

Author Queries

Journal: Biology Letters

Manuscript: rsbl20110295

- Q1** Please supply author name and year for the unpublished data.
- Q2** Support for the research... Please check the edit of the sentence.
- Q3** Please supply complete details for ref. [22].
- Q4** Figure 1 is low resolution. Please provide better resolution figure (at least 300 ppi at 80 mm).

Consistent avoidance of human disturbance over large geographical distances by a migratory bird

Zsolt Végvári^{1,3,*}, Zoltán Barta²,
Pekka Mustakallio⁴ and Tamás Székely⁵

¹Department of Conservation Biology, and ²Department of Evolutionary Zoology, University of Debrecen, Debrecen 4010, Hungary

³Hortobágy National Park Directorate, 4024 Debrecen, Hungary

⁴Finnish Crane Working Group, Helsinki 00100, Finland

⁵Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, UK

*Author for correspondence (vegvári@hmp.hu).

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 geographical 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 subarctic 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.

Keywords: carry-over; human disturbance; personality; common crane; wetland conservation

1. 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 owing to the challenges of tracking animal behaviour over large geographical distances.

Here we investigate the behavioural consistency in a long-distance migratory bird, the common crane, using disturbance-tolerance behaviour. Human disturbance has a 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 hypothesized 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.

2. MATERIAL AND METHODS

We collected data between 1995 and 2007 in Hortobágy National Park in Hungary (47°30' N, 21°0' E, Hortobágy henceforth), which 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 (figure 1a). Locations of nest sites were collected by P.M., and resighting data were acquired from the Hungarian Bird Ringing Center (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 data), respectively: proximity (km⁻¹) to the nearest (i) tarmac road and (ii) human settlement, and perturbation, i.e. density (ha⁻¹) of (iii) tarmac roads, (iv) human settlements, and (v) human population. Since common crane territories are approximately 3–4 ha [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].

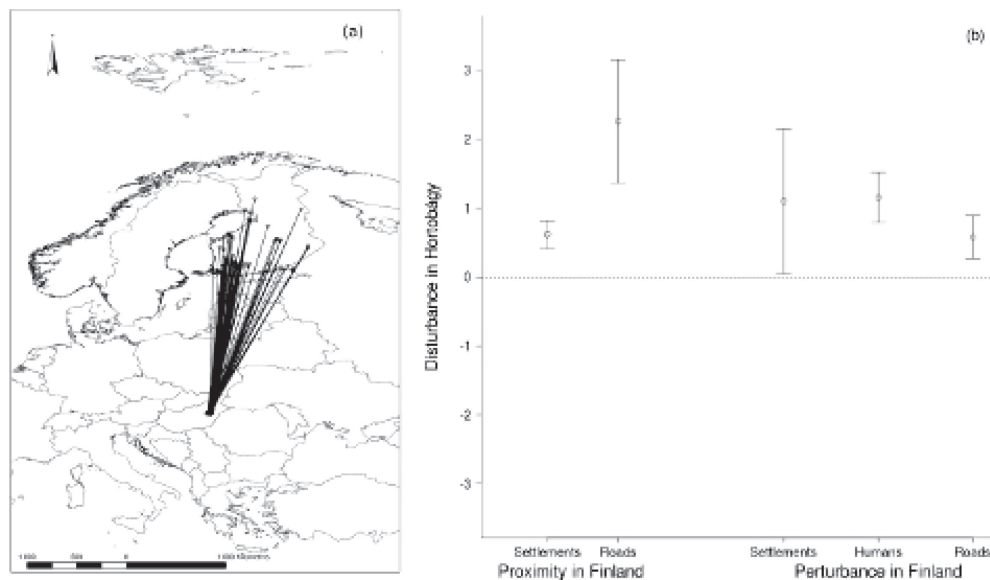


Figure 1. Disturbance tolerance in a long-distance migratory bird, the common crane. (a) Natal and migratory stop-over sites of 273 resighted cranes in Finland and Hungary, respectively. (b) The average effect size of the disturbance variables in Finland calculated as the mean of Student's *t*-values over the Hortobágy disturbance variables from linear mixed-effects models (for details, see §2 and table 1). Proximity refers to distances from human settlement and roads, and perturbation refers to density of settlements, human population and roads. Means \pm 95% confidence intervals are shown. Q4

Table 1. Repeatability of disturbance-tolerance behaviour ($r \pm$ s.e.) in common cranes in migratory stop-over site. Significant relationships are in bold, and d.f. refers to between- and within-group degrees of freedom.

variable	$r \pm$ s.e.	d.f.	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)

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 that 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].

3. RESULTS

Cranes used 10.24 ± 1.03 (mean \pm s.e.) different roost sites in Hortobágy each year, and those cranes that were observed several times within a year used three (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 their 95% confidence intervals did not include zero (figure 1b). Q2

4. 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 one that demonstrates long-lasting individual differences in response to human disturbance using individually marked birds. Consistent disturbance-tolerance behaviour may emerge in three

Table 2. Student's *t*-values from linear mixed-effects models (LMMs) fitted to disturbance-tolerance variables in the migratory stop-over site in Hortobágy (dependent variable, migratory site) and the 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)

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 lasts 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 contexts, 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 geographical 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.

- Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004 The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**, 734–739. (doi:10.1111/j.1461-0248.2004.00618.x)
- Dingemanse, N. J., Kazem, A. J. M., Réale, D. & Wright, J. 2010 Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol. Evol.* **25**, 81–89. (doi:10.1016/j.tree.2009.07.013)
- Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K. & van Noordwijk, A. J. 2002 Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.* **64**, 929–938. (doi:10.1006/anbe.2002.2006)
- Cote, J., Fogarty, S., Weinersmith, K., Bordin, T. & Sih, A. 2010 Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proc. R. Soc. B* **277**, 1571–1579. (doi:10.1098/rspb.2009.2128)
- Gosling, S. D. 2001 From mice to men: what can we learn about personality from animal research? *Psychol. Bull.* **127**, 45–86. (doi:10.1037/0033-2909.127.1.45)
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007 Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318. (doi:10.1111/j.1469-185X.2007.00010.x)
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W. & Blokhuis, H. J. 1999 Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* **23**, 925–935. (doi:10.1016/S0149-7634(99)00026-3)
- Dingle, H. 1996 *Migration: the biology of life on the move*. New York, NY: Oxford University Press.
- Newton, I. 2010 *Bird migration*. London, UK: Collins.
- Snow, D. W. & Perrins, C. M. 1998 *The Birds of the Western Palearctic. Concise edition*. Oxford, UK: Oxford University Press.
- Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994 Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446.
- Sutherland, W. J. 1998 The importance of behavioural studies in conservation biology. *Anim. Behav.* **56**, 801–809. (doi:10.1006/anbe.1998.0896)
- Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R. & Bearhop, S. 2010 Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.* **80**, 4–18. (doi:10.1111/j.1365-2656.2010.01740.x)
- Dingle, H. & Drake, A. 2007 What is migration. *Bioscience* **57**, 113–121. (doi:10.1641/B570206)
- Blumstein, D. T. 2006 Developing an evolutionary ecology of fear: how life history and natural history traits

- 385 affect disturbance tolerance in birds. *Anim. Behav.* **71**,
 386 389–399. (doi:10.1016/j.anbehav.2005.05.010)
- 387 16 Marzluff, J. M., Bowman, R. & Donnelly, R. (eds) 2001
 388 *Avian ecology and conservation in an urbanizing world*.
 389 Boston, MA: Kluwer Academic.
- 390 17 Underhill, J. E. & Angold, P. G. 2000 Effects of roads on
 391 wildlife in an intensively modified landscape. *Environ.*
 392 *Rev.* **8**, 21–39. (doi:10.1139/er-8-1-21)
- 393 18 Végvári, Z. & Tar, J. 2002 Roost site selection of the
 394 Common Crane *Grus grus* in the Hortobágy National
 395 Park, Hungary between 1995–2000. *Ornis Fenn.* **79**,
 396 101–110.
- 397 19 Harper, D. G. C. 1994 Some comments on the repeat-
 398 ability of measurements. *Ring. Migr.* **15**, 84–90.
- 399 20 Crawley, M. J. 2007 *The R Book*. London, UK: UK
 400 Imperial Collage London at Silwood Park.
- 401 21 R Development Core Team. 2010 The R project for
 402 statistical computing. See <http://www.r-project.org> (last
 403 visited 01 May 2010).
- 404 22 Swanberg, P. O. 1974 Notes on the population of
 405 Common Crane in Scandinavia and Finland: a prelimi-
 406 nary survey. In *Crane research around the world*,
 407 pp. 184–185.
- 408 23 Sokolowski, M. B. & Levine, J. D. 2010 Nature–nurture
 409 interactions. In *Social behaviour: genes, ecology and*
 410 *evolution* (eds T. Székely, J. Komdeur & A. J. Moore).
 411 Cambridge, UK: Cambridge University Press. 449
- 412 24 Dingemans, N. J., Wright, J., Kazem, A. J. N., Thomas,
 413 D. K., Hickling, R. & Dawnay, N. 2007 Behavioural
 414 syndromes differ predictably between 12 populations of
 415 stickleback. *J. Anim. Ecol.* **76**, 1128–1138. (doi:10.
 416 1111/j.1365-2656.2007.01284.x) 450
- 417 25 Martin, J. & Réale, D. Animal temperament and human
 418 disturbance: implications for the response of wildlife to
 419 tourism. *Behav. Process.* **77**, 66–72. 451
- 420 26 English, S., Nakagawa, S. & Clutton-Brock, T. H. 2010
 421 Consistent individual differences in cooperative behav-
 422 iour in meerkats (*Suricata suricatta*). *J. Evol. Biol.* **23**,
 423 1597–1604. 452
- 424 27 Gunnarsson, T. G., Gill, J. A., Newton, J., Potts, P. M. &
 425 Sutherland, W. J. 2005 Seasonal matching of
 426 habitat quality and fitness in a migratory bird. *Proc.*
 427 *R. Soc. B* **272**, 2319–2323. (doi:10.1098/rspb.2005.
 428 3214) 453
- 429 28 Webster, M. S. & Marra, P. P. 2005 The importance of
 430 understanding migratory connectivity and seasonal
 431 interactions. In *Birds of two worlds. The ecology and*
 432 *evolution of migration* (eds R. Greenberg & P. P. Marra),
 433 pp. 199–209. Baltimore, MD: Johns Hopkins University
 434 Press. 454
- 435 455
- 436 456
- 437 457
- 438 458
- 439 459
- 440 460
- 441 461
- 442 462
- 443 463
- 444 464
- 445 465
- 446 466
- 447 467
- 448 468
- 449 469
- 450 470
- 451 471
- 452 472
- 453 473
- 454 474
- 455 475
- 456 476
- 457 477
- 458 478
- 459 479
- 460 480
- 461 481
- 462 482
- 463 483
- 464 484
- 465 485
- 466 486
- 467 487
- 468 488
- 469 489
- 470 490
- 471 491
- 472 492
- 473 493
- 474 494
- 475 495
- 476 496
- 477 497
- 478 498
- 479 499
- 480 500
- 481 501
- 482 502
- 483 503
- 484 504
- 485 505
- 486 506
- 487 507
- 488 508
- 489 509
- 490 510
- 491 511
- 492 512