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RESEARCH PAPER

Behavioural responses of grey herons *Ardea cinerea* and great egrets *Ardea alba* to human-caused disturbance

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Abstract. This study examined the effects of different types on anthropogenic disturbance on behaviours of grey herons *Ardea cinerea*, and great egrets *Ardea alba*, that gather in an Important Bird Area near Belgrade (Serbia), during their autumn migration, with the goal of assessing how diverse human-caused stimuli affect the behaviours of foraging and resting birds. I obtained behavioural data through scan sampling, with six categories of behaviour distinguished: vigilant, flying, feeding, comfort, inactive and other. In total, I collected 5,065 observations of individual birds: 1,293 for grey herons and 3,772 for great egrets. Significantly more birds were vigilant or in flight when they were disturbed by construction vehicles, military jets, and rural free-ranging dogs, whereas no statistical significance was associated with shooting and passing cars. Using a linear mixed model, it was shown that a greater proportion of birds was vigilant during disturbance than following disturbance or in the absence of disturbance, whereas air temperature and wind speed were not statistically significant. This study demonstrates that anthropogenic disturbance can alter the behaviour of the study species, which could aid future management and conservation planning.

Key words: anthropogenic disturbance, vigilance, flight response, behaviour, IBA

Introduction

Various human activities, from those involving alterations of the landscape to those represented by the mere presence of people, can disturb wildlife (Price 2008). Responses of animals to anthropogenic disturbance are diverse and dependent on the intensity and frequency of disruption, but also the biological characteristics of the disturbed individuals, as well as of environmental conditions (Tablado & Jenni 2017). The most basic form of reaction, which occurs after detection of disturbance, involves physiological and behavioural responses to anthropogenic stimuli (Tablado & Jenni 2017). These responses may further reduce the fitness of disturbed animals, and affect the

way they use suitable habitats; e.g. disturbed animals may suffer prolonged stress, abandon their nests or profitable feeding areas (Anderson 1988, Ellenberg et al. 2007). Ultimately, frequent disturbance events or those affecting areas containing a large part of a population may lead to reduction in population size and a change in the spatial distribution of populations (Thiel et al. 2008, Tablado & Jenni 2017).

Behavioural reactions to anthropogenic disturbance typically resemble those that would be caused by predators (Frid & Dill 2002). Animals have evolved antipredator responses to any potentially threatening stimulus, and thus approaching humans, vehicles, or noise produced by aircraft may elicit flight or increased

vigilance in disturbed animals, even though these activities usually do not harm them directly (Frid & Dill 2002, Berger-Tal & Saltz 2016). Antipredator behaviours in such situations are redundant, may increase the level of stress, and divert animals from feeding or other fitness enhancing activities (Burger & Gochfeld 1998, Fernández-Juricic et al. 2007, Ciuti et al. 2012). The link between behavioural responses to human disturbance and its impact on animal welfare, however, is not always straightforward. For example, animals remaining in a disturbed area may misleadingly appear unaffected by disturbance while suffering chronic stress, whereas animals leaving the area may benefit by moving to better quality sites (Beale 2007, Gill 2007). Nevertheless, as direct indicators of the impact of human activities on animals, such as survival and fecundity, are often difficult to estimate, many studies measure behavioural responses. Irrespective of its limitations, behavioural research may still provide useful information on how animals react to different sources of disturbance (Gutzwiller & Cole 2005, Sutherland 2007), which may be valuable in early phases of the assessment of human impacts on wildlife.

