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MASTER THESIS

Influence of human encounters on movement of blackbirds (*Turdus merula*) in hedgerows



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Abstract

Outdoor recreation is increasing in intensity and space. Areas previously inaccessible are now being visited by ever-growing numbers of people, which increases human-wildlife encounters across taxa. Animals often perceive humans as predators and mount physiological and behavioural responses that can have negative consequences. Human disturbances, even at low levels, are likely to impact species during sensitive breeding season in a sex- and status-specific way. However, experimental studies on movement behaviour for the same individual during consecutive days are lacking.

Here, we experimentally disturbed blackbirds in hedgerows over several days and quantified their flying distances and movement events using radio-telemetry. We compared the movement before, during and after a disturbance using linear mixed effects models (LME).

We showed that Blackbirds of unknown status increased their flying distances during disturbance to the non-disturbed periods directly before and after (+95.5 m/10min / +114 m/10min) and showed a strong tendency to increase numbers of movement events. Contrary to our expectations, we did not find a clear long lasting effect despite the trend that females with unknown status remained at the same flying distances as during disturbance. For feeding blackbirds we found a sex-specific tendency that females reduced flying distances while males moved more during disturbance. In general, incubating females moved little with preferences for short distance movement.

Furthermore, we wanted to investigate whether birds which were not accustomed to human encounters get habituated or whether they become sensitized during disturbance series. The sample size was too small to draw conclusions, but the data showed a tendency indicating a sensitization. The flying distances increased for during disturbance (experiment 6) and also for after disturbance (experiment 5 and 6) period. Additionally, trees had a pronounced positive effect on flying distances for either flying distances or movement events.

We observed sex- and status-specific responses of blackbirds to human encounters disrupting their daily routine behaviour. These findings suggest, that further studies should incorporate sex-, status- and also personalities of individuals investigating the negative impact on fitness parameters of the parents and/or the nestlings. In addition, the sensitization trend of blackbirds to human encounters must be proved, especially for not accustomed individuals over a couple of days. Moreover, visitor guidance and prevention of trail construction in undeveloped semi-natural habitats would reduce impact on modified movement pattern thru recreationists most efficiently.

Key words: human disturbance, recreation, flying distances, movement events, radio-telemetry

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1 Introduction

Outdoor recreation has increased in intensity and space over the past decades (Boyle & Samson 1985, Balmford et al. 2009). Areas previously inaccessible are now being visited by ever-growing numbers of people. This has increased human-wildlife encounters across taxa (Carney & Sydeman 1999, Balmford et al. 2009, Buckley 2009). Human disturbance has been found to negatively affect wildlife (Bötsch et al. 2017).

As suggested by previous research, animals often perceive humans as predators (Frid & Dill 2002, Beale & Monaghan 2004). Human-wildlife interactions begin with visual, auditory or olfactorial detection (Utne-Palm 2001, Smith et al. 2004, Whittingham et al. 2004, Bates et al. 2007, Hagelin & Jones 2007, Fernández-Juricic et al. 2012). Prey has evolved antipredator responses to generalized threatening stimuli (Dill 1974). When such stimuli exceed a threshold, prey responds, even if the specific source is new to the prey's evolutionary history (Frid & Dill 2002). Physiological or behavioural responses can have consequences at the level of individual fitness and habitat use, and subsequent impacts on populations or species (Tablado 2015).

1.1 Theoretical background

The optimal escape theory (OET) evaluates escape decisions made by prey. It states that the prey will initiate escape when the risk of remaining and the costs of leaving are equal (Ydenberg 1986). In contrast, the Flush Early and Avoid the Rush (FEAR), states that prey will generally flee soon after they detect a predator. The FEAR hypothesis – reflects a widespread phenomenon that drives escape behaviour in birds and explained escape behaviour for 79% of species studied (Blumstein 2010). However, whether recreational tourism affects the individuals' escape decisions is still not understood. Geffroy et al. (2015) proposed that nature-based tourism reduces the fearfulness and antipredator behaviour leading towards boldness. This could indirectly influence the reaction to predators, because human presence might lead to a decrease in natural predators and thus prey might become less wary. Consequently, this habituation to humans might lead to bolder individuals and make them thus more vulnerable to predation. Other authors mentioned, that the boldness-syndrome strictly applies to nonthreatening human-wildlife interactions only. Alternatively, physiological stress might promote refuge-seeking behaviour thereby affecting conspecifics through social learning or causing evolutionary adaption that collectively increases the average timidity levels of surviving individuals (Arlinghaus et al. 2016). Whether or not, boldness or timidity does more likely occur, several studies showed that animals encountering potential predators had a lower Flight initiation distance (FID) in high-predator density areas (Atwell et al. 2012, Piratelli et al. 2001, Rodriguez-Prieto et al. 2009). The FID is the distance at which an individual takes flight when approached by a potential predator such as a humans (Blumstein 2010). Further studies argue that not only habituation but also risk allocation produced shorter FID. In parks with higher pedestrian rates, blackbirds *Turdus merula* showed lower

FID than in parks with lower pedestrian rates, in response to both usual and novel potential predators (radio-controlled vehicle) approaches. Apparently, the blackbirds adjusted their antipredator behavior (FID) to the specific level of pedestrian rate every morning in each park and no habituation was present. Otherwise the blackbirds would have known the pedestrians from previous encounters and the FID should have been lower. Nevertheless, habituation was also present, because the rate at which FID was reduced in individuals from low-visited parks compared to high-visited parks was greater for pedestrians than for novel potential predators (Rodriguez-Prieto et al. 2009).

