distinguish between individuals (Tibbetts and Dale 2007; Yorzinski 2017), and the signals they produce, whereby the information content of the signal provides cues to individual identity (Crowley et al. 1996; Blumstein et al. 2004; Terry et al. 2005; Tibbetts and Dale 2007; Pollard and Blumstein 2011; Colombelli-Négrel and Evans 2017). Potential benefits of individual discrimination include differential responses to conspecifics, partner, offspring, competitors and neighbors, allowing individuals to target specific responses to kin, reciprocal altruism partners and/or social allies and competitors. Individual distinctiveness may also carry costs, since a recognizable individual may be remembered and penalized if they cheat and/or neglect to engage in reciprocal altruism (Raihani et al. 2012).

Potential cues to individuality have several important implications in the evolution of behavior, especially for the evolution of cooperation. In short, altruistic or helper behavior directed towards kin (i.e., relatives) is an investment that increases inclusive fitness (Hamilton 1964). In contrast, in unrelated individuals, reciprocal altruism based on tit-for-tat models predicts that two unrelated individuals should engage in reciprocal behaviors and help each other if they have the opportunity to meet again in the future (Axelrod and Hamilton 1981). However, reciprocal altruism is unstable because it will often pay to cheat—as cheaters do not repay a favor received—which poses a threat to the stability of cooperation (Riehl and Frederickson 2016). Trivers (1971), therefore, identified preconditions for the persistence of reciprocal altruism, including stable groups, long life, individual recognition, and the ability to make cheating costly (Zahavi and Zahavi 1997; Dugatkin 2000), such as

through punishment (Mulder and Langmore 1993; Fischer et al. 2014).

Many examples of individuality signaling in animals focus on so-called vocal signatures in the acoustic domain (Jones et al. 1993; Elie and Theunissen 2018). Vocal signatures of individual identity have been found in the signature whistles of bottlenose dolphins (*Tursiops truncatus*; Janik and Sayigh 2013), maternal calls of Australian sea lions (*Neophoca cinerea*; Charrier et al. 2009), various calls in Australian fairywrens (*Malurus* spp.; Colombelli-Négrel et al. 2012, 2014; Dowling et al. 2016; Colombelli-Négrel and Evans 2017), spotted hyenas (*Crocuta crocuta*; Mathevon et al. 2010; Lehmann et al. 2022) and bonobos (*Pan paniscus*; Keenan et al. 2020), to list a few examples. Research into the occurrence and biological function of visual signals of individuality is only beginning, with evidence in Australian sea lions (e.g. Deb et al. 2018; Birenbaum et al. 2022; Charrier et al. 2022).

Greylag Geese (*Anser anser*) satisfy several preconditions for reciprocal altruism: they live in large groups (100+ flock members) (e.g. Nilsson et al. 1999), are long-lived (25 years), and have individually distinct vocalizations (e.g. distance calls; Guggenberger et al. 2022). Therefore, in principle, tit-for-tat repayment of favors could occur among unrelated individuals across longer time scales. Greylag Goose flocks have female-clan substructure where female lineages but not male lineages co-occur spatially (Kotrschal et al. 2010) and social proximity is a strong predictor of social alliance (Scheiber et al. 2005, 2013). Greylag Geese have individually distinct distance calls that may coordinate within-pair activity (Guggenberger et al. 2022) and use departure calls in the context of purportedly coordinated group movement (Schmitt 1990; Lorenz 1991). In the visual domain, Konrad Lorenz could famously recognize and name

each Greylag Goose in ‘his’ flock by sight (Nisbett 1977, p. 168), suggesting that Greylag Geese have visual features that allow individual recognition, at least by skilled human observers.

In this study, we first asked whether distinctive individual features of Greylag Geese faces can be recognized by automated facial recognition software. Second, we used an experimental behavioral approach to measure geese’s individual- or category-level (e.g. partner vs non-partner) behavioral response to goose photographs presented in the field. We hypothesized that the extent of individual differences in goose faces would be great enough to be detected by AI and by other geese. If so, we predicted that birds should show stronger affiliative responses (measured by a faster approach, more time in close proximity, and/or more contact calls) when exposed to photographs of their breeding partner compared with photographs of another familiar flock member or an unfamiliar goose (tested using a photograph of the goose itself).