Here I examined the effects of various types of anthropogenic disturbance on behaviours of grey herons Ardea cinerea (hereafter herons) and great egrets Ardea alba (hereafter egrets), during their autumn migration within an Important Bird Area that is recognized as a significant breeding and wintering habitat, as well as a migratory stopover for various species of waterbirds (Puzović et al. 2009). In general, it is well documented how herons and egrets react to human activities while in their breeding colonies, particularly for species breeding in North America (e.g. Vos et al. 1985, Rodgers & Smith 1995, Skagen et al. 2001, Fernández-Juricic et al. 2007). However, information on the behavioural responses of the two species when exposed to different human-caused disturbance outside the breeding period is strikingly absent from the literature. In addition, the study area has been proposed as a protected nature reserve, and thus information on how human activities affect the behaviour of birds may be important for the development of future conservation strategies. Therefore, I aim to investigate how diverse anthropogenic stimuli affect the behaviours of herons and egrets that gather to forage and rest during the period of autumn migration.

Material and Methods

The study was conducted in Beljarica, Serbia (44.91 N, 20.36 E), from 19 September to 26 November 2019. The study area is the Danube floodplain in the vicinity of Belgrade (distanced 20 km from the city centre), situated between the river and a 10 km long embankment. Much of the area is covered with the riparian forest dominated by willow (Salix sp.) and poplar (Populus sp.), as well as poplar plantations, intersected by backwaters and ponds. The study location is also an Important Bird Area used for recreational activities, including birdwatching, fishing, and hunting. Grey herons and great egrets use ponds along the embankment for foraging and resting during and outside the breeding season (Puzović et al. 2009, Sekulić & Sekulić 2013).

Prior to the onset of data recording, I constructed an ethogram for the two studied species. To describe behaviours, using a digital camcorder, I recorded 30 focal individuals (19 herons, 11 egrets) whose behaviour was subsequently observed; the median duration of focal observations was 3 min (range 1-5 min). The following categories of behaviour were distinguished: 1) vigilant, 2) flying, 3) feeding, 4) comfort, 5) inactive and 6) other types of behaviour. Vigilance is typically described as the state of alertness allowing animals to detect stimuli from their surroundings (Beauchamp 2015). In birds, a common indication of antipredator vigilance is a behavioural posture with an upright head allowing individuals to inspect the environment (Beauchamp 2014). Although vigilance may be induced by conspecifics, it is typically considered to be disturbance-related behaviour (Riddington et al. 1996, Sastre et al. 2009, Beauchamp 2015). In observed herons and egrets vigilance was distinguished from other behaviours by noticeable prolonged gaze (lasting more than several seconds), not necessarily directed toward the source of disturbance, as laterally placed eyes allow birds to scan a wide portion of the space that surrounds the head (Martin 2007). In addition to vigilance, flight can also be a consequence of disturbance, as birds usually tend to move away from the source of disturbance (Fernández-Juricic et al. 2001, Sastre et al. 2009, Burger et al. 2010). To avoid recording birds whose behaviours was not related to conditions at the study site, I did not record individuals flying high over the study area. Details on all behavioural patterns observed in herons and egrets are listed in Table 1.

Observations were conducted during daylight (8-15 h), three to four hours during each visit; in total, the birds were observed ten days within the study period, with a 0-10 days interval between subsequent visits. The approximate area where I was able to

Table 1. General categories of behaviour observed in grey herons and great egrets.

Behaviour	Description
Vigilant	Stationary or walking, watching ahead or above (with bill horizontal or pointed up, respectively), often tilting or moving head from side to side, with or without stretched neck
Flying	Flying low above the study area, flying up or flying down; birds flying high over the study area were not recorded
Feeding	All aspects of food acquisition (searching for, attacking, capturing and swallowing prey) and drinking
Comfort	Preening, scratching, stretching, shaking, wing flapping, sunbathing, bathing, panting
Inactive	Inactivity, including resting and sleeping
Other	All other behaviours (e.g. social, yawning)