1.2 Consequences from human encounters

Regularly disturbed areas may also be avoided or used only when humans are not present, altering spatial use and/or activity patterns (Tuite et al. 1983, Pfister et al. 1992, Bejder et al. 2006, Bejder et al. 2009). This can lead to a shift in home range and displace wildlife into suboptimal habitats, either permanently or temporarily, with consequences for animal body condition and fitness (Tablado & Jenni 2015). Human disturbances, even at low levels, are likely to impact bird species. Bötsch et al. (2017, 2018b) discovered that the number of territories and species richness in disturbed plots were substantially reduced compared with control plots.

Within a fragmented landscape in parks, increasing levels of pedestrians reduced species richness and overall abundance within circular plots. The abundance of foraging individuals and their breeding densities decreased with increasing disturbance levels for the four species magpies *Pica pica*, blackbirds *Turdus merula*, starling *Sturnus unicolor* and woodpigeon *Columba palumbus* (Fernández-Juricic 2000a). Another study on the impact of recreational disturbance on the distribution and the reproductive performance of breeding Golden Plover *Pluvialis apricaria* close to the Pennine Way (UK). During resurfacing less people strayed from the footpath which reduced the impact of recreational disturbance on distribution significantly. The avoided areas of Golden Plover were four times smaller during chick-rearing period. Despite the clear behavioural change, there was no detectable impact of disturbance on reproductive performance (Finney et al. 2005).

1.3 Antipredator behaviour

In birds human presence typically induces an immediate orienting reflex (also called ‘alert’ position). The birds cease their current activity (foraging, singing, etc.) and focus their senses on the anthropogenic stimulus, increasing vigilance to gather further information about the potential threat to assess the danger (Gabrielsen et al. 1985, Knight & Gutzwiller 1995). As daily routine and vigilance are mutually exclusive, antipredatory responses is at the expense of feeding, sleeping or preening (Randler 2006). After the perception of a threat, an individual will respond accordingly by staying immobile to avoid being seen (i.e. hide or freeze and remain cryptic) or by actively escaping from or fighting the threat (Lima & Dill 1990, Lima 1993, Bracha 2004). The alert distance varies among species and appears to be a more conservative indicator of tolerance than FID, because it includes the

differences between alert and flight distance (Fernández-Juricic et al. 2001). As well as the alert distance, the FID can be viewed as species-specific trait (Blumstein et al. 2003).

The sensory response (and the corresponding alert reflex) may be followed by behavioural and physiological antipredator responses (Gabrielsen & Smith 1995, Berger et al. 2007, Blumstein 2010).

1.4 Factors modulating behavioural stress response raised by human encounters

If individuals respond behaviourally or physiologically to the presence of recreationists, e.g. by a change of habitat use or a reduced reproductive output, their survival and thus their fitness may be compromised. This can happen both through a single disturbance event and through continuous or frequent disturbances (Wingfield 1984, Bowles 1995, Knight & Gutzwiller 1995, Frid & Dill 2002, Buckley 2009). Human recreation will tend to have a higher impact on breeding success, survival, habitat selection in areas with frequent, continuous or intense human use (i.e. higher number of people using an area at the same time) and for individuals or species that fail to habituate to the disturbance (Robert & Ralph 1975, Harper & Eastman 2000, Thiel et al. 2008, Wheeler et al. 2009, French et al. 2011).

If disturbances are frequent or continuous, they may also cause negative effects through chronic stress (i.e. continuous activation of HPA axis and disruption of negative feedback, which impeded the return to basal CORT levels), longer-term changes in activity budget patterns, behaviour (e.g. movement patterns) and energy expenditure (Wingfield 1984, Knight & Gutzwiller 1995, Frid & Dill 2002, Romero 2004). The perception of humans as a possible predator or a disturbance induces the activation of physiological stress responses which in turn trigger behavioural changes. These responses may allow individuals to cope with stressful stimuli, but repeated or long-term exposure may have detrimental individual effects which could have implications on the populations level (Tarjuelo et al. 2015).

In a park in Madrid it was shown that pedestrians were the main cause of flushing responses, followed by magpies *Pica* and dogs accompanying visitors (Fernández-Juricic & Tellería 2000). Birds spent more time being vigilant and moving away from people and less time searching for food which decreased food intake. Active birds (foraging, searching for food, feeding) decreased with increasing numbers of pedestrians during the day and the quantity of blackbird individuals was negatively related to the numbers of visitors. This finding confirmed that blackbird feeding strategies in urban parks are negatively affected by human disturbance. Additionally, human disturbance ultimately modified spatial and temporal patterns of habitat selection and abundance. Also, behavioural adjustments are affected by duration and frequency of disturbance (Fernández-Juricic & Tellería 2000). Investigation on an endangered steppe bird, the little bustard *Tetrax tetrax*, showed behavioural responses due to human activities peaked during the weekends, in particular during hunting. Little bustards spent more time vigilant and flying during the weekends than during the week and more time foraging in morning

