Comparing behavioural responses of Greylag Geese *Anser anser* and Egyptian Geese *Alopochen aegyptiaca* to human disturbance in an urban setting

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Abstract

When animals first colonise urban areas, they may perceive disturbance from humans and their pets as a novel form of predation risk. Adaptation to predation risk is important in an evolutionary sense: caution could be beneficial for reducing the risk of injury and mortality; on the other hand, reacting too soon and too often can cause stress, costs energy and may lower survival. This study compares the extent of tolerance to human disturbance in two introduced but established waterfowl species, Greylag Geese *Anser anser* (Anserinae) and Egyptian Geese *Alopochen aegyptiaca* (Tadorninae). After their recent colonisation of the city of Stuttgart in southwest Germany, Greylag Geese first hatched a brood in 1995, while Egyptian Geese only latterly colonised the city (first successfully fledged brood in 2010), but subsequently showed exponential population increase. There are many potential reasons for this; they may have a broader ecological niche (*i.e.* are able to use a wider array of available nesting sites), and have larger broods with higher fledging rates, but Egyptian Geese may also show higher tolerance towards disturbance than Greylag Geese in an urban setting. We investigated the last of these hypotheses by comparing variation between the two species in their reaction to disturbance stimuli between 5 June and 22 August 2018. Our behavioural observations showed that Egyptian Geese reacted to disturbance stimuli > 50% more frequently than Greylag Geese, and with more intense behaviours. In addition to species-specific differences, we found that reaction to disturbance also varied with location, the type of disturbance, social status, time of day and ambient temperature. Both species reacted most strongly (*i.e.* were alerted or displaced at greater distances) when disturbed by dogs. Egyptian Geese were generally more cautious than Greylag Geese to equivalent stimuli from human presence. Such cautiousness may, in addition to ecological differences, partly explain the greater success of Egyptian Geese as an invading species in novel environments. Alternatively, this difference between the two species may reflect a longer habituation period, or perhaps genetic adaptation to disturbance stimuli by Greylag Geese.

Key words: fear, invasive species, novel habitat, tameness.

Animals that adapt to living in cities face different challenges to those occurring in their original habitat (Callaghan *et al.* 2019). For instance, close encounters with humans and their pets (*e.g.* dogs) may form or be perceived as a novel predation risk (Fernández-Juricic & Jokimäki 2001), and individuals may respond to these disturbances and associated risks very differently. Some react early, whilst others do not show much reaction at all (Beale & Monaghan 2004; Møller 2008). Individual variation in reaction time and flight initiation distance reveals much about the perceptions of the predation risk by birds (Blumstein 2019). In an evolutionary sense, it may pay to be cautious. On the other hand, acute or chronic stress caused by disturbances may have an adverse effect on individual fitness (Rebolo-Ifran *et al.* 2015); thus individuals "tame" to human activities may have an evolutionary advantage in cities. Cities therefore can be regarded as testbeds for evolutionary change, as selection pressures are often very different in comparison to those in the wild (Beans 2019). For instance, urbanisation has been identified as the most important factor underlying variation in escape behaviour in birds, being lower in the city (Møller 2008; Samia *et al.* 2017). Moreover, Carrete & Tella (2010) hypothesise that within a population only tamer birds use urban areas, whereas less tame birds remain in a rural setting. It is currently unclear whether phenotypic plasticity explains personality traits or microevolutionary processes (Vincze *et al.* 2016; Miranda *et al.* 2013). The longer a species lives in a novel urban habitat, the more adapted it may become genetically to tolerate disturbance in an evolutionary sense; *i.e.* natural selection should favour tamer individuals in an urban setting (Samia *et al.* 2017).

For herbivorous geese, the parks of the city of Stuttgart with regularly mown lawns and grasslands offer high quality grazing almost year round, with safe nesting places and no hunting. However, by exploiting such areas, geese encounter humans at close range and must deal with the disturbances caused by *e.g.* pedestrians, joggers, dogs, cyclists, small children, cars or mowing machines. The Greylag Goose *Anser anser* has been resident in the city since the second half of the 20th century, with first breeding detected in 1995, and its numbers have been more or less stable since 2010. In contrast, the Egyptian Goose *Alopochen aegyptiaca*, has become established in Stuttgart relatively recently, with breeding first confirmed in 2010, and has increased rapidly in numbers, and seems to be doing well in the urban setting. We hypothesise that, irrespective of ecological differences between the two species, Egyptian Geese are more tolerant towards disturbances compared to Greylag Geese, and that this behavioural flexibility may partly explain their prompter success in colonising new areas (Sol *et al.* 2002), with several other studies reporting that some bird species are particularly successful in anthropogenically modified habitats (Case 1996). Alternatively, Greylag Geese may prove to be more tolerant towards disturbances than Egyptian Geese, because they colonised the area earlier and therefore have had more time to habituate, or that natural selection favours tamer individuals sooner (Samia *et al.* 2017).

Egyptian Goose numbers have increased noticeably in many European countries over the last years, where they cause problems in the urban environment, *e.g.* by their droppings fouling and contaminating public pools, gardens or golf courses (Cornelissen 2013). Private and public owners therefore seek ways to discourage Egyptian Geese, along with other urban goose species (Fox 2019), from using such sites (*e.g.* through sward management, chemical repellents, habitat management, and elimination of human provision of food). Disturbing and displacing Egyptian Geese using falconry-flown birds of prey or drones are among the deterrents used to date in urban areas when other measures are not possible but experience shows the geese quickly adapt to these and lose their fear (Atkins *et al.* 2017). In this context, our comparison of the behaviour of the two goose species towards disturbance may provide useful information upon which to base more effective management decisions.

