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1. Title: Consistent avoidance of human disturbance over large geographic distances by a migratory bird

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3. Summary

Recent works on animal personalities have demonstrated that individuals may show consistent behaviour across situations and contexts. These studies were often carried out in one location and/or during short time intervals. Many animals, however, migrate and spend their life in several geographically distinct locations, and they may either adopt specific behaviours to the local environment or keep consistent behaviours over ecologically distinct locations. Long-distance migratory species offer excellent opportunities to test whether the animals maintain their personalities over large geographic scale, although the practical difficulties associated with these studies have hampered such tests. Here we demonstrate for the first time consistency in disturbance-tolerance behaviour in a long-distance migratory bird, using the common crane *Grus grus* as an ecological model species. Cranes that hatched in undisturbed habitats in Finland choose undisturbed migratory stop-over sites in Hungary, 1300 - 2000 km away from their breeding ground. This is remarkable, because these sites are not only separated by large distances, they also differ ecologically: the breeding sites are wooded bogs and sub-Arctic tundra, whereas the migratory stop-over sites are temperate zone alkaline grasslands. The significance of our study goes beyond evolutionary biology and behavioural ecology: local effects on behaviour may carry over large distances, and this hitherto hidden implication of habitat selection needs to be incorporated into conservation planning.

4. Key words: carry-over; human disturbance; personality; common crane; wetland conservation

5. Introduction

Animals in the same population usually differ in their behaviour and underlying physiology [1-2]. Moreover, the same set of animals may show the same kind of differences in different situations (e.g. in level of predator avoidance at different foraging sites) and contexts (e.g. boldness in foraging and social interactions). For instance, great tits *Parus major* show consistent individual differences in exploring open field areas [3], and in mosquito fish *Gambusia affinis* asocial individuals show greater dispersal tendency [4]. Although individuals may adjust their behaviour depending on situations, nevertheless consistent differences between individuals usually remain. These are frequently characterized as animal personalities [5], temperament [6], behavioural syndromes or coping styles [7].

Many animals spend their life in several geographically distinct locations, and previous studies that investigate personality traits in a given location over short periods of time may not be able to estimate the importance of behavioural consistencies across contrasted ecological settings. Migratory insects, fishes, birds and mammals encounter wide range of habitats during their annual movements [8-9]; for instance Arctic terns *Sterna paradisea* fly over 70,000 km each year and cover vast range of habitats between their Arctic breeding ground and their wintering sites near Antarctica [10].

Animals may adopt two behavioural strategies when they encounter different ecological settings. On the one hand, they may exhibit different types of behaviour depending on local conditions during migration. On the other hand, they may show consistent behaviour even across highly contrasted environments [11].

Migratory species provide excellent opportunities to test these possibilities. Although the ability of migratory animals to exhibit consistent behavioural responses over large geographical areas has been suspected [12-13], no study has yet demonstrated such behaviour due to the challenges of tracking animal behaviour over large geographic distances.

Here we investigate the behavioural consistency in a long-distance migratory bird, the common crane using disturbance-tolerance behaviour. Human disturbance has large effect on the distribution, ecology and behaviour of animals [14-15], for instance, the spatial distribution of human settlements and density of roads influence avian habitat selection [16-17]. We hypothesised that the cranes' behavioural responses to human disturbance are consistent between their natal site and their migratory stop-over site that are separated by over 1000 km.

6. Material and Methods

We collected data between 1995-2007 in Hortobágy National Park in Hungary (N 47°30' E 21°0', Hortobágy henceforth) that is the largest alkaline steppe in Europe (80,200 ha), an UNESCO World Heritage Site and protected by Ramsar Convention. Hortobágy is surrounded by 18 settlements (min - max no. of inhabitants: 1950 - 50,000).

We use data on 273 cranes that were marked as chicks in Finland between 1985 and 2007 by individual combinations of colour rings, and resighted in Hortobágy between 1995 and 2007 (Fig 1a). Locations of nest sites were collected by PM, and resighting data were acquired from the Hungarian Bird Ringing Centre (Budapest). Five proxy variables of human disturbance were estimated from 1:16,000 maps of the National Land Survey of Finland (http://kansalaisen.karttapaikka.fi/kartanhaku/osoitehaku.html), and the Hortobágy National Park's GIS map (unpublished), respectively: proximity (km^{-1}) to the nearest (1) tarmac road and (2) human settlement, and perturbance i.e. density (ha^{-1}) of (3) tarmac roads, (4) human settlements and (5) human population. Since common crane territories are approximately 3-4 hectares [10], we estimated these variables within a 1 km radius around nests. On migration, the cranes move between roost sites and feeding sites, and since these are within 10 km, we estimated all five variables in a 10 km radius around roost sites [18].

Out of 273 cranes, 138 were observed at least twice (up to 10 times) in Hortobágy. For individuals observed several times in a year, we calculated the within-year repeatability of the disturbance variables. For those cranes which have been recorded repeatedly in different years we calculated between-year repeatability of the disturbance variables [19]. To investigate the consistency in behaviour between natal sites in Finland and migratory sites in Hortobágy, we fitted Linear Mixed Effects Models (LMMs) using disturbance-variables on the migratory site as response variables, and disturbance variables on the natal sites as fixed effects for all possible pairwise combinations (25 models in total, [20]). A positive *t* value, a proxy of effect size, indicates consistent result with the working hypothesis. Regions within Finland (as a control for spatial autocorrelation), and Bird ID were included in LMMs as nested random factors. We performed all statistical analyses in R [21].