after weekends (Tarjuelo et al. 2015). A different study showed variation in feeding behaviour of five species (common gallinule *Gallinula chloropus*, sora rail *Porzana Carolina*, glossy ibis *Plegadis falcinellus*, little blue heron *Egretta caerulea* and Louisiana heron *Egretta tricolor* at Loxahatchee, part of the Everglades, in Southern Florida. The feeding behaviour was largely explained by presence and number of people and the amount of noise made by the people. Studies about the energy budget of the Brent Geese *Branta b. bernicla* living along a stretch of the north Norfolk coast in Norwich during high- and low-disturbance days, showed that birds feed less and are more vigilant when disturbance is increased (Riddington et al. 1996).

The number of pedestrians was positively correlated with blackbirds distance to pathways and negatively to distance to protective cover (Fernández-Juricic & Tellería 2000). Habitat structure modifies alert distances of different species. For four species (*Passer domesticus*, *Turdus merula*, *Columba palumbus*, and *Pica pica*) in urban parks in Madrid (Spain), the birds' tolerance increased with greater availability of escape cover (shrub and coniferous cover, and shrub height) (Fernández-Juricic et al. 2001).

Next to habitat, differences in magnitude of behavioural responses could also be influenced by various forms of recreational activities and the spatial context in which the activities occur. The FID, area of influence (probability that an animal will flush or become alert at a given perpendicular distance from a trail), and distance moved is greater when activities occur off-trail versus on-trail for American robin *Turdus migratorius*, vesper sparrow *Pooecetes gramineus* and western meadowlark *Sturnella neglecta* in a study in the USA. The smallest effects on area of influence, FID and distance moved resulted from the dog-alone treatment, while the response for pedestrian-alone and dog-on-leash (pedestrian with dog) were greater for vesper sparrow *Pooecetes gramineus* and western meadowlark *Sturnella neglecta*. In forests, American robins *Turdus migratorius* behaviour (area of influence, FID and distance moved) did not differ between pedestrian-alone and dog-on-leash treatments (Miller et al. 2001). In a study in the Mountain woodland of Argentina on different forest species, researchers revealed more insights to different components of flight distances (horizontal, vertical and diagonal) and their relation of different spatial interactions to human disturbances. All flight distance components increased linearly with body size and the physical structure of the vegetation affected differently flight distances to all species in various ways (Fernández-Juricic et al. 2004, Blumstein et al. 2005). A widespread assumption is that direct approaches are more disturbing than tangential approaches. Four out of five grassland species in Argentina showed, greater FID response to tangential than direct approaches (Fernández-Juricic et al. 2005).

Species specific differences in FID may partially explain the predominance of species with higher ecological plasticity in cities. Shorter FID are, most likely, an important adaptive trait in urban habitats (Moller et al. 2015, Piratelli et al. 2015). Reduction in FID is partly explained by differences in the community of predators, longer history of urbanization and use of birdfeeders, increasing availability

and reliability of food (Bötsch et al. 2018a, Moller et al. 2015). Another study focused on predator–prey systems such as condition-dependent use of feeding areas (Hilton et al. 1999). They revealed that turnstones *Arenaria interpres* with enhanced condition by supplementary feeding showed greater responsiveness to standardized human disturbance. They fly away at greater distances from the observer, scan more frequently for predators and fly further when flushed (Beale & Monaghan 2004). The findings that birds in manipulated areas were consistently more risk averse due to more response options by enhanced body condition are not consistent with other studies. Different results on behavioural responses dependent on body condition could be induced by interactions between habituation, body condition and bird species.

Few studies have evaluated the impact of urban life on co-divergence of hormonal and behavioural traits in natural systems. A comparison between the population of the dark-eyed junco *Junco hyemalis* from a recently established urban population in San Diego, California, with birds from a nearby wild population and with birds raised in a captive common garden, showed persistent population differences. Both, CORT responses and exploratory behaviour were reduced, and a significant negative co-variation between maximum CORT and exploratory behaviour was observed. These results suggest contemporary adaptive evolution of correlated hormonal and behavioural traits associated with colonization of an urban habitat (Atwell et al. 2012).

Besides these findings other impacts on wildlife could be demonstrated. A classification of recreational-use impact on wildlife from interviews with refuge managers mentioned lower productivity, reduced use of refuge, reduced use of preferred habitat for refuge and aberrant behaviour (Pomerantz et al. 1988).

2 Research gap

According to previous studies and our own experience during the pilot project of this study, birds alter their spatial use and activity pattern when humans are present (Tuite et al. 1983, Pfister et al. 1992, Bejder et al. 2006, Bejder et al. 2009). Despite the large amount of studies on how the human encounters may affect the behaviour of birds, no general pattern has emerged. Several studies suggested, disturbance by human activity may modify bird foraging behaviour (Burger & Gochfeld 1991, Fernández-Juricic & Tellería 2000), patch selection (Fernández-Juricic 2000b) and reproduction (Giese 1996). A review about disturbances found that only 21% of studies, that used a behavioural approach to study human disturbance, focused on multiple species (Blumstein et al. 2005) and most studies focused on few single behavioural responses or movement parameters (e.g. FID, Flying distance, vigilance or foraging). Little is known about the behavioural responses to human activity of single individuals over a couple of days. Thus, a realistic initial design about recreationist encounters (pedestrians along hedgerows) was performed.