observe birds was 9 ha. To obtain behavioural data, at regular intervals (10-15 min), all herons and egrets observable on the pond and nearby vegetation were scanned, from one vantage point on the embankment at an approximate distance of 300-600 m. I did not record behaviours of birds closer than 300 m, as many of them appeared to be alert to my presence. The birds were observed using a 30 × 77 spotting scope (Kowa TSN-770), with the behaviour of each individual dictated on a voice recorder. In addition to behavioural data, I also recorded the occurrence of anthropogenic disturbance as "no disturbance", "during disturbance" (i.e. disturbance occurring during bird scanning), and "after disturbance" (i.e. disturbance occurring two-three minutes prior to bird scanning). The following types of disturbance were distinguished: 1) shooting heard from a nearby forest; 2) cars passing along the embankment; 3) construction vehicles engaged in maintenance activities on the shore; 4) military jets flying above the study location; 5) rural free-ranging dogs. I was not able to determine the distance to the source of shooting, as hunting of wild boar (Sus scrofa) takes place within a broad area of the riparian forest (D. Simić, pers. comm.), in proximity to the ponds where herons and egrets were observed. Similarly, it was not possible to determine distance to military jets, which frequently changed their height above the study area. For that reason, I considered that the noise produced by aircraft and shooting had a potential to disturb all birds present in the study area regardless of their position relative to the source of disturbance. However, other types of disturbance were localized, occurring at the particular site of the shore or the embankment. Thus, cars passing along the embankment were recorded as disturbance (either as "during" or "after" disturbance) when passing along the embankment in line (± 50 m) with birds; the distance between focal birds and passing vehicles ranged from 50 to 250 m. Likewise, the activity of construction vehicles and

free-ranging dogs was recorded as disturbance only for birds within an approximately 200 m radius. As there were no visual obstructions between ponds, where herons and egrets were observed, and the embankment and shore, where these activities occurred, I considered that cars, construction vehicles and dogs had a potential to disturb all the birds within the above specified portion of the pond. At the beginning of each scan sampling, I also recorded the ambient temperature and wind speed using a digital thermometer/anemometer.

To examine differences in the behaviour of birds during, after, and in the absence of human disturbance, I used a Chi-square test, with Bonferroni correction for pairwise comparisons. The Chi-square test was also used to examine differences in the behaviour of birds when exposed to different types of human disturbance; for the latter analysis, vigilance and flight were combined into a single, disturbance-related behavioural category. Data recorded when more than one source of disturbance was present were not included in this analysis (e.g. both shooting and construction vehicles acted at the same time).

Vigilance is affected by a number of social and environmental variables (Beauchamp 2015), therefore I conducted a multiple regression analysis where some of those confounding variables were accounted for. At first, I considered the following explanatory variables: disturbance, time of day (expressed as the number of hours passed since eight o'clock in the morning), air temperature, and wind speed. However, as the two variables – time of day and air temperature – where highly correlated (r = 0.79, P < 0.001), time of day was not included in analysis. Hence, the linear mixed model included the percent of birds being vigilant per scan sample as a response variable, whereas disturbance (none, during, and after), air temperature, and wind speed where used

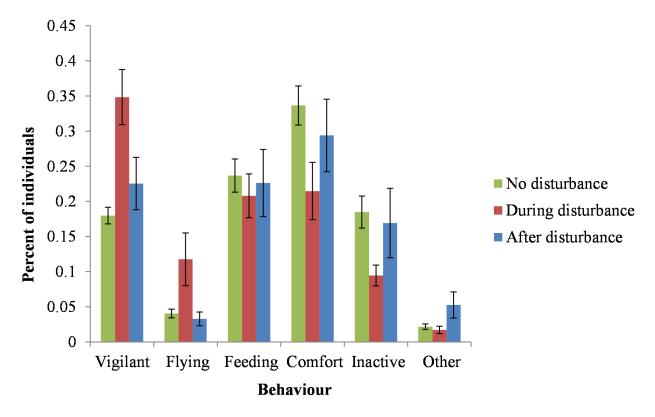


Fig. 1. Mean proportion of grey herons and great egrets (± SE) engaged in various types of behaviour in the absence of human-caused disturbance, during disturbance, and after disturbance.