7. Results

Cranes used 10.24 ±1.03 [mean ± SE] different roost sites in Hortobágy each year, and those cranes that were observed several times within a year used 3 (2-4.75) sites per year. Four of the five disturbance-tolerance variables were significantly repeatable both within and between years for individual cranes (Table 1). This indicates a high level of behavioural consistency both within a particular year, and over the study period for a given individual.

Out of 25 pairwise models, 24 showed positive relationships between disturbance tolerance in the natal and migratory sites (binomial test using 0.5 expectation, $p < 10^{-5}$, Table 2). Support for the research hypothesis was also indicated by the positive average *t*-values, and that their 95% confidence intervals did not include zero (Fig 1b).

8. Discussion

Common cranes show consistent disturbance-tolerance behaviour between years, and between natal and migratory sites separated by over 1000 km. As far as we are aware, our study is the only that demonstrates long-lasting individual differences in response to human disturbance using individually marked birds. Consistent disturbance-tolerance behaviour may emerge in three mutually non-exclusive ways. First, young cranes may be imprinted to certain levels of human disturbance by the location of their nest, and they seek out these features during migration. Second, common cranes have extensive parental care that last up to 10 months after hatching [10]. Therefore, the young crane's migratory behaviour may be influenced by their parents' behaviour [22]. This carry-over of information may lead to cultural transmission of habitat preference in regards to disturbance [23]. Third, habitat preference may have a genetic component so that certain genotypes tolerate more disturbance than others.

Previous studies demonstrated consistent behaviour in various context including exploration, aggression, anti-predator behaviour, parental provisioning and cooperation [24-26]. Our work adds to these by showing personality-related traits in disturbance-tolerance behaviour. Also, we expand the scope of personality by showing that cranes behave consistently over a long time period and between habitats with very different ecological conditions, such as northern wooded bogs, subarctic tundra and temperate zone alkaline grassland.

It would be interesting to investigate whether habitat preference correlates with other personality traits e.g. flushing distance, exploration behaviour, or physiological reactions to handling. Unfortunately, we are unable to address this proposition here because of the lack of appropriate data from individually marked cranes.

The process we demonstrate here is similar to the ecological carry-over, whereby events during one period of the annual cycle in migratory animals influence reproductive success in a subsequent season [13, 27-28]. We propose that both the carry-over from one season to another, and the consistent behavioural responses to disturbance we demonstrate here, imply that conservation-decisions for migratory species should be made at a larger geographic scale than is currently the case.

To conclude, disturbance sensitivity, a consistent personality trait is retained in migratory species over large temporal and spatial scales as well as habitat types, and thus affecting habitat choice. These effects should be incorporated into conservation planning and policies.

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Tables

Table 1. Repeatability of disturbance-tolerance behaviour (r ± SE) in common cranes in migratory stop-over site. Significant relationships are in bold, and df refers to between and within group degrees of freedoms.

variable	r ± SE	df	F (p)
Within-year repeatability			
Distance to human settlement	0.658 ± 0.027	32; 48	5.709 **(<0.001)**
Distance to road	0.437 ± 0.300	32; 48	2.896 **(<0.001)**
Settlement size density	0.623 ± 0.029	32; 48	5.053 **(<0.001)**
Human population density	0.192 ± 0.019	32; 48	1.58 (0.074)
Road density	0.545 ± 0.300	32; 48	3.931 **(<0.001)**
Between-year repeatability			
Distance to human settlement	0.203 ± 0.021	127; 195	1.643 **(<0.001)**
Distance to road	0.229 ± 0.023	127; 195	1.748 **(<0.001)**
Settlement size density	0.032 ± 0.005	127; 195	1.084 (0.304)
Human population density	0.190 ± 0.020	127; 195	1.592 **(0.002)**
Road density	0.174 ± 0.019	127; 195	1.531 **(0.004)**

Table 2. Student's *t*-values from Linear Mixed Effects Models (LMMs) fitted to disturbance-tolerance variables in migratory stop-over site in Hortobágy (dependent variable, migratory site) and natal site in Finland (predictor variable). Random effects (Regions within Finland and Bird ID) were included in LMMs as nested random factors. Significant relationships ($p < 0.05$) are in bold. The numbers in parentheses give parameter estimates.

Disturbance tolerance in Finland

Dependent variables	Distance to human settlement (km^{-1})	Distance to road (km^{-1})	Human population density (ha^{-1})	Settlement size density (ha^{-1})	Road density (ha^{-1})
Settlement distance	0.428 (0)	0.529 (0)	-0.366 (-0.001)	0.845 (0)	0.544 (0.001)
Distance to road	0.448 (0.001)	**3.012 (0.014)**	**2.332 (0.03)**	0.817 (0.003)	0.503 (0.007)
Settlement size density	0.998 (5.595)	**2.263 (17.925)**	0.014 (0.284)	1.839 (9.827)	1.184 (26.75)
Human population density	0.633 (30.769)	**3.028 (207.278)**	1.847 (366.444)	1.219 (61.743)	0.319 (69.412)
Road density	0.561 (0.033)	**2.441 (0.204)**	1.649 (0.4)	1.032 (0.064)	0.331 (0.088)

Figure legends

Figure 1. Disturbance tolerance in a long-distance migratory bird, the common crane. (a) Natal and migratory stop-over sites of 273 resighted cranes in Finland and Hungary, respectively. (b) The average effect size of the disturbance variables in Finland calculated as the mean of Student's *t*-values over the Hortobágy disturbance variables from Linear Mixed Effects Models (for details see Methods and Table 1). Proximity refers to distances from human settlement and roads, and perturbance refers to density of settlements, human population and roads. Means ± 95% confidence intervals are shown.