Methods

Study site and species

This study was conducted in a flock of 111 free-flying Greylag Geese (*Anser anser*) in Grünau im Almtal, Upper Austria, Austria (47°48′50.5″ N 13°56′51.0″ E). The geese are descended from a flock transferred from the Max Planck Institute by Konrad Lorenz in 1973 and now reside as the free-flying habituated resident flock in the valley of the river Alm. The geese are supplementally fed with barley and grass pellets twice per day in outdoor feeding troughs (Hemetsberger 2001) and their attendance at the feeding site is voluntary. Each goose in the flock is individually color-banded and the life history of all flock members has been monitored since 1973 (Hemetsberger 2001; Hemetsberger et al. 2010; Scheiber et al. 2013). Birth year, sex, pairing status, and length of the pairing are known for every individual (Hemetsberger 2001). From 2019 to 2023, we collected 516 photographs of flock members (89 geese within the same year across days or weeks, and 84 geese across 2–4 years), recording the left side of their face. The behavioral experiments at photographs were conducted in October and November 2021, during the non-breeding season.

Goose face photograph library

Photographs of all individuals were taken from the ground at goose eye level ~3 m from the goose, using either a Canon EOS 7D with a 100–400 mm lens or an iPhone. Several photographs were taken from each individual with different backgrounds across years (2019–2023) to ensure varying

lighting conditions and to test our pre-processing steps for the software (see below). For efficient photographic storage and management, we created a master file containing all photographic (date taken, camera type, location) and individual details (name, sex, age, date banded) for each photograph taken.

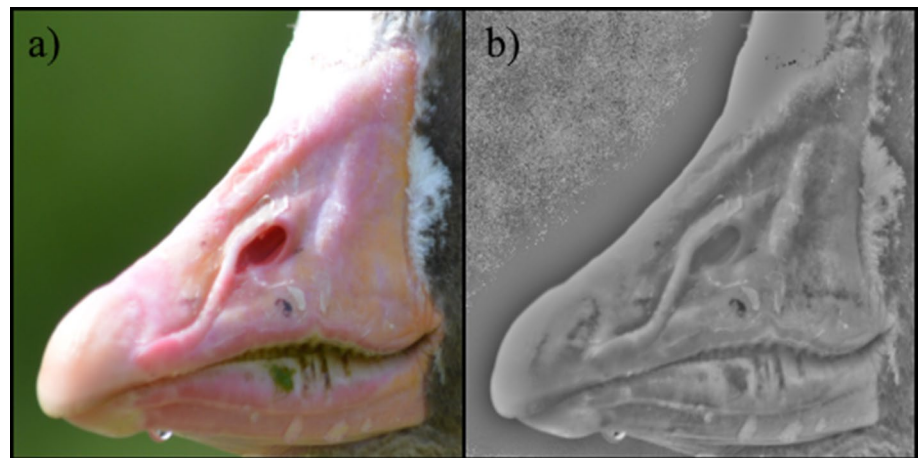
Facial recognition software

To determine whether goose faces were visually unique, we developed an automated facial recognition software using the similarity between images of goose bills. Feathers are subject to variation, depending on whether the bird is dry or wet or whether the bird is molting; therefore, we focused on identification using the bill, which is less likely to be affected by such variations. Prior to identification, we passed each input image through three different stages: first, we geometrically normalized the image to ensure a robust identification regardless of changes in position, scale, and rotation (Fig. S1). Second, we assessed the quality of the image using a combination of image quality measures (see supplemental material) to determine its suitability for identification (Figure S2). Finally, we further normalized each image by adjusting its luminance and enhancing its details and edges, to ensure identification was robust to changes in illumination (Fig. 1).