Study sites

Stuttgart is the state capital of Baden-Württemberg, southwest Germany (48°46'N, 09°10'E), with roughly 600,000 inhabitants. It is located at 230–550 m above sea level in a hilly landscape. Stuttgart's public parks extend along an 8 km corridor with a total area of 5.6 km^2, where lawns provide ample grazing for the geese and many small lakes offer safe roosting places. Within the city, the geese use several sites (see Käßmann & Woog 2008 for further details). This study was conducted from 5 June–22 August 2018 at the inner city parks and also 5 km to the north along the River Neckar, at the "Max-Eyth Lake" which was formerly a gravel pit. The inner city parks were created in the early 19th century as an "English Garden" and consist of large grasslands and lawns with scattered old trees which are amongst the many nesting opportunities available for Egyptian Geese. Greylag Goose nesting sites are restricted almost entirely to the few islands at the Max-Eyth Lake, where incubating females are undisturbed and the risk of damage or predation of the eggs is minimal. Both sites are heavily used for recreational purposes. Dogs are allowed only on a leash and this is mostly accepted by dog owners. Unleashed dogs very rarely occur.

Study species

Both goose species are mainly herbivores and benefit from frequently mown pastures with grasses and herbs with a high protein and low fibre content (Drent & Prins 1987). Greylag Geese usually nest once a year, mostly on islands or in reedbeds. Clutch size comprises 4–9 eggs. Parents stay with their young for a prolonged period, often until the next breeding season (Bauer *et al.* 2012). The average breeding success in Baden-Württemberg was reported to be 2.9 fledglings per pair (Hölzinger *et al.* 2018). Greylag Geese were first recorded in Stuttgart in the 1980s and are descended from released captive wild-type individuals (Hölzinger *et al.* 2018). The first successful brood was encountered in 1995 but the number of breeding pairs increased only slowly, to five pairs in 2005 and peaking at 26 pairs in 2015 before declining in more recent years (Fig. 1a), presumably due to a limited availability of safe nesting sites, such

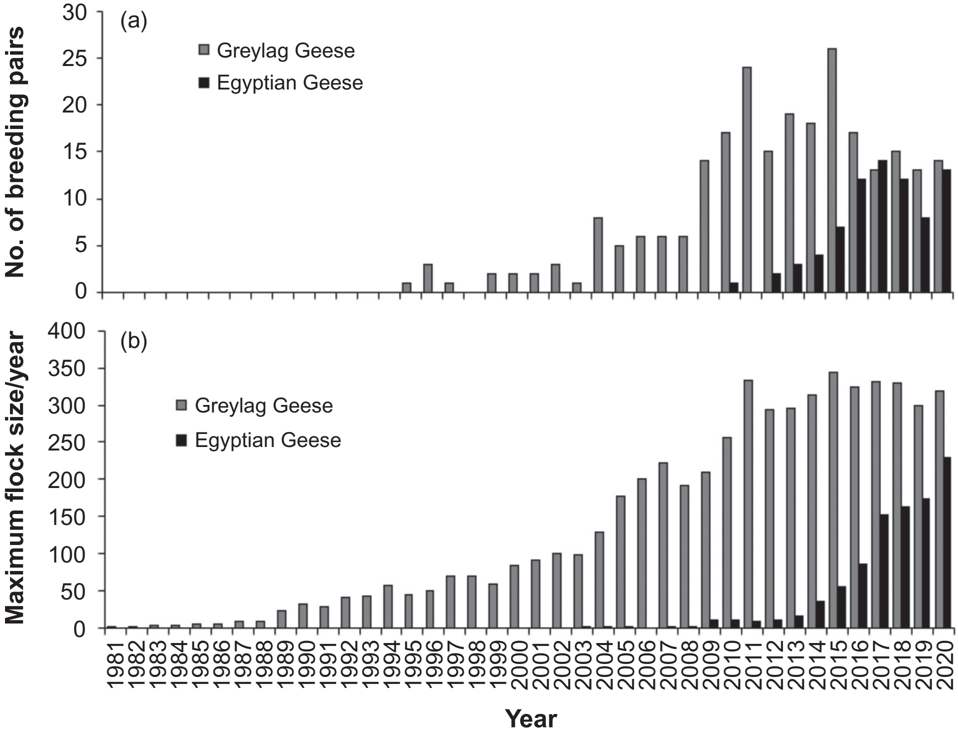

Figure 1. The number of: (a) breeding pairs, and (b) the largest weekly flock size recorded within a given year for Greylag Geese (grey bars) and Egyptian Geese (dark bars) in the Stuttgart study area.

as on islands. In contrast, the number of Egyptian Geese breeding in Stuttgart has risen from one successful pair in 2010 to 14 pairs 10 years later in 2020 (Fig. 1a). The maximum weekly count in the study area in 2020 comprised 319 Greylag and 230 Egyptian Geese (Fig. 1b). Between 2002 and 2020, 1,250 Greylag Geese were ringed in the Stuttgart area, but only 39 Egyptian Geese. Among the Greylag Geese in Stuttgart, the proportion of non-breeders is high, again probably due to a limited number of breeding sites. Between 2007 and 2020, on average only 20% of the Greylag Geese present had nests (12–28%; Ehret 2016; F. Woog, unpubl. data). Ring recoveries have shown that the Stuttgart Greylag Geese are non-migratory and that they stay in the area throughout the year, even during cold winters (Käßmann & Woog 2007).