3 Aim of this study

This study aims to get a better understanding of the influence of human encounters on movement distances (subsequently as flying distances) and frequency of movement (subsequently movement events) of black birds in hedgerows.

This study investigated the small-scale movement of blackbirds in hedgerows during the breeding season. Therefore, we quantified the movement when birds were disturbed and undisturbed, respectively. We tracked 20 individuals over several days with a VHF-transmitter which provided detailed information on the individual scale. We predicted that disturbed (during disturbance) blackbirds fly more often and for longer distances than during daily routine (before disturbance) with potential lasting effects on movement (after disturbance). For the after disturbance period we expected blackbirds to move either more (compensation) or less (vigilance). Furthermore, we investigated how single blackbirds modified movement over a couple of days with repeated encounters by recreationists. By comparing flying distances between experiments, we aimed to answer, whether blackbirds either habituate or sensitize to human presence.

4 Method

4.1 Bird species

This study focuses on common blackbirds *Turdus merula* (subsequently blackbird) a hedge-breeding species that is big enough to carry an appropriate transmitter. Blackbirds are non-threatened and classified as Least Concern (LC) on the Red List for Switzerland (Keller et al. 2010).

4.2 Study side

We chose hedgerows as study sites because breeding birds are easy to survey due to the overseeable structure of this habitat type. Hedgerows are non-crop linear areas with bushes, trees and scrub in the open landscape (Holm & Laursen 2011). They provide an increasingly important habitat for certain species of birds (Hinsley & Bellamy 2000). Our pilot study showed that the birds were easy to observe and to track with radio telemetry. For practical reasons, we concentrated on hedgerows without forest in the surroundings. Our experience showed that blackbirds with territories close to forests tend to shift their home range after a few experimental disturbances.

We conducted our study in 13 different hedgerows in the surroundings of Lake of Sempach, Switzerland (Fig. S1). There were no paths or trails along the 13 hedgerows accessible to the public for recreation (e.g. walking, biking).

Several reasons such as avoidance of humans, altering spatial use and/or activity pattern can lead to a shift in home range and displace wildlife into suboptimal habitat, either permanently or temporarily. If alternative habitats are not available, animals may be reluctant to abandon an area (Gill et al., 2001; Weidinger 2002; Lambert & Kleindorfer, 2006; Bejder et al., 2009). Therefore, we focused on areas without access for recreationists to be sure that territorial selection of the bird will not be biased by other anthropogenic influence. This approach will allow us to make conclusions about behavioural responses in hedgerows with prediction for other habitats on the study species. Although there were anthropogenic influences of agriculture (harvesting, mowing, manuring or livestock grazing) nearby, encounters by tractors deemed less disruptive as recreationists and frequency was very low with no more than one occasion per week (own observations). Predators as cats, foxes and birds of prey were monitored and embedded in the statistical models as explanatory variable. The hedgerows mainly consisted of indigenous shrubs and some trees. The density and composition varied among the hedgerows with common hazel *Corylus avellana*, blackberry *Rubus fruticosus*, common dogwood *Cornus sanguinea*, blackthorn *Prunus spinosa*, hawthorn *Crataegus sp.*, european spindle *Euonymus europaeus*, briar rose *Rosa canina*, dwarf honeysuckle *Lonicera xylosteum* and podunculate oaks *Quercus robur*, European beech *Fagus sylvatica*, and European ash *Fraxinus excelsior* as the dominating shrub- and tree species.

4.3 Experimental design

In order to answer whether or how the movements of a bird differ after a disturbance event, we conducted experiments (disturbance series) with recreationist/bird encounters and recorded the behaviour of the time periods directly before-, during- and directly after the disturbance event. This method was developed and proved by the Swiss Ornithological Institute during a pilot project in 2016.

The first time period, before the disturbance event, represented daily routine condition and lasted for 30 minutes. The observers were hidden to ensure that the bird was not disturbed and behaved naturally. Then we simulated encounters with recreationists (=disturbance period) by 2 persons walking along the hedgerow talking in a normal conversation volume. This period started when the recreationists were at a distance double the FID. The FID was estimated beforehand by own observations during the pilot project taking into account all the relevant landscape features, which could modify FID. The disturbance period varied in time between the experiments, birds and hedgerows. The third period started immediately after the disturbance and again lasted 30 minutes.

To assess accurate positions of the bird we used radio telemetry from at least two positions. While two disturbers one with (T2; Fig 1) and one without telemetry (D1; Fig 1) will walk along one side of the hedgerow, a third person tracked the bird in a rectangular angle to get an accurate position of the bird. When the circumstances did not allow for locating the bird with accurate precision (for e.g. hillier landscape), another additional telemetry position improved the data quality sufficiently (T3). Every 10 seconds, the most accurate position of the bird was determined and recorded. We used digital voice recorder WS-853 from OLYMPUS for the recording, walkie-talkies TLKR T80 Extreme from Motorola for communication and Telemetry receiver R-1000 from communication specialists, inc. and telemetry antenna from titley scientific for telemetry. The disturbance experiment was repeated 6 times per bird alternating in the morning and in the evening on 6 continuous days. The birds were surveyed during the breeding season 2017 between 16 April and 10 July. The telemetry protocols were done by 2 groups of 3 people each. Three of them were experienced field assistants. One of them always supervised the entire experiment.