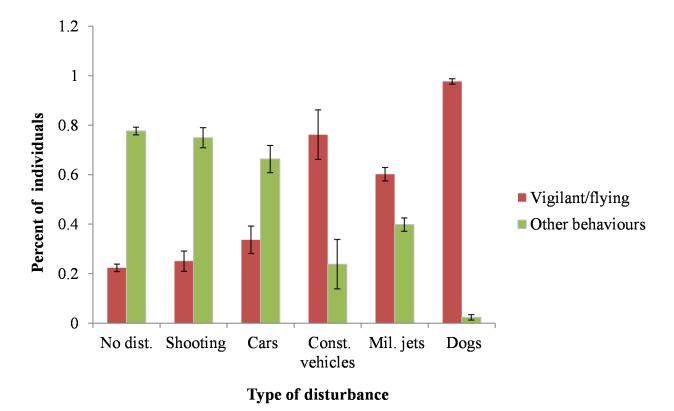


Fig. 2. Mean proportion of grey herons and great egrets (± SE) exhibiting disturbance-related behaviours (vigilance and flight) and all other behaviours in the absence of disturbance (No dist.) and during disturbance caused by: shooting, passing cars, construction vehicles engaged in maintenance activities on the shore (Const. vehicles), military jets flying above the study location (Mil. jets), and rural, free-ranging dogs.

Table 2. Summary of the main effect of independent variables on measures of the proportion of vigilant grey herons and great egrets. The table provides coefficient estimates for numerical variables - temperature and wind - and least square means for multiple comparisons of categorical variables - three levels of anthropogenic disturbance: "no disturbance", "during disturbance" and "after disturbance".

Variables	Coefficients or Least square means (SEM)	<i>P</i> -value	
Temperature	-0.001 (0.007)	0.921	
Wind speed	0.006 (0.022)	0.801	
Disturbance		< 0.001	
During-after	0.190 (0.056)	0.002	
During-none	0.249 (0.042)	< 0.001	
After-none	0.059 (0.054)	1.000	

as explanatory variables; the date of observation was treated as a random factor. The disturbance variable combined all types of disturbance, as there were too few data to analyse the effect of each category of disturbance separately. To normalize the data, the response variable was log₁₀-transformed after adding a small constant (McDonald 2014). Group size, distance to nearest neighbour, and position within a group exert strong influence on vigilance (Beauchamp 2015). Nevertheless, herons and egrets were spread out across a large surface of water, with well-distanced foraging birds, and birds resting on logs and trees in close proximity. For that reason, it was difficult to discern which birds constituted a flock, particularly if they were far away, and thus these variables were not included in the model. Model validation was conducted using diagnostic plots (a histogram of residuals, Q-Q plot, and residuals plotted vs. fitted values); the auto-correlation of residuals was examined using the ACF function (Zuur et al. 2009). All statistical analyses were carried out using R v4.4.1. (R Core Team 2021), using the packages: car (Fox & Weisberg 2019), nlme (Pinheiro et al. 2021), emmeans (Lenth 2021), predictmeans (Luo et al. 2021), and rcompanion (Mangiafico 2021).

Results

I conducted 103 scan observations (5,065 observations of individual birds: 1,293 grey herons and 3,772 great egrets), 47 of which occurred with no disturbance, 40 during disturbance, and 16 after disturbance; the number of individuals per scan sample ranged from 10 to 129 individuals; the median was 42. On average, 25% of scanned birds were observed being vigilant, 7% were in flight, 22% were feeding, 28% were engaged in comfort activities, 15% were inactive and 3% were observed engaging in other behaviours. Significantly more birds were vigilant compared to other behaviours during disturbance than in the absence of disturbance ($\chi^2 = 364.91$, P <