Egyptian Geese are native to Africa (Bauer *et al.* 2012). Introduced birds have spread from the Netherlands throughout the rest of Europe and the species is now established in many European countries (Gyimesi & Lensink 2012). In Germany, the Lower Rhine area (located most closely to the Netherlands) was colonised in the late 1980s (Hüppeler 2000) but southern

Germany was colonised more than 20 years later (see below). Ring recoveries have shown that Egyptian Geese move larger distances than Greylag Geese (Bauer *et al.* 2019).

Egyptian Geese use a variety of nesting sites near water bodies. Often they reuse nests built by other birds in trees, but they also nest underneath bushes, in dense vegetation, tree and earth holes, caves, crevices, and on floating or real islands (Bauer *et al.* 2012). During the breeding season they protect a territory *c.* 1 ha in size. In Europe they can breed up to three times a year and throughout the year, with a peak nesting period during April–June (Bauer *et al.* 2018). Clutch size is of 6–10 eggs, and the parents stay with their young for several months (Bauer *et al.* 2012). In Stuttgart, the first brood was observed in 2010 (Woog *et al.* 2010) and by 2019 at least 16 nests (mostly in trees) had been recorded, which subsequently have often been used on a regular basis (F. Woog pers. obs.). Breeding success in Baden-Württemberg ranges between 2.7–3.8 fledglings (Bauer *et al.* 2018) and the population is increasing (Fig. 1b). The EU has classified the Egyptian Goose as an invasive species (European Commission 2017).

It is not yet fully known if Egyptian Geese have any negative effects on native species in Europe on a population level. Some individuals show strong aggressive behaviour towards conspecifics but also towards other species. Sometimes they may kill individuals of other species, *e.g.* Common Moorhen *Gallinula chloropus* and Common Shelduck *Tadorna tadorna* chicks, with reports even including a flamingo at Stuttgart zoo (see Woog *et al.* 2010). This behaviour, however, does not appear to threaten bird populations on a larger geographic scale (Gyimesi & Lensink 2012). Since 2015, Greylag and Egyptian Geese have both been huntable in the state of Baden-Württemberg from 1 September to 15 January. Hunting is, however, prohibited in public parks.

Methods

Disturbance observations

Between 5 June and 22 August 2018, disturbance observations were carried out for a total of 172 hours (n = 101 h for Greylag Goose; n = 71 h for Egyptian Goose flocks). Within each hour, all potential disturbance stimuli in view of the observer were recorded, whether or not the geese reacted, and the type of behaviour observed. We followed the definition by Stock *et al.* (1994) where disturbance is a visible reaction to a disturbance stimulus. This may lead to displacement, change in physiology or even limit breeding success and/or survival (Cayford 1993). Disturbance stimuli recorded during our study included: pedestrians, joggers, cyclists, Nordic walkers, people with buggies, children on foot, cars, supplemental feeding of birds, dogs and helicopters. Reactions by the geese were modified from Inglis (1977) and classified as follows: (1) vigilance with head up or extreme head up positions; (2) avoidance (small scale movement); (3) walking away; (4) running away; (5) flight on foot to lake; (6) flight on wing to lake; (7) aggression; (8) approaching; (9) leaving the area for an unknown destination; and (10) no reaction.

All observations were carried out in hourly blocks between 8:30–10:30 h and 12:00–15:00 h. Only complete hourly observation blocks were used. Data are described as the number of disturbance events resulting in different types of behaviour within these hourly observation blocks, including when no disturbance was recorded during a 1 h observation period. Although the flock was treated as the observation unit, reactions of geese within that flock were not always the same, and behaviour was recorded only for the individual that reacted first. Individuals in flocks share vigilance duties and an early reaction enables fellow flock members to become aware of and avoid potential predators. As Egyptian Geese were not ringed, and rings of the Greylag Goose that reacted first were not always visible, the same individual may have contributed to the dataset more than once. If the geese left the area before the end of the observation hour, these observations were not included in the analyses. A total of 1,967 disturbance events were recorded (n = 1,077 for Greylag Goose, n = 890 for Egyptian Goose flocks). The flocks of the two species usually did not mix, so mixed flocks were not included in the analyses.

Reaction distances have been shown to vary due to a number of factors, including sociality and flock size (Laursen *et al.* 2005; Blumstein 2019). Therefore, on estimating the reaction distance of the first individual to respond to a disturbance stimulus (recorded to the closest metre), flock size and social status (family, non-breeder) were also noted. Families and non-breeders formed separate flocks. As we did not collect data on an individual level, we could not take individual flight initiation distances and instead refer to "reaction distances", which were estimated by eye after training. The observation unit was a flock at a given site, and the behaviour and reaction distance of the individual within that flock that reacted first were noted. Flock sizes ranged between 2–120 individuals, were not stable over time and frequently changed in composition (see above).

Goose counts

In the years 1985–2000 inclusive, goose counts were carried out through opportunistic observations of unmarked birds by a variety of observers, from 2001–2006 weekly counts were conducted by a well-trained group of observers, and from 2007–2019 weekly counts were conducted by the same observer (H. Haag). To describe population size, we present the maximum weekly count of geese recorded within a year. Breeding pairs include those seen with young and also failed breeders.