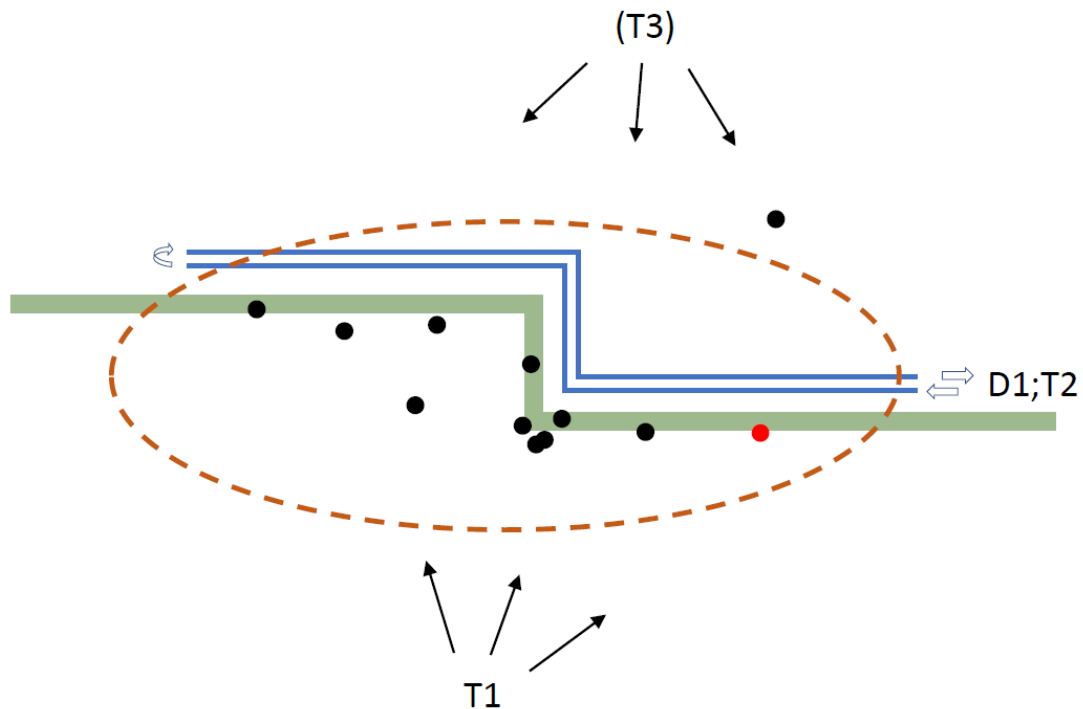


Fig. 1 Experimental disturbance design; green: hedgerow, red point: birds position at the start of the experiment, black points: possible birds positions, T1: observing and doing telemetry, T2: observing and doing telemetry / performing disturbance by walking along the hedgerow, D: field assistant performing disturbance by walking along the hedgerow forth and back (blue arrows), T3: additional telemetry position, dashed brown line: estimated home range of the bird.

Sample size was 20 individuals. The focus lied on a balanced ratio of females and males. The capture of the birds took place around the nestling's age of 5 (± 1) days for the females to avoid brood desertion. When the fledglings reached the age of 5 days we use Japan nets to catch the bird for tagging. It was not always possible to assign the males to a specific nest due to their polygynous behaviour. We used radio-tags (PIP3 Ag379) from Biotrack, which was combined with activity-loggers. The lifetimes for the radio-tags was 28. The radio-tags were attached to the birds by a leg-loop Harness produced by the Swiss Ornithological Institute. This study focused on the analysis of radio-tag data. The analysis of the activity-loggers was subject of a parallel study. After one day of adaptation to the transmitter, the disturbance series were performed during 6 consecutive days. Once the disturbance series was finished, the bird was recaptured immediately. The bird was measured (weight and body fat) before and after the experimental disturbance series.

Radio-tags are a reliable method tool to get an insight on natural behaviour and movement. The main advantage is that there is no need to recapture the bird to get the data. GPS-loggers were not suited for our study because they have to be recaptured for downloading the data and because the position accuracy is not precise enough for our question.

4.4 Vegetation surveys

We recorded the vegetation structure and composition to account for influences on movement behaviour. After the disturbance series we knew the home range of the bird (based on own observational experience) and the surroundings. We did a stratified sampling along the hedgerow and recorded the vegetation at points every twelve meters, in the centre of the hedgerow for the description of the home range and at two more points outside the home range. Surveys of the hedgerows composition were done at four different locations 1 m away from each point into the four main cardinal directions (Fig. 2). At each location, we estimated *density* (%) and *shrub cover* on a 1x1 m area and took the mean among the four locations. The *density* comprised two variables. For the first variable we used a 3 m rod and counted all branches and leaves with contact. For the second variable we measured the density by looking through a toilet paper tube and assessed the proportion of canopy against the sky in the visual field of the observer (done by only one observer). Both variables were proportional weighted and represent *density* (%). Additionally, we measured the *height* and *width* at each point and counted the *trees* 6 m back and forth of each point (Fig. 2). The vegetation surveys were conducted after the experiment series, when the vegetation was fully developed (August).