0.001) or after disturbance ($\chi^2 = 119.86$, P < 0.001), whereas the difference between the number of birds being vigilant in the absence and after disturbance was not significant ($\chi^2 = 0.16$, P = 1.00). Similarly, more birds were in flight during disturbance than in the absence of disturbance (χ^2 = 292.71, P < 0.001) or after disturbance (χ^2 = 61.92, P < 0.001), while there was no significant difference between the number of flying birds after disturbance and in the absence of disturbance ($\chi^2 = 1.67$, P = 0.59), (Fig. 1). In addition, significantly more birds were vigilant or in flight when they were disturbed by construction vehicles $(\chi^2 = 524.94, P < 0.001)$, military jets $(\chi^2 = 61.45,$ P < 0.001), and rural free-ranging dogs ($\chi^2 = 626.84$, P < 0.001), compared to undisturbed birds, whereas no statistical significance was associated with shooting and cars passing along the embankment (Fig. 2). In the mixed model, a greater proportion of birds was vigilant during disturbance than in the absence or after disturbance. Air temperature and wind speed were not statistically significant in the model (Table 2).

Discussion

Anthropogenic disturbance initiates immediate behavioural responses in disturbed animals, typically antipredator responses, such as vigilance or flight (Frid & Dill 2002). Many studies have shown that the incidence of vigilant or fleeing animals, or the time they devote to vigilance, increases when they are disturbed. For example, several species of aquatic birds increased the number of look-ups per unit time in the presence of people (Burger & Gochfeld 1998). In piping plovers Charadrius melodus time being vigilant increased with the number of people in their proximity (Burger et al. 1995), whereas Eurasian coots Fulica atra increased both the frequency and duration of vigilance bouts when exposed to dog barking (Randler 2006). Also, the proportion of vigilant whooper swans Cygnus cygnus and the number of common terns Sterna hirundo flying above the colony increased with the intensity of anthropogenic disturbance (Burger 1998, Rees et al. 2005). In the present study, the proportion of herons and egrets that were vigilant or in flight was similarly observed to be greater when exposed to certain types of human-caused disturbance, while fewer birds were engaged in foraging, resting and comfort activities. Although the behavioural responses of disturbed animals do not necessarily imply fitness consequences, several studies have demonstrated energetic costs of disturbance due to increased flight at the expense of feeding, e.g. in snow geese Anser caerulescens, American coots Fulica americana and knots Calidris tenuirostris and C. canutus (Bélanger & Bédard 1990, Schummer & Eddleman 2003, Rogers et al. 2006), which ultimately may lead to decreased survival or reproductive success (Villegas-Amtmann et al. 2015, Pirotta et al. 2018).

Not all forms of disturbance equally affected herons and egrets: they reacted strongly to free-ranging dogs, military jets, and construction vehicles operating on the shore, whereas the sound of shooting and cars on the embankment had little effect on them. The activity of roaming dogs caused vigilance in the majority of observed individuals, particularly as the dogs approached close to the birds. Birds often respond to freeranging dogs with vigilance and escape. Free-ranging dogs were the most greatest source of disturbance to great bustards Otis tarda, with the probability of disturbance exceeding 50% (Rees et al. 2005). Similarly, shorebirds show considerable sensitivity to unleashed dogs and react by fleeing at longer distances to dogs than to pedestrians (Lafferty 2001). Such sensitivity of birds toward free-ranging dogs may be due to the unpredictable movements of dogs, which is often accompanied by approaches and chasing (Lafferty 2001, Rees et al. 2005). Manoeuvres of military jets also increased the proportion of vigilant herons and egrets. Goudie (2006) concluded that because these aircraft produce substantial high-amplitude noise, they could be a major stressor of birds; in his study, harlequin ducks Histrionicus histrionicus exhibited more alert behaviours and inactivity when disturbed by military jets than by other types of aircrafts producing less noise. Similarly, noise and noise-induced structural vibrations produced by supersonic transport aircraft most likely caused flushing of waterbirds, which was absent when other types of aircraft passed overhead (Burger 1981). The activity of construction vehicles in the study area was another factor disturbing herons and egrets by increasing the proportion of flying