Weather data

Weather records were available from the Environmental Office in Stuttgart. The weather station is located in town close to the study area. From the daily records we calculated the hourly mean, minimum and maximum temperatures within the city for each hour of observation. As there was almost no rain, rainfall was not included in the analyses.

Statistics

Studies on waterfowl disturbance in urban areas have shown that social status, weather conditions and the type of disturbance influence the reaction of birds (Blumstein *et al.* 2005). We therefore controlled for these factors in our comparison of the probabilities of the geese reacting towards disturbances. Generalized linear models on disturbance reactions were calculated using R (R Core Team 2019, RStudio Team 2020) with a binomial model, where the response variable was treated as a 0/1 variable (0 = no reaction, 1 = reaction). Explanatory variables were species, location, disturbance stimulus, social status, time of day and ambient temperature. First, backward selection was performed using the Akaike Information Criteria (AIC) and the model with the lowest AIC-value was selected. Results are presented only for the latter (best-fit) model.

Mean reaction distances recorded for Greylag and Egyptian Goose flocks in relation to the most important disturbance stimuli were tested using Welch's T-tests (Field *et al.* 2012) in IBM SPSS Statistics 24 (IBM 2016). Data from both species had equal variances for all of the disturbance stimuli tested (Levene 1960); *i.e.*, for pedestrian, jogger, bicycle, walker, buggy, child, car, supplemental feeding and dogs.

The influence of flock size on reaction distances was analysed using a Pearson correlation in IBM SPSS Statistics 24 (IBM 2016).

Results

Egyptian Geese reacted more frequently towards disturbance stimuli than Greylag Geese and with more intense behaviours (Fig. 2a,b). Moreover, in addition to species (*i.e.* Greylag Goose *versus* Egyptian Goose), including location, social status, disturbance stimulus, time of day and ambient temperature as explanatory variables in a generalized linear model best explained the probability of disturbance (GLM: χ^2_{14}= 1434, P < 0.001; Table 1, Fig. 3). Egyptian Geese reacted more frequently towards disturbance (40%) than Greylag Geese (25%), see Fig. 3a. The frequency of disturbance was higher at the Max-Eyth Lake in comparison to the inner city parks (Fig. 3b). Whereas in Greylag Geese, families reacted more frequently towards disturbances, the non-breeding birds did so among the Egyptian Geese. In the complete model, however, this difference was only slight, with non-breeders showing a higher probability of reaction towards a disturbance (Table 2, Fig. 3c). Whereas pedestrians including joggers and cyclists caused only few reactions, getting fed by pedestrians, and the occurrence of dogs and helicopters caused more disturbances (both in attracting and alerting/displacing the birds) for both goose species (Fig. 3d). The probability of the geese reacting towards disturbances increased during the day (Fig. 3e). Ambient temperatures increased until mid-day but the warmer the temperatures, the less likely the geese reacted (Fig. 3f).

Reaction distance

Reaction distance was at < 10 m in both species when disturbed by pedestrians, joggers, bicycles, Nordic walkers or buggies. Egyptian Geese reacted earlier when children on foot were involved. Both species reacted towards cars and feeding events at a larger distance, and the reaction distance was highest when the birds were disturbed