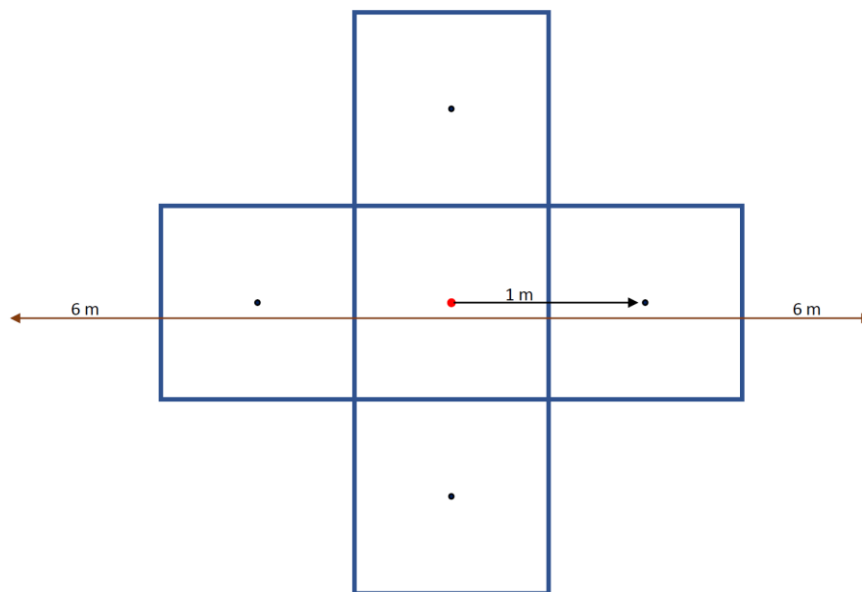


Fig. 2 Points in the middle of the hedgerows for recording vegetation structure and composition of shrubs and trees.

4.5 Statistical Analyses

In order to examine how movement parameters of blackbirds differed between before, during and after disturbances periods, we started with two linear mixed effects models (LME), with either the logarithmic flying distances (*meters per 10 minutes*) or logarithmic movement events per 10 minutes (*events per 10 minutes*) per period as the dependent variables (both following a Normal distribution). According to our experimental design the position of the bird was recorded every 10 seconds, hence

with a very high temporal resolution. With these data we calculated the flying distance and movement events per 10 seconds. Due to the zero inflation and the variation in time between disturbance periods, we summed the distances for each disturbance period to 10 minutes or events per 10 minutes and used the natural logarithm to transform data (both following a Normal distribution). As explanatory variables we included *disturbance* (factor levels: 0; before-, 1; during- and 2; after disturbance), *sex* (factor levels: 1; male and 2; female), *status* (factor levels: feeding, unknown, incubating), temperature (*temp_sc*), time (in minutes) elapsed since sunrise (*sun_diff_sc*), predation (number of potential predators: *predation_sc*) and vegetation characteristics (*width_sc*, *tree_count_sc*, *dens_mean_sc*). Variables which showed correlations among each other (Pearson correlation coefficient < 0.5) were not included in the models. These were *temperature* with *jdate* (0.683), *density* with *height* (0.519) and *density* with *shrub count* (0.796). Therefore, we excluded *jdate*, *height* and *shrub count* because of their less meaningful context. We included the interactive effect between *disturbance* and *status* to test for the impact of disturbance on the differences between status levels and the interactive effect between *disturbance* and *sex* to control for potential differences between sexes due to disturbance. As random factors we included *experiment* (only for the model with distances as dependent variable because of inability to do estimates for experiments within the model for events as dependent variable), which accounted for the correlations among differences in movements behaviour between experiments and *disturbance* nested in *ringnr*, to account for differences among personalities of birds (Table 1). The Akaike information criterion (AIC) was used to rank the models. The model best fitted the data didn't contain *temp_sc*, *sun_diff_sc*, *predation_sc* and *width_sc* and was used to draw inferences about logarithmic distances- and logarithmic events per 10 minutes per period. Discarding the other models seemed appropriate without losing biological meaningful explanatory variables.

In order to explore differences between experiments, we performed one additional linear mixed effects model (LME). These started with a similar structure as the previous initial ones but additionally included *experiment* as explanatory variable as well as the interaction between *disturbance* and *experiment*. In contrast, we excluded *experiment* as random factor. For all models the maximum likelihood (ML) was used since the interest was in the fixed effects.

All analyses were conducted in R version 3.4.1 (Ihaka and Gentleman 1996; R Core Team 2016) using the *glmer* function from the R-package *lme4* (Bates et al. 2015). For calculating the 95% credible intervals (CrI) of the model estimates, we used the Bayesian framework (function *sim* from the R-package *arm* (Gelman and Su 2015)), simulating 2000 random samples of the joint posterior distribution of the model parameters. For all models, we evaluated whether model assumptions were fulfilled via analysis of the residuals and checking for overdispersion after Korner-Nievergelt et al. (2015). To facilitate model convergence, all numeric explanatory variables were centred and standardized (mean = 0, SD = 1).