birds. Bulldozers and dump trucks, which were flattening the terrain close to a pond used by birds, produced both visual and auditory stimuli, causing birds either to temporarily abandon their foraging and resting sites, or to engage in vigilance. By contrast, the behaviour of birds was not significantly affected by shooting and passing cars, as these were the most common anthropogenic stimuli at the site. Animals often habituate to predictable nonthreatening stimuli (Knight & Temple 1995). Although herons and egrets were observed during the migration period, the wild boar hunting season in Serbia occurs throughout much of the year, so at least some of the birds, if exposed to gunfire close to their breeding colonies, may have become habituated. In addition, the level of noise needs to achieve a certain threshold to cause behavioural reaction in animals (Brown 1990, Bowles 1995). Shooting never occurred at the study site while I was observing herons and egrets, thus the stimulus may not have been loud enough to trigger a response. Similar to other research where animals exposed to frequent encounters with vehicles showed little reaction to passing cars (MacArthur et al. 1982, Stolen 2003), the birds here did not alter their behaviour in an obvious manner when cars were passing. It should be noted, however, that in most situations vehicles were passing along the embankment at a steady speed, which typically affects birds less in comparison with vehicles that stop or slow near birds (Stolen 2003). On one occasion, when a person stopped and left his vehicle, the birds reacted by increased vigilance and flight compared to behaviours in the absence of disturbance.

The proportion of vigilant birds in the linear model was significantly higher during disturbance, but with no difference between birds observed in the absence of disturbance and shortly after disturbance. This result could indicate that the incidence of antipredator responses rapidly declined after individuals were exposed to anthropogenic stimuli, although it should be noted that all categories of disturbance were combined within the model, so the recovery time for birds exposed to different sources of disturbance may had been different. For example, the recovery time of whooper swans was longer when they were disturbed by pedestrians than motor vehicles and aircrafts (Rees et al. 2005). In addition, even when disturbed individuals rapidly resume their foraging activities, they may suffer foraging depression due to lower foraging and/or capturing rates, as reported for the little blue heron Egretta caerulea, and tricolored heron Egretta tricolor (Burger & Gochfeld 1998).

TAIL!

As an area of high wildlife importance, the study area has been proposed as a nature reserve, being a habitat for protected and endangered species of animals and plants (Sekulić & Sekulić 2013). An additional value of the area is the fact that it is situated close to a densely-populated city, facilitating public education in the value of biodiversity and sustainable environmental practices. This study demonstrated that anthropogenic disturbance can alter the behaviour of the study species, and although the impact of such behavioural responses to the survival and energy budget of birds remains unknown, the findings presented here may serve as a foundation for future research and can be integrated in management and conservation planning.

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Data Availability Statement

The data that support the findings of this study are available in the FigShare repository under the name "data ardea glmm.csv": https://dx.doi.org/10.6084/m9.figshare.19802896.v1.



Literature

- Anderson D.W. 1988: Dose-response relationship between human disturbance and brown pelican breeding success. *Wildl. Soc. Bull.* 16: 339–345.
- Beale C.M. 2007: The behavioural ecology of disturbance responses. *Int. J. Comp. Psychol.* 20: 111–120.
- Beauchamp G. 2014: Social predation: how group living benefits predators and prey. *Academic Press, London, UK*.
- Beauchamp G. 2015: Animal vigilance: monitoring predators and competitors. *Academic Press, Oxford, UK*.
- Berger-Tal O. & Saltz D. 2016: Behavioural rigidity in the face of anthropogenic change. In: Berger-Tal O. & Saltz D. (eds.), Conservation behaviour. *Cambridge University Press, Cambridge, UK:* 95–120.
- Bélanger L. & Bédard J. 1990: Energetic cost of maninduced disturbance to staging snow geese. *J. Wildl. Manag.* 54: 36–41.
- Bowles A.E. 1995: Responses of wildlife to noise. In: Knight R.L. & Gutzwiller K.J. (eds.), Wildlife and recreationists: coexistence through management and research. *Island Press, Washington D.C., USA:* 109–156.
- Brown A.L. 1990: Measuring the effect of aircraft noise on sea birds. *Environ. Int.* 16: 587–592.
- Burger J. 1981: The effect of human activity on birds at a coastal bay. *Biol. Conserv.* 21: 231–241.
- Burger J. 1998: Effects of motorboats and personal watercraft on flight behaviour over a colony of common terns. *Condor 100: 528–534*.
- Burger J. & Gochfeld M. 1998: Effects of ecotourists on bird behaviour at Loxahatchee National Wildlife Refuge, Florida. *Environ. Conserv.* 25: 13–21.
- Burger J., Gochfeld M., Jenkins C.D. & Lesser F. 2010: Effect of approaching boats on nesting black skimmers: using response distances to establish protective buffer zones. *J. Wildl. Manag.* 74: 102–108.
- Burger J., Gochfeld M. & Niles L.J. 1995: Ecotourism and birds in coastal New Jersey: contrasting responses of birds, tourists, and managers. *Environ. Conserv.* 22: 56–65.
- Ciuti S., Northrup J.M., Muhly T.B. et al. 2012: Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLOS ONE 7: e50611*.
- Ellenberg U., Setiawan A.N., Cree A. et al. 2007: Elevated hormonal stress response and reduced reproductive output in yelloweyed penguins