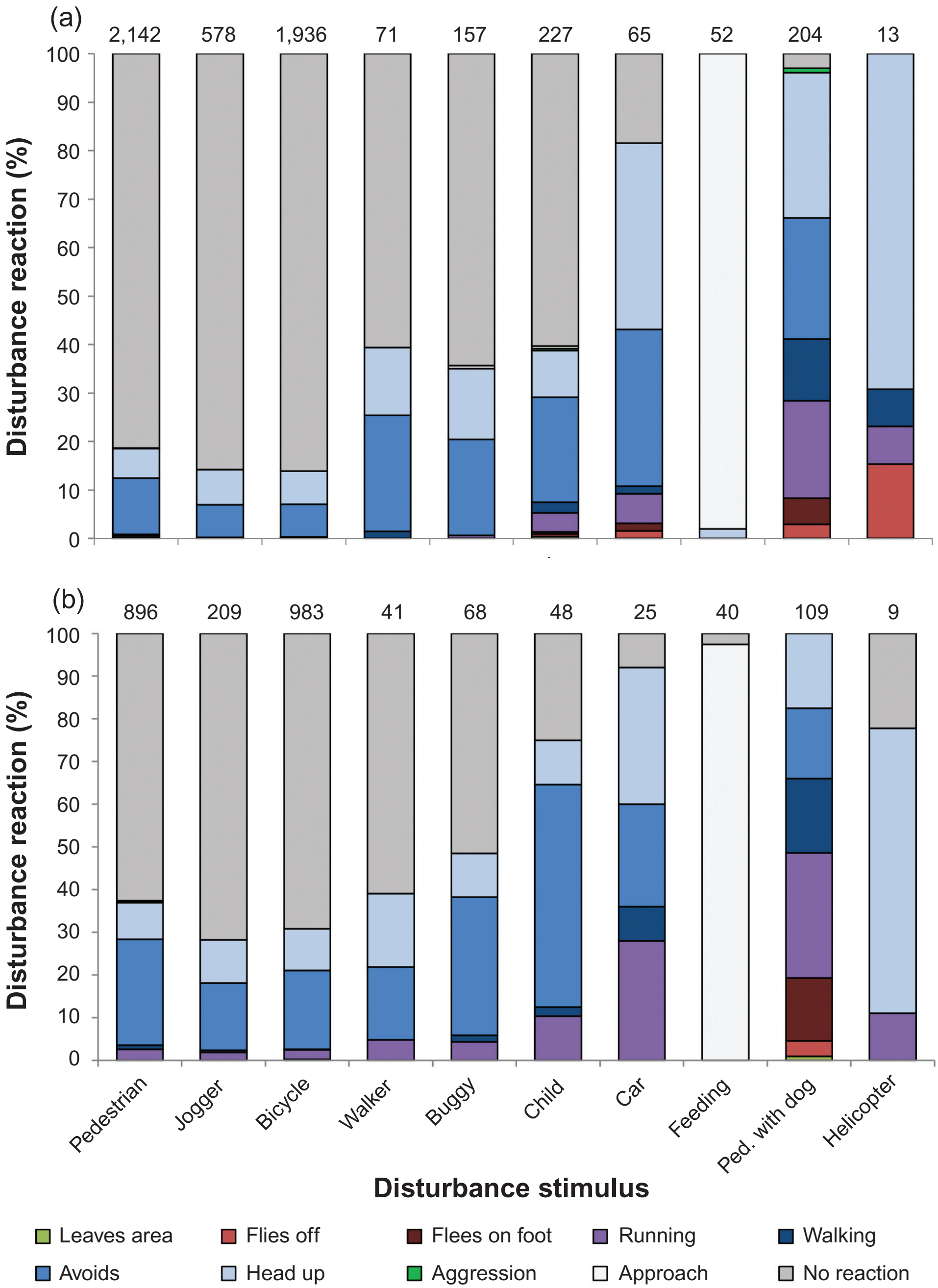

Figure 2. Percentages of behavioural reactions towards different types of disturbance in: (a) Greylag Geese, and (b) Egyptian Geese.

Table 1. Generalized linear model (GLM) of factors influencing whether or not geese respond to disturbance, in relation to the following references: species = Greylag Goose, location = Max-Eyth Lake, social status = family, disturbance stimulus = pedestrian. Confidence intervals are larger when the type of disturbance seldom occurs. Note: *P* values may be inflated because multiple observations may have been made of unmarked individuals during the course of the study.

Variables	B	s.e.	z	*P*	Odds ratio	95% CI
Species: Egyptian Goose	0.73	0.08	9.04	0.0001	2.07	1.77–2.42
Time of day (h)	0.11	0.02	5.16	0.0001	1.11	1.07–1.16
Location: Inner City Parks	–0.69	0.07	–9.41	0.0001	0.50	0.43–0.58
Ambient temperature (°C)	–0.04	0.01	–5.62	0.0001	0.96	0.95–0.97
Social status: non-breeder	0.27	0.09	3.08	0.002	1.31	1.10–1.55
Disturbance stimulus:						
Jogger	–0.32	0.12	–2.58	0.01	0.73	0.57–0.92
Bicycle	–0.29	0.08	–3.84	0.0001	0.75	0.65–0.87
Walker	0.57	0.24	2.35	0.02	1.77	1.09–2.84
Buggy	0.79	0.16	4.90	0.0001	2.20	1.60–3.00
Child	1.22	0.15	8.20	0.0001	3.40	2.54–4.56
Car	2.66	0.34	7.74	0.0001	14.24	7.54–29.33
Feeding	5.58	1.01	5.53	0.0001	264.06	58.01–4,674
Dog	5.26	0.51	10.36	0.0001	193.31	81.41–630
Helicopter	3.94	1.04	3.79	0.0002	51.24	10.18–933

by a dog (Fig. 4). Reaction distances differed between the two species only for disturbances by dogs, which was higher in Egyptian Geese (Table 2).

In Greylag Geese, the reaction distance increased with flock size (Pearson correlation: $r = 0.31$, $n = 1{,}249$, $P < 0.001$; Fig. 5a) but in Egyptian Geese there was no such effect (Pearson correlation: $r = -0.02$, $n = 986$, $P = 0.45$, n.s.; Fig. 5b).

Discussion

In a large comparative study on 150 bird species, Blumstein *et al.* (2005) found that larger animals tend to be more prone to disturbance than smaller ones. Contrary to this prediction, in our study the smaller Egyptian Geese reacted more often and more strongly than Greylag Geese to human disturbance stimuli. In addition to species-