5 Results

5.1 Descriptive statistics

In total 20 birds were used for analysis, 10 females from 9 different hedgerows and 10 males from 9 different hedgerows. 4 males were feeding chicks and for 6 the status was unknown. For the females, 5 were feeding, 3 were incubating and 2 had unknown status (Table 1).

Table 1 Sample size of blackbirds separated per status and sex.

Status	Sex	Sample size N
Incubating	Female	3
Feeding	Female	5
Feeding	Male	4
Unknown	Female	2
Unknown	Male	6

5.2 Flying distances and movement events

Birds with unknown status moved 95.5 m/10min more during disturbance than before disturbance (mean \pm SD: 219.3 \pm 166.8 m/10min versus 123.6 \pm 147.3) and 114 m/10min more compared to the after- disturbance period (mean \pm SD: 105.3 \pm 96.6 m/10min) (Fig. 3, Table 2). The effect of enhancing flying distances during disturbance compared to before- and after disturbance periods was more distinct for males than for females (Fig. 3). Females with unknown status show a trend remaining at the same flying distances than during disturbance (Fig. 3). Incubating birds (only females) decreased flying distances in general (Fig. 3, Table 2). This reflects that females spent a lot of time heating the nestlings during the first few days. During the feeding period both sexes contributed to feed the nestlings (Hill et al. 1999). Feeding females showed a strong trend reducing flying distances during disturbance while feeding males showed a weak tendency in contrary direction (Fig. 3, Table 2). Furthermore, the number of trees (*tree_counts_sc*) positively affected the flying distances (Table 2).

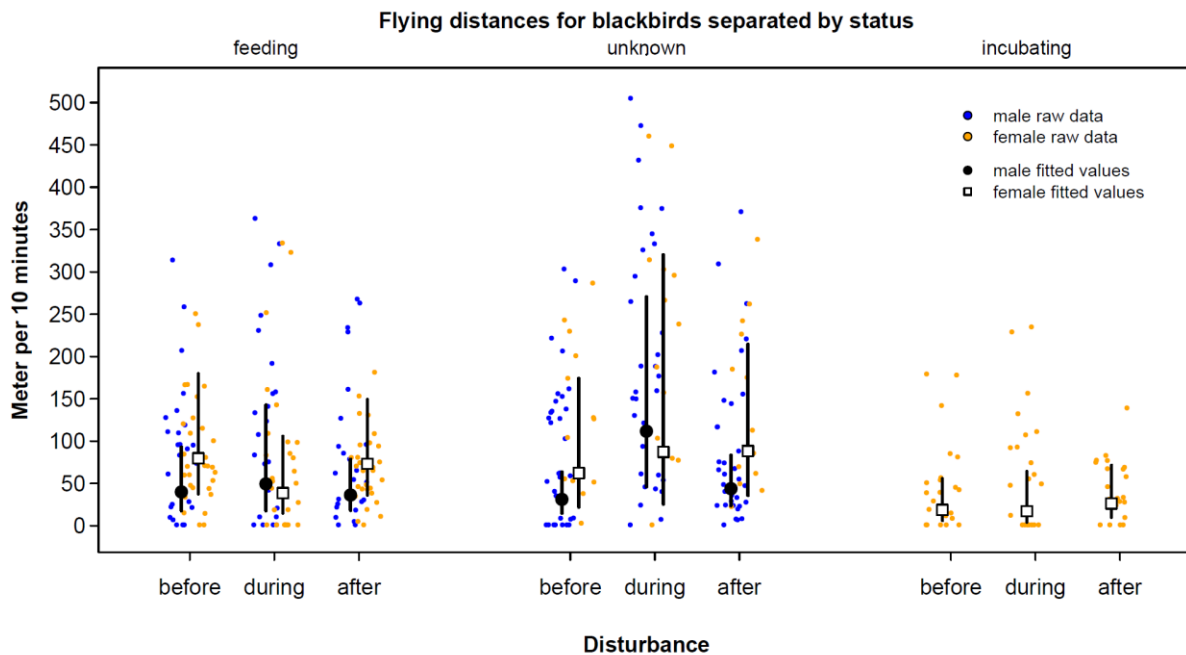


Fig. 3 Flying distances in meter per 10 minutes (\pm 95% CrI), for feeding, incubating and birds with unknown status before, during and after disturbance, separated for male and female birds (in black) with raw data in colour.

For the number of movement events, we found similar patterns but to a weakened extend. The events tended to increase during disturbance periods for birds with unknown status (Fig. 4, Table 2). The contrary tendency, decreasing movement for feeding females during disturbance and increasing for males, respectively, was also present, while the number of trees (*tree_counts_sc*) still showed a clear positive effect on movement (Table 2). Furthermore, incubating birds showed decreased movement events (females) (Fig. 4, Table 2) in relation to the other two status, the same pattern as for flying distances but to a lower ratio. This could be interpreted, that the incubating females move, but for shorter distances.