- exposed to unregulated tourism. *Gen. Comp. Endocrinol.* 152: 54–63.
- Fernández-Juricic E., Jimenez M.D. & Lucas E. 2001: Bird tolerance to human disturbances in urban parks of Madrid (Spain): management implications. In: Marzluff J.M., Bowman R. & Donelly R. (eds.), Avian ecology and conservation in an urbanizing world. *Kluwer, Dordrecht, Netherlands*: 259–274.
- Fernández-Juricic E., Zollner P.A., LeBlanc C. & Westphal L.M. 2007: Responses of nestling black-crowned night herons (*Nycticorax nycticorax*) to aquatic and terrestrial recreational activities: a manipulative study. *Waterbirds* 30: 554–565.
- Fox J. & Weisberg S. 2019: An R companion to applied regression, 3rd ed. Sage, Thousand Oaks, USA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/
- Frid A. & Dill L.M. 2002: Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6: 11.
- Gill J.A. 2007: Approaches to measuring the effects of human disturbance on birds. *Ibis* 149: 9–14.
- Goudie R.I. 2006: Multivariate behavioural response of harlequin ducks to aircraft disturbance in Labrador. *Environ. Conserv.* 33: 28–35.
- Gutzwiller K.J. & Cole D.N. 2005: Assessment and management of wildland recreational disturbance. In: Braun C.E. (ed.), Techniques for wildlife investigations and management. *The Wildlife Society, Bethesda, USA:* 779–796.
- Knight R.L. & Temple S.A. 1995: Origin of wildlife responses to recreationists. Knight R.L. & Gutzwiller K.J. (eds.), Wildlife and recreationists: coexistence through management and research. *Island Press, Washington D.C., USA: 81–91.*
- Lafferty K.D. 2001: Birds at a Southern California beach: seasonality, habitat use and disturbance by human activity. *Biodivers. Conserv.* 10: 1949–1962.
- Lenth R.V. 2021: Emmeans: estimated marginal means, aka least-squares means. R package version 1.7.0. https://CRAN.R-project.org/package=emmeans
- Luo D., Ganesh S. & Koolaard J. 2021: Predictmeans: calculate predicted means for linear models. R package version 1.0.6. https://CRAN.R-project.org/package=predictmeans
- MacArthur R.A., Geist V. & Johnston R.H. 1982: Cardiac and behavioural responses of mountain sheep to human disturbance. *J. Wildl. Manag.* 46: 351–358.
- Mangiafico S. 2021: Recompanion: functions to support extension education program evaluation. R