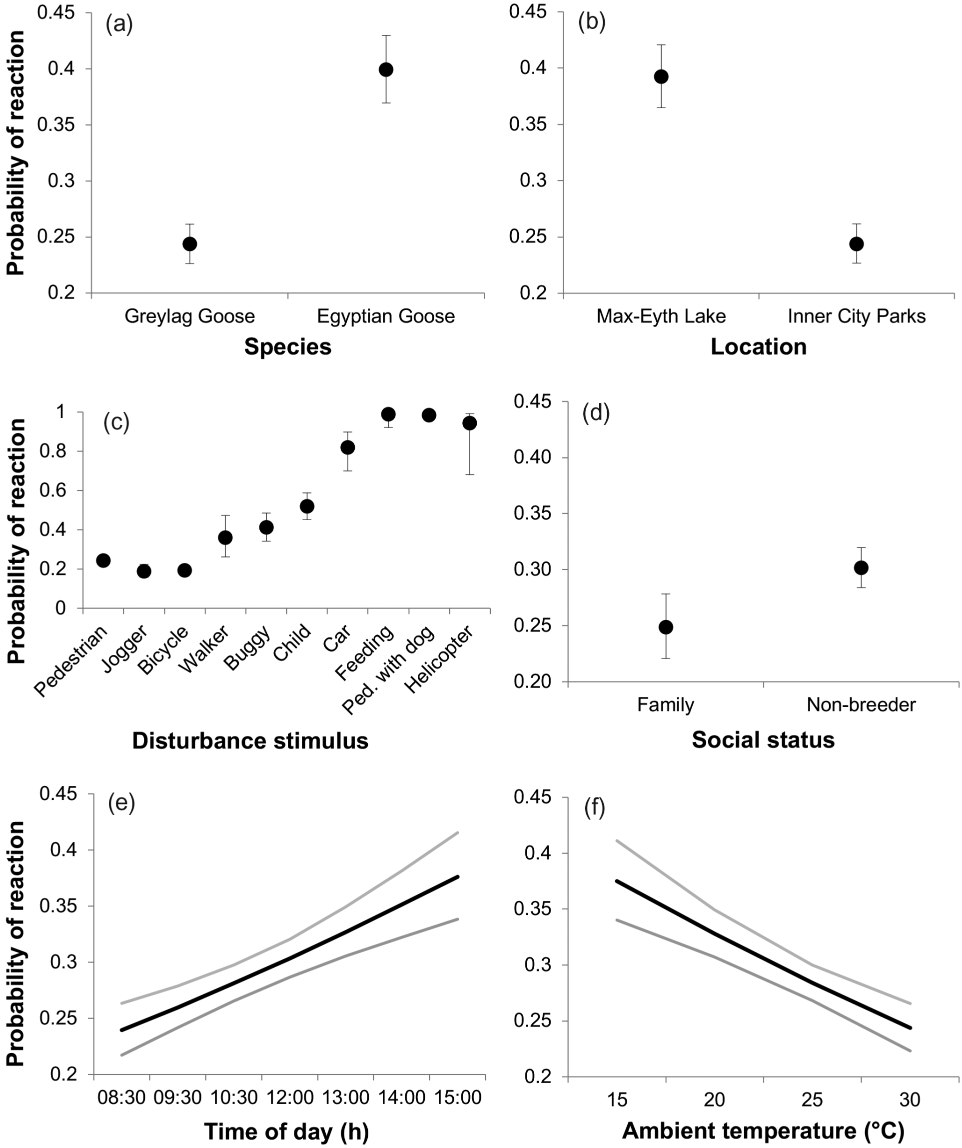

Figure 3. Probability of reaction towards a disturbance stimulus (± 95% CI) in relation to: (a) goose species, (b) location, (c) type of disturbance, (d) social status, (e) time of day and (f) ambient temperature.

specific differences, we showed that reactions to disturbance also varied with location, the type of disturbance stimulus, social status, time of day and ambient temperature.

At the Max-Eyth Lake both goose species reacted more frequently to disturbance stimuli than in the inner city parks. This may be due to differences in human use: at the

Table 2. Test of differences between the two goose species in their mean reaction distances at the time of maximal disturbance, in relation to the most important disturbance stimuli (Welch's *t*-tests). Only disturbance by dogs proved statistically significant, being slightly higher in Egyptian Geese (as illustrated in Fig. 4).

Disturbance type	***t***	**d.f.**	***P***
Pedestrian	–1.69	704	0.092
Jogger	1.17	121	0.243
Bicycle	0.80	512	0.422
Walker	1.40	36	0.171
Buggy	–0.25	87	0.806
Child	–1.06	39	0.295
Car	–0.05	73	0.962
Feeding	0.00	87	0.999
Dog	–3.07	164	0.003***

inner city parks people usually stay on the paths whereas at the Max-Eyth Lake people also leave the paths to have picnics on the lawn. Wildfowl in Lower Saxony likewise showed less reaction when people stay on paths (Hohmann 2016).

The probability of disturbance varied with the type of disturbance stimulus. Pedestrians, joggers and people on bicycles did not cause many reactions; however, Nordic walkers with their walking sticks, buggies and children had more impact on the geese. Supplemental feeding by visitors attracted both goose taxa, changing their behaviour and leading to an increase of aggressive encounters between geese (also see Käßmann & Woog 2013). Disturbances by helicopters were rare in Stuttgart, but always led to a very strong reaction especially in Greylag Geese, even resulting in the death of birds by collision with trees during flight (F. Woog, unpubl. data). Strong reactions towards helicopters has also been observed in Barnacle Geese *Branta leucopsis* (Mosbech 1992), Brent Geese *Branta bernicla* (Holm 1997) and Whooper Swans *Cygnus cygnus* (Rees *et al.* 2005). In contrast, Kahlert (2006) reported habituation of Greylag Geese towards helicopters in an area with frequent helicopter traffic (up to 52 flights a day). Geese in Stuttgart were habituated neither to cars nor to helicopters which may explain their strong reaction towards them.

Both species reacted most strongly when being exposed to dogs and kept at a long distance especially from large dogs (Schwarz, unpubl. data; see also Wascher *et al.* 2011 for Greylag Geese; Randler 2003 for feral domestic Swan Geese *Anser cygnoides domesticus*). This is not surprising as medium to large-sized dogs resemble foxes and wolves, which are natural predators of geese. Dogs showed a large variety of behaviours towards the geese and some still demonstrated a hunting instinct. Thus, for as long as dog behaviour remained unpredictable, and adverse experiences and occasional predation by dogs occurred, the geese did not habituate towards them. Using dogs to deter geese from using areas where there may be a conflict with humans (*e.g.* swimming pools) therefore warrants further investigation.