Experiment with photographs in the field

In 2021, we measured the geese’s behavioral response to photographs presented in the field at the Konrad Lorenz Research Center for Behavior and Cognition. To do so, we placed a wooden board (900 × 1200 mm) at five sites around the flock’s traditional feeding area for two weeks to habituate the geese and then pinned a life-sized goose photograph (840 × 1180 mm) to the board on the trial days (described below). The five trial sites spanned a total area of 4800 m² around the research center. The sites were (1) in front of the research center (building), (2) on the grassy meadow adjacent to the traditional feeding trays (meadow), (3) close to the water fountain and its runoff water (fountain), (4) adjacent to the river Alm (river), and (5) next to a pond (pond). We demarcated a 2 m radius around each board using stones and placed a separate stone to demarcate the start of the 1 m radius. As the geese inhabit the pebble shores of the Alm, the stones are a natural part of the landscape. At each board, there was a food bowl (10 cm × 20 cm) placed 10 cm in front of each (photograph) board and filled with the usual food pellets at 0800, the daily supplemental feeding time of the geese since 1973. We placed a GoPro Hero 7 Black (GoPro, Inc., San Mateo, CA, U.S.A.) on a tripod 2.2 m in front of each photograph and began recording continuously.

Fig. 1 Examples of **a** a normalized input image and **b** its detail-enhanced version used for identification



We used a random generator to select treatment types presented on a given day, and this resulted in the following sample sizes: control board ($N = 72$), photo of flock mate ($N = 68$), photo of partner ($N = 11$), and photo of self ($N = 12$). Six geese received all three photo treatments, eight received two treatments, and 57 received one treatment type only (55/57 cases, photo of flock mate).

The presence of geese in the area was determined using binoculars, and then researcher BH placed photographs on the boards that satisfied the random presentation order planned for the different categories, though there was no certainty that the geese present on that day would approach. Once a target goose had completed a trial, it was no longer considered on that day. Field notes with time stamps supplemented goose trial identification and labelling. We analyzed the response to the trials from the GoPro video recording, identifying the bird by the color bands visible on the video. We used Solomon Coder beta 19.08.02 (<https://solomon.andraspeter.com>) to code the behavior from the videos for 5 min per goose after it entered the 2 m arena; the analysis of behavioral response was restricted to behaviors within the 2 m radius. Across the sampling month, we only analyzed the first photograph type experienced by each goose per category (control, photo self, photo other, photo partner) to ensure that we only scored the first encounter with each treatment type. We kept notes on which goose had received which treatment daily.

From the video recordings, we scored affiliative behavior as (1) latency (s) of approach from 2 to 1 m, (2) minimum approach distance (m) to the photo, (3) time (s) spent feeding within 1 m of the photo, and (4) number of contact call bouts. We measured agonistic behavior as (1) number of forward-extended neck postures, (2) number of upward-extended neck postures (vigilance), (3) number of hisses, and (4) peck contact with photo (no, yes).

Statistical analysis

All analyses were performed using SPSS v 25 for Windows (SPSS Inc., Chicago, IL, U.S.A.). We used principal component analysis (PCA) to calculate a derived PC Affiliative Response variable with eigenvalue 2.41 that explained 60.3% of the variance with factor loadings for latency to 1 m (-0.91), minimum distance (-0.90), feeding duration at photo (0.77), and number of contact calls (0.43). Geese with high PC Affiliative Response scores approached more quickly and more closely, spent more time feeding near the photograph, and produced more contact calls. We used generalized linear mixed models with a Gaussian distribution, and PC Affiliative Response as the response variable to test for effects of treatment type (control, photo self, photo other, photo partner), trial location (building, meadow, fountain, river, pond) and sex as fixed factors, and Goose ID as a random effect. The frequency of agonistic behaviors was too low to be statistically analyzed (see Table 2).