- package version 2.4.1. https://CRAN.R-project.org/package=rcompanion
- Martin G.R. 2007: Visual fields and their functions in birds. *J. Ornithol.* 148: 547–562.
- McDonald J.H. 2014: Handbook of biological statistics, 3rd ed. *Sparky House Publishing, Baltimore, USA*.
- Pinheiro J., Bates D., DebRoy S. et al. 2021: nlme: linear and nonlinear mixed effects models. R package version 3.1-152. https://CRAN.R-project.org/package=nlme
- Pirotta E., Booth C.G., Costa D.P. et al. 2018. Understanding the population consequences of disturbance. *Ecol. Evol. 8*: 9934–9946.
- Price M. 2008: The impact of human disturbance on birds: a selective review. In: Lunney D., Munn A. & Meikle W. (eds.), Too close for comfort: conflicts in human wildlife encounters. *Royal Zoological Society of New South Wales, Sydney, Australia:* 163–196.
- Puzović S., Sekulić G., Stojnić N. et al. 2009: Important bird areas in Serbia. Ministry of Environment and Spatial Planning, Institute for Nature Conservation of Serbia, Provincial Secretariat of Environmental Protection and Sustainable Development, Belgrade, Serbia. (in Serbian)
- R Core Team 2021: R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.*
- Randler C. 2006: Disturbances by dog barking increase vigilance in coots *Fulica atra*. Eur. *J. Wildl. Res.* 52: 265–270.
- Rees E.C., Bruce J.H. & White G.T. 2005: Factors affecting the behavioural responses of whooper swans (*Cygnus c. cygnus*) to various human activities. *Biol. Conserv.* 121: 369–382.
- Riddington R., Hassall M., Lane S.J. et al. 1996: The impact of disturbance on the behaviour and energy budgets of brent geese *Branta b. bernicla*. *Bird Study* 43: 269–279.
- Rogers D.I., Piersma T. & Hassell C.J. 2006: Roost availability may constrain shorebird distribution: exploring the energetic costs of roosting and disturbance around a tropical bay. *Biol. Conserv.* 133: 225–235.

- Rodgers J.A., Jr. & Smith H.T. 1995: Set-back distances to protect nesting bird colonies from human disturbance in Florida. *Conserv. Biol. 9: 89–99*.
- Sastre P., Ponce C., Palacín C. et al. 2009: Disturbances to great bustards (*Otis tarda*) in central Spain: human activities, bird responses and management implications. *Eur. J. Wildl. Res.* 55: 425–432.
- Schummer M.L. & Eddleman W.R. 2003: Effects of disturbance on activity and energy budgets of migrating waterbirds in south-central Oklahoma. *J. Wildl. Manag.* 67: 789–795.
- Sekulić N. & Sekulić G. 2013: Conservation study "Foreland of the left bank of the Danube near Belgrade". *Institute for Nature Conservation of Serbia, Belgrade, Serbia. (in Serbian)*
- Skagen S.K., Melcher C.P. & Muths E. 2001: The interplay of habitat change, human disturbance and species interactions in a waterbird colony. *Am. Midl. Nat.* 145: 18–28.
- Stolen E.D. 2003: The effects of vehicle passage on foraging behaviour of wading birds. *Waterbirds* 26: 429–436.
- Sutherland W.J. 2007: Future directions in disturbance research. *Ibis* 149: 120–124.
- Tablado Z. & Jenni L. 2017: Determinants of uncertainty in wildlife responses to human disturbance. *Biol. Rev.* 92: 216–233.
- Thiel D., Jenni-Eiermann S., Braunisch V. et al. 2008: Ski tourism affects habitat use and evokes a physiological stress response in capercaillie Tetrao urogallus: a new methodological approach. *J. Appl. Ecol.* 45: 845–853.
- Villegas-Amtmann S., Schwarz L.K., Sumich J.L. & Costa D.P. 2015: A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere 6: 1–19.*
- Vos D.K., Ryder R.A. & Graul W.D. 1985: Response of breeding great blue herons to human disturbance in northcentral Colorado. *Col. Waterbirds 8:* 13–22.
- Zuur A.F., Ieno E.N., Walker N.J. et al. 2009: Mixed effects models and extensions in ecology with R. *Springer, New York, USA*.