Both goose species adjusted their reaction to the severity of disturbance.

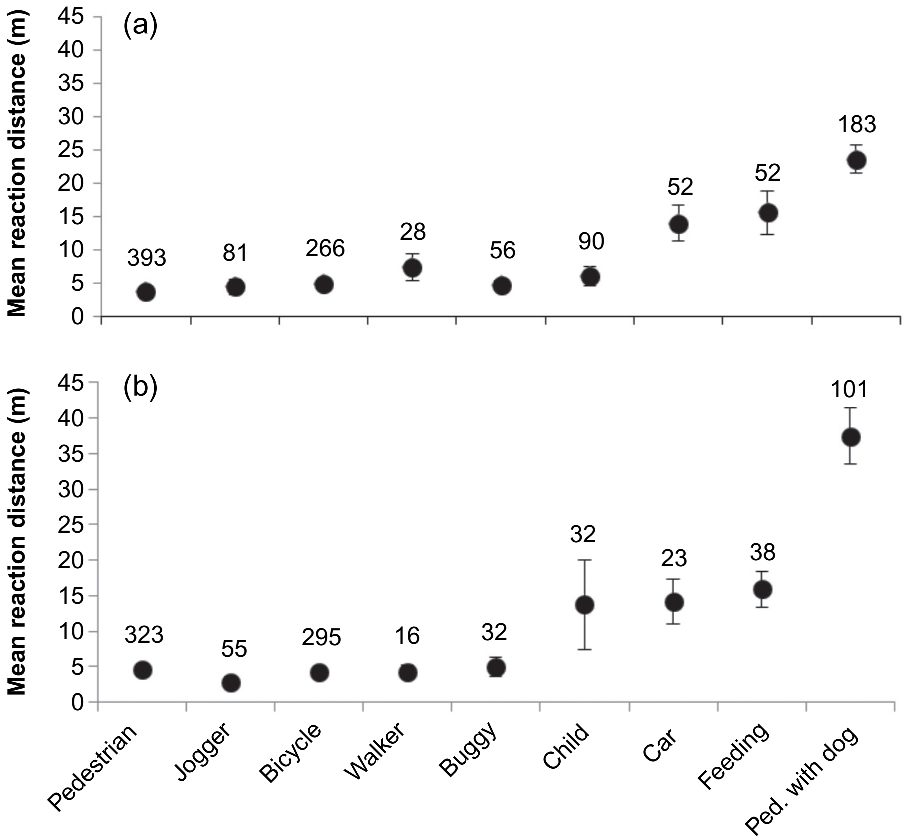

Figure 4. Mean reaction distance (± s.e.) by: (a) Greylag Geese, and (b) Egyptian Geese, in relation to the main disturbance stimuli. Sample sizes are indicated above the error bars.

The most frequent disturbance stimuli (pedestrians, cyclists and joggers) resulted in the lowest number of reactions (Bauer *et al.* 1992). This was similarly shown in a study by Schwarz (2010) in Greylag Geese, as well as a study on feral domestic Swan Geese (Randler 2003). Wascher *et al.* 2011 found that heart rate responses of Greylag Geese differed between familiar and unfamiliar humans, showing how learned experience shaped individual birds' responses to the same stimuli.

The social status of the geese also influenced their responses: Greylag Goose family groups reacted more frequently towards disturbance than non-breeding birds. Greylag Goose parents were extremely alert (also see Schwarz 2010). It was surprising that Egyptian Geese showed the opposite pattern, perhaps because they showed a higher level response by completely avoiding areas of known intensive disturbance. Egyptian Geese often stayed in close proximity to the water and were thus