Results

Facial recognition software

Results were obtained from two datasets: images taken within a single year and images taken at least 1 year apart (to account for possible effects of ageing, for example). For the first dataset (images taken within a single year), 21 individual geese with two images and 68 other individuals with a single image passed the quality threshold. This gave us a total of 110 images and 5996 possible image-pair combinations. For the second dataset (images taken 1 year apart), 26 individual geese with two images and 58 other individuals with a single image passed the quality threshold. This provided a total of 110 images and 5994 possible image pair

a)					b)				
	Total Image Pairs: 5996	Positive Match	Negative Match			Total Image Pairs: 5996	Positive Match	Negative Match	
	Positive Match	True Positive 14	False Positive 92			Positive Match	True Positive 16	False Positive 163	
	Negative Match	False Negative 7	True Negative 5883			Negative Match	False Negative 10	True Negative 5805	
		Sensitivity 66.67%	Specificity 98.46%				Sensitivity 61.54%	Specificity 97.27%	
		Accuracy = 98.35%					Accuracy = 97.11%		

Fig. 2 Confusion matrixes showing the identification results for **a** images taken within the same year, and **b** images taken 1 year apart

Table 1 The average affiliative response (mean $\pm$ SE) during a photo presentation trial in Greylag Geese (*Anser anser*)

	Control	Photo self	Photo other	Photo partner
Latency to 1 m	180.2 $\pm$ 14.4	208.3 $\pm$ 39.3	260.5 $\pm$ 11.2	106.6 $\pm$ 22.9
Minimum distance	88.6 $\pm$ 7.2	113.3 $\pm$ 17.8	140.4 $\pm$ 6.2	44.6 $\pm$ 13.2
Feeding duration	32.6 $\pm$ 6.8	0.4 $\pm$ 0.3	5.4 $\pm$ 2.2	16.1 $\pm$ 8.6
#Contact calls	0.4 $\pm$ 0.2	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1	1.1 $\pm$ 0.4

The control condition was a wooden board of the same size dimension as the life-sized goose photos, and the photos were either of the focal goose, a flock mate, or the partner. The data are shown for latency (s) to approach to 1 m, minimum distance (m) of approach, feeding duration (s) within 1 m, and number of contact calls

combinations. Figure 2 shows the confusion matrixes for the two datasets.

Results from the facial recognition software showed that identification of individual geese using images of their bill was possible and validated the idea that geese are visually unique. An accuracy of 98.4% was obtained for the first dataset (images taken within a single year) (Fig. 2a). For the second dataset (images taken 1 year apart), the accuracy was 97.1% (Fig. 2b).

Behavioral response to photographs in the field

Tables 1 and 2 show summary data for the affiliative and agonistic behavioral response of Greylag Geese that encounter a wooden board (control) or life-sized goose photo while walking on a grassy field (Fig. 3).

The affiliative response patterns differed across treatments: geese had the strongest affiliative response if they encountered a photograph of their partner compared to any of the other treatments (ANOVA: $F = 10.67$, $df = 3, 169$, $P < 0.001$; Fig. 4). Tukey's post-hoc pairwise tests showed a significant difference between the response to 'photo

Table 2 The average agonistic response (mean $\pm$ SE) during a photo presentation trial in Greylag Geese (*Anser anser*)

	Control	Photo self	Photo other	Photo partner
Threat	0	0.8 $\pm$ 0.3	0.1 $\pm$ 0.1	0
Vigilance	1.0	0	1.6 $\pm$ 0.6	5.0
Contact	0	0	0	0
#Hiss calls	0	0	0	0

The control condition was a wooden board of the same dimension as the life-sized goose photos, and the photos were either of the focal goose, a flock mate, or the partner. The data are shown for threat (neck forward posture), vigilance (upright neck posture), peck/contact in the photo, and a number of his vocalizations. The frequency of agonistic behaviors was too low to be statistically analyzed

other' and 'photo partner' ($P < 0.001$), 'photo other' and 'control' ($P < 0.001$), and a non-significant trend for a stronger response to 'photo partner' than 'photo self' (Fig. 4). There were no significant effects of trial location, sex, or of the random effect of Goose ID (GLMM results Table 3) on affiliative behavioral response.