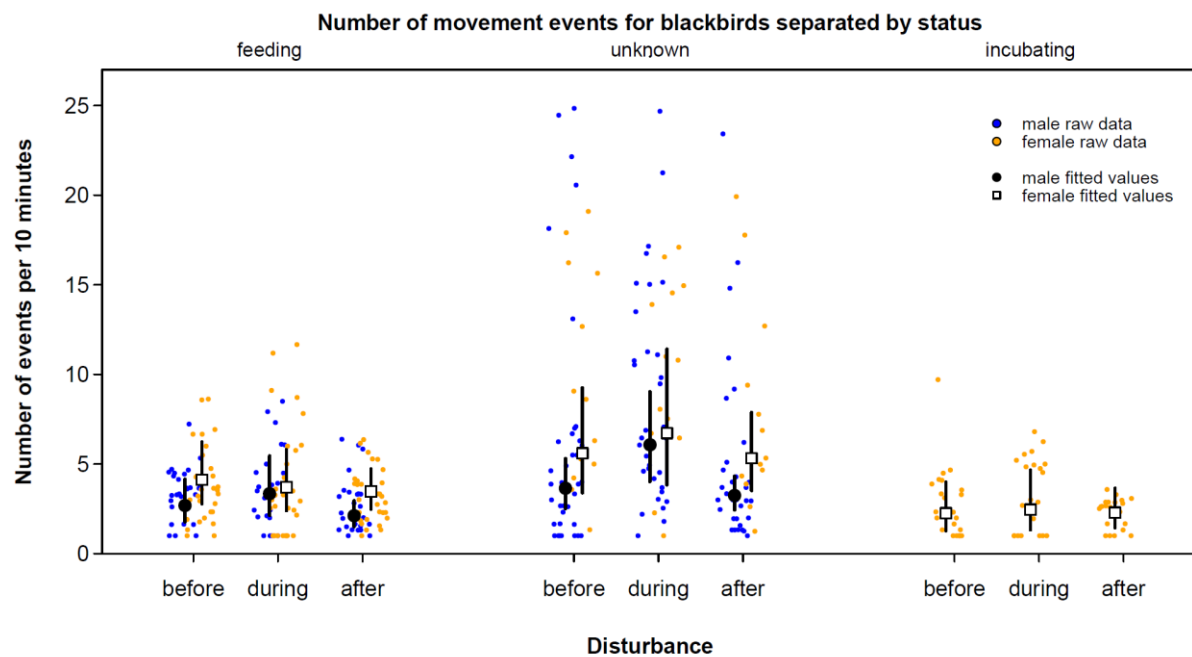


Fig. 4 Number of movement events per 10 minutes (\pm 95% CrI) for feeding, incubating and birds with unknown status before, during and after disturbance, separated for male and female birds (in black) with raw data in colour.

Table 2 Model estimates (\pm 95% CrI) of the effects tested in the LMEs investigating the influence of specified predictors on flying distances and number of events. The corresponding level of each factor is given in parentheses after the variable name. The missing factor levels (Sex1 = Males, Disturbance0 = Before Disturbance, Statusfeeding) are the ones used as reference categories in the models. Disturbance1 = During Disturbance, Disturbance2 = After Disturbance, Sex2 = Females.

Dependent variable	Meter per 10 Minutes	Number of events per 10 Minutes
Intercept	3.715 (2.861; 4.571)	0.989 (0.555; 1.403)
Sex2	0.656 (-0.316; 1.638)	0.431 (-0.091; 0.905)
Disturbance1	0.206 (-0.533; 0.997)	0.224 (-0.073; 0.499)
Disturbance2	-0.110 (-0.804; 0.599)	-0.235 (-0.525; 0.062)
Statusincubating	-1.438 (-2.819; -0.129)	-0.602 (-1.280; 0.085)
Statusunknown	-0.253 (-1.271; 0.736)	0.307 (-0.196; 0.807)
Tree_count_sc	0.434 (0.229; 0.636)	0.242 (0.155; 0.324)
Dens_mean_sc	-0.005 (-0.191; 0.188)	0.076 (-0.005; 0.156)
Disturbance1 \times Statusincubating	0.659 (-0.599; 1.847)	0.194 (-0.256; 0.641)
Disturbance2 \times Statusincubating	0.441 (-0.623; 1.492)	0.173 (-0.303; 0.635)
Disturbance1 \times Statusunknown	1.087 (0.152; 1.968)	0.285 (-0.063; 0.652)
Disturbance2 \times Statusunknown	0.446 (-0.362; 1.230)	0.111 (-0.242; 0.463)
Sex2 \times Disturbance1	-0.947 (-1.881; 0.040)	-0.333 (-0.677; 0.022)
Sex2 \times Disturbance2	0.012 (-0.776; 0.838)	0.068 (-0.289; 0.423)

Distribution = Norm; link function = natural logarithm; random factors = experiment, ringnr, and disturbance/ringnr

We were also interested how specific behaviour of a certain status changed between the experiments. After inspection of the raw data we could see some exceptional patterns for feeding birds which was confirmed by the models. Birds showed increased flying distances for the after disturbance period in experiment 5 and 6 and also for the during disturbance period in experiment 6 (Fig 5. males, Fig. 6 females and Table 3). This trend could probably indicate a sensitization to human encounters over a couple of days; however sample size is too low to be conclusive.