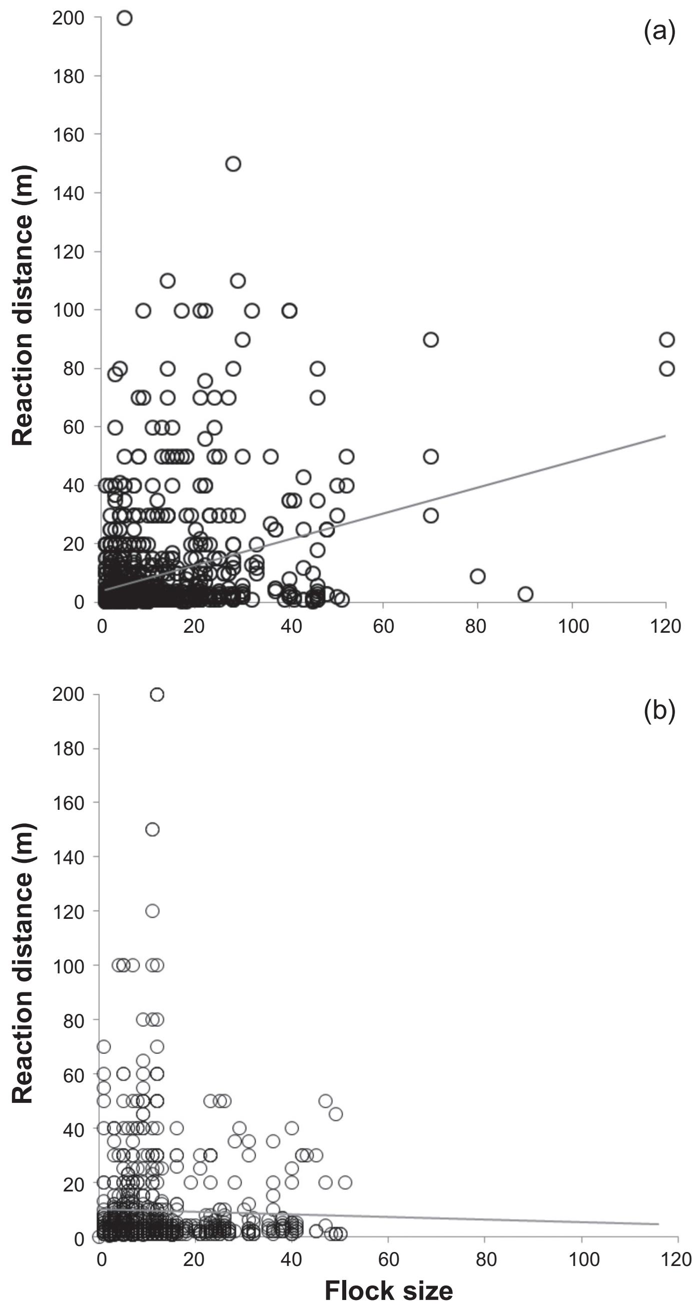

Figure 5. Reaction distance in (a) Greylag Geese (n = 1,294) and (b) Egyptian Geese (n = 986) in relation to flock size. All distances measured are shown.

able to flee to safety quickly at any one moment.

The probability of a reaction increased during the course of the day. This may be explained by daily routines of the geese. Geese usually flew or walked from their roost to grazing areas, and took a break from feeding in the middle of the day to loaf either on the lawns or at the small lakes nearby (Lorenz 1991). The probability of disturbance was low and restricted to the paths in the morning, when the geese were mainly grazing. Later, more people appeared as the geese loafed on paths and pastures, increasing the probability of disturbance. At the same time, temperatures increased during the course of the morning, reducing the probability of reaction by the geese. Maybe in the heat they tried to save energy by not moving more than necessary (Townsend *et al.* 2003).

In general, birds in urban areas show lower flight initiation distances than in rural areas (Møller 2008; Samia *et al.* 2017). We found that the mean reaction distances for both species were, on average, at < 10 m. In contrast, Bregnballe *et al.* (2009) describe reaction distances for Greylag Geese in Danish wetlands of up to 230 m. These differences are striking and potentially may have an effect on survival and reproductive success (Stankowich & Blumstein 2005). The reaction distances indicate that birds in the study area have learnt that some disturbance stimuli (pedestrians, joggers, bicycles) are predictable because these stay on the paths, whereas children and dogs move unpredictably and are therefore potentially more dangerous. Dogs are known to have injured geese in the study area (F. Woog, pers. obs.)

Only among Greylag Geese did reaction distance increase with flock size, a relationship also found by Kahlert (2006) in moulting Greylag Geese. It may be explained by the increased likelihood of a vigilant individual being a member of the flock or alternatively an increased chance of a false reaction among greater numbers of birds (Kahlert 2006). This may also point towards the more sophisticated social system that exists among Greylag Geese. By sharing vigilance duties among a larger group, they have more time for resting and feeding (*i.e.* Scheiber *et al.* 2013). Thus they profit from an early warning system but, for this benefit, they pay the addition cost of more frequent flight initiation, which expends energy.

The number of generations in an area is an important factor for the susceptibility to disturbance (Møller 2008). Greylag Geese have been established in the area of Stuttgart for a longer time period than Egyptian Geese, so natural selection may already have favoured individuals that are tamer. In Great Tits *Parus major* risk taking was 19.3% heritable (Van Oers *et al.* 2003) and in Black Swans *Cygnus atratus* the dopamine D4 receptor gene responsible for fear varied as a function of urbanisation (Van Dongen *et al.* 2014). Species-specific differences clearly point towards a genetic basis of tameness. This certainly needs further study.

To flee or to stay – this decision is an important one for birds (Cooper *et al.* 2015). To stay could mean to be injured or to even die; to flee may cost the expenditure of unnecessary energy. In Denmark, moulting Greylag Geese lost on average 19 min feeding time per disturbance (Kahlert 2006). In comparison to wild geese, for urban geese it may be essential for their survival and reproductive success to be "tamer" in an environment with frequent disturbance but comparatively little real danger to their lives. In Stuttgart, reaction distances of Egyptian Geese were much higher than those of Greylag Geese. Other advantages appear to override the lack of behavioural adaptation: unlimited nesting sites and a prolonged breeding season allow Egyptian Geese to reproduce up to three times a year in Europe (Lensink 1999; Hölzinger *et al.* 2018).

Within our small study population, we found that newly-colonising Egyptian Goose individuals showed more pronounced reactions toward disturbances in an urban setting than resident Greylag Geese. To be more "tame" may save energy by avoiding costly and unnecessary reactions and avoid stress, which may be especially important for large-bodied animals. It remains unclear whether the lower disturbance tolerance in Egyptian Geese explains higher gosling survival in this species or if this is due to another behavioural adaptation. To test for a possible adaptation to the urban environment, imilar studies are needed from more rural areas. It will be important to study further the ecological and life history traits that most associate with successful and unsuccessful species in urban environments. Furthermore, studies of fear behaviour and its genetics in long-lived individuals that are sampled repeatedly are needed to understand the basis of individual variation (Blumstein 2019) especially in a changing environment.

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Photograph: Greylag Goose chasing an Egyptian Goose in Stuttgart, by Gabriele Rohde