Fig. 3 View of the presentation of life-size goose photographs in the field. Left: view of a goose photo with stones that demarcate the 2 m and 1 m observation area, and GoPro just outside the central 2 m stone. Right: adult goose feeding next to a photo of another adult goose

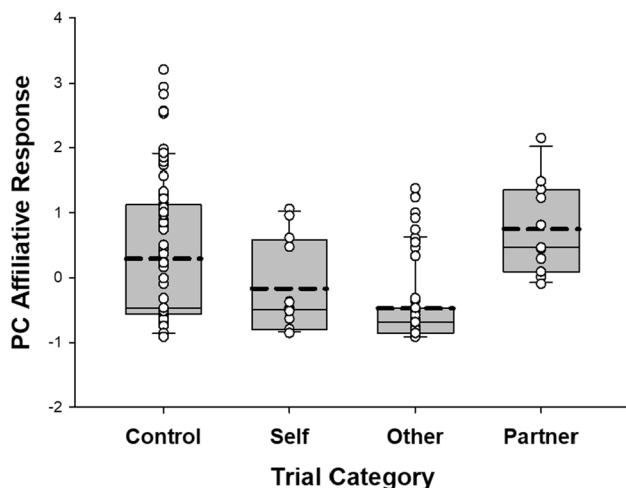


Fig. 4 The average PC Affiliative Response (mean $\pm$ SE) during a photograph presentation trial in Greylag Geese (*Anser anser*). Free-ranging geese were filmed with GoPro cameras in a grassy field when they approached: a wooden board (control) ($N=88$), a photograph of self ($N=12$), a photograph of a familiar flock mate (other) ($N=68$), or a photograph of their breeding partner ($N=11$). Geese had the strongest affiliative response (faster and closer approach, more time feeding in close proximity, and more contact calls) to a photograph of their partner. Horizontal lines within the boxes represent means (dashed) and medians (straight). Whiskers represent $\pm$ SE. White circles indicate individual data points

Discussion

We developed facial recognition software that correctly identified individual Greylag Geese using photographs of their bills with an accuracy of $\sim 97\%$. Consistent with claims by Konrad Lorenz that he could identify each goose by face, we confirmed that each goose face is sufficiently distinct to be detected algorithmically. Furthermore, whole-geese images can be discriminated by other geese: we found that geese responded to photographs in the field in a pattern suggesting that they distinguished their partners from other geese. Geese that encountered a photograph of their partner in the field approached the photographs more quickly, spent longer feeding near the photograph, and were more likely to give contact calls than geese that encountered a photograph of another flock mate (familiar goose) or themselves (an unfamiliar goose). It is of course likely that geese use other traits than just the bill to distinguish between conspecifics. These findings add to the growing literature suggesting that individuals can be identified and monitored using photographs, and thus without the need for capture (Kelly 2001; Speed et al. 2007; Sherley et al. 2010; Bolger et al. 2012; Kühl and Burghardt 2013; Urian et al. 2015; Gore et al. 2016). Furthermore, our methods offer new ways to investigate the proximate and functional significance of individuality signaling in a basal avian lineage.

There are many potential roles for cues to individuality in Greylag Geese. Individuality signaling could be favored

Table 3 Summary of results from the GLMM testing the derived affiliative response score (PCA affiliative response) against the fixed factors treatment (control, photo self, photo other, photo partner), trial location, and sex of the focal bird, and random effect Goose ID

Factors	Estimate	Standard Error	95% CI lower	95% CI upper	Test statistic	P value
Fixed factors						
Intercept	1.40	0.36	0.69	2.11	3.80	<0.001
Treatment	-1.23	0.30	-1.83	-0.64	-4.12	<0.001
Trial location	-0.64	0.34	-1.31	0.03	-1.90	0.059
Sex	-0.15	0.20	-0.55	0.25	-0.74	0.46
Random factor						
Goose ID	0.082	0.11	0.01	1.16	0.74	0.46

The test statistic was t for fixed factors and Z for random factors

by natural selection if it enhances fitness through benefits gained by, for example, selectively provisioning offspring or selectively deploying tit-for-tat favors among unrelated individuals. Mobbing behavior of predators has been tested as one example of reciprocal altruism, and individuality cues could reduce costly cheating in such systems. For example, in Pied Flycatchers (*Ficedula hypoleuca*), birds provided mobbing assistance to neighbors only if the neighbors had previously also provided mobbing assistance, and did not support neighbors that had previously defected from providing such assistance (Krams et al. 2007). A range of species have individually distinct alarm calls, such as Speckled Ground Squirrel (*Spermophilus suslicus*) (Matrosova et al. 2009, 2010), Silky Sifaka Lemur (*Propithecus candidus*) (Patel and Owren 2012), and an Australian songbird, the Superb Fairywren (*Malurus cyaneus*), where birds show stronger response to alarm calls and distress calls of familiar or related birds (Colombelli-Négrel and Evans 2017; Camerlenghi et al. 2023). Variance between geese in mobbing behavior or anti-predator behavior has not been studied in any detail at the individual level. We know that individual geese have different flight initiation distances to an unfamiliar human approach simulating a predator (Kleindorfer, unpublished data), and hence that geese differ in their boldness and other personality traits (Kralj-Fišer et al. 2007, 2010; Kurvers et al. 2010). Future research should address this gap in knowledge to test if anti-predator behavior in geese could be a fruitful area of research to further investigate tit-for-tat behavior and reciprocal altruism.

Our findings add to considerable previous evidence of relatively sophisticated cognitive abilities in Greylag Geese. Cognitive traits that facilitate recognition of relative social category and dominance rank of group members would be advantageous to maximize the benefits of targeted alliance formation (Frigerio et al. 2003; Scheiber et al. 2005, 2008, 2009a, b) and reduce the costs of conflict (Weiß and Kotrschal 2004; Weiß et al. 2008). For example, Greylag Geese can make judgments about relationships using transitive inference (Weiß et al. 2010). Transitive inference refers to the capacity to infer relationships, such as, for example, if A is dominant to B and B is dominant to C, then A is probably also dominant to C. Greylag Geese also have the capacity for gaze following (Kehmeier et al. 2011). The capacity of Greylag Geese for transitive inference of relationship hierarchies and visual attention towards conspecifics measured as gaze following is in line with the findings of this study, where geese adjusted their behavioral response to a photo in relation to the dyadic relationship between the goose in the photo and other flock mates (partner vs non-partner).

Greylag Geese have increased aggression against individuals who were recently involved in a conflict with the aggressor's social allies, pointing to the possibility they may understand third-party relationships (Weiß et al. 2008).

Third-party inference is a cognitive feat that involves transitive inference and has been demonstrated in primates (Cheney and Seyfarth 2005; Subiaul et al. 2008), hyenas (Engh et al. 2005; Holekamp et al. 2007), and corvids (Clayton and Emery 2007; Massen et al. 2014). Ravens for example have been shown to provide social support to conspecific allies during conflicts (Fraser and Bugnyar 2012), engage in reconciliation after conflicts (Fraser and Bugnyar 2010), and remember long-term allies even after a period of separation (Boeckle and Bugnyar 2012). In the highly social Greylag Goose, paired males isolated from their mates for 48 h had elevated corticosterone stress response and increased parasite load that only returned to baseline after four weeks (Wascher et al. 2012; Ludwig et al. 2017). In another study, bystander geese increased their heart rate when observing agonistic interactions among flock mates, especially if their partners were involved (Wascher et al. 2009). Thus, short bursts of intense social stress can have strong measurable impacts on physiological stress response and, in some cases, immune function. Do Greylag Geese use third-party intervention to reduce stress in targeted flock members? Future research could explore this possibility in more detail, given the findings here showing that geese likely use visual information, also in combination with individually distinct calls (Guggenberger et al. 2022), to reliably discriminate between flock mates.

Finally, we are in the midst of the Anthropocene and a biodiversity crisis (Lewis and Maslin 2015; Cazalis et al. 2020; Sandor et al. 2022). Novel approaches, including animal monitoring with drones, are increasing in frequency (Linchant et al. 2015; Hodgson et al. 2016). Concurrently, citizen scientists are playing an increasingly important role to collect data across large temporal and spatial scales (He et al. 2016; Miller et al. 2017; Locke et al. 2019). Animals with individually distinct faces and/or body patterns can be monitored using photographs and this creates the opportunity for large-scale citizen science involvement. In addition to the benefits of citizen science engagement for transforming human attitudes about wildlife (Frigerio et al. 2018, 2019; Bruckermann et al. 2021; Ostermann-Miyashita et al. 2021; Greving et al. 2023), the specific use of photographs that capture individually distinct animals can be used to assess individual movement patterns (for example, using sightings of the same individual across space) and more accurately assess population size by avoiding re-counts of the same individual (Zero et al. 2013; Rahman et al. 2016; Landeo-Yauri et al. 2020).

Animal welfare could be enhanced through the use of photographs in captivity. For example, a photograph might reduce the sense of isolation in a social species held in captivity or could serve as a sort of 'soft introduction' before a new animal is introduced into the enclosure, though care should be given to avoid photos of a deceased relative, ally

or dominant. Perhaps captive individuals in group-living species express reduced anxiety when exposed to a photograph of an unknown and smaller conspecific. Some researchers are exploring the use of computer touchscreens for animals in captivity as a form of enrichment (Egelkamp and Ross 2019; Scheer et al. 2019; Webber et al. 2020; Kleiber et al. 2021). In captive Sumatran Orangutans (*Pongo abelii*), individuals interacting with a touchscreen preferred to view photographs of conspecifics over humans (Adams and MacDonald 2018).

In summary, our study contributes to understanding morphological cues to individuality in animals. First, we developed an algorithm for facial recognition that can in principle be applied to any species, involving the identification of points of marked difference and comparison of photos to a photo library. Second, we field-tested 2D photos in the wild and showed that focal geese can discriminate between individual geese in the flock, at least in regards to their partner versus other geese. We suggest that individuality cues could be favored by selection if they provide benefits by avoiding cheating conspecifics, which requires further research. While there is growing evidence that primates can discriminate between conspecifics in photographs (Vonk and Hamilton 2014), this study shows that such a capacity—which we tested using 2D photos—also occurs in Greylag Geese, an ancestral avian lineage. Birds and mammals diverged about 310 mya (Hedges and Kumar 2004), and while our results cannot distinguish between homology and convergence in birds and primates, they suggest that the capacity for individual discrimination has a long evolutionary history. Future research could address cognitive mechanisms that underpin morphological discrimination. For example, how many different geese can a goose keep track of, and how does cognitive capacity covary with group size, group stability, and migration distance? From an ultimate perspective, individuality cues may be more likely to occur in systems with reciprocal altruism and/or high-risk high-gain communication contexts that, for example, enhance coordinated group movement and escape from threat.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-023-02113-4>.

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are the descendent geese of the flock Lorenz transferred to Grünau im Almtal after Lorenz’ retirement from the Max Planck Institute in 1973.

Author contributions SK and DCN designed the research; SK wrote the first draft of the paper; SK, BH, JH and DF collected the data; DT developed the facial recognition software program; SK, DCN, BH and DT analyzed the data; all authors edited the manuscript.

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Data availability Data are available on the Flinders University data repository at DOI: <https://doi.org/10.25451/flinders.24082680>.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical statement This study complies with all current Austrian laws and regulations and was supported by Animal Experiment License Number 66.006/0026-WF/V/3b/2014 issued by the Austrian Federal Ministry for Science and Research (EU Standard, equivalent to the Animal Ethics Board). All data collected for this study were obtained using non-invasive methods. Birds were habituated to the presence of humans as the flock has been observed at the Konrad Lorenz Research Center for Behavior and Cognition (KLF) since 1973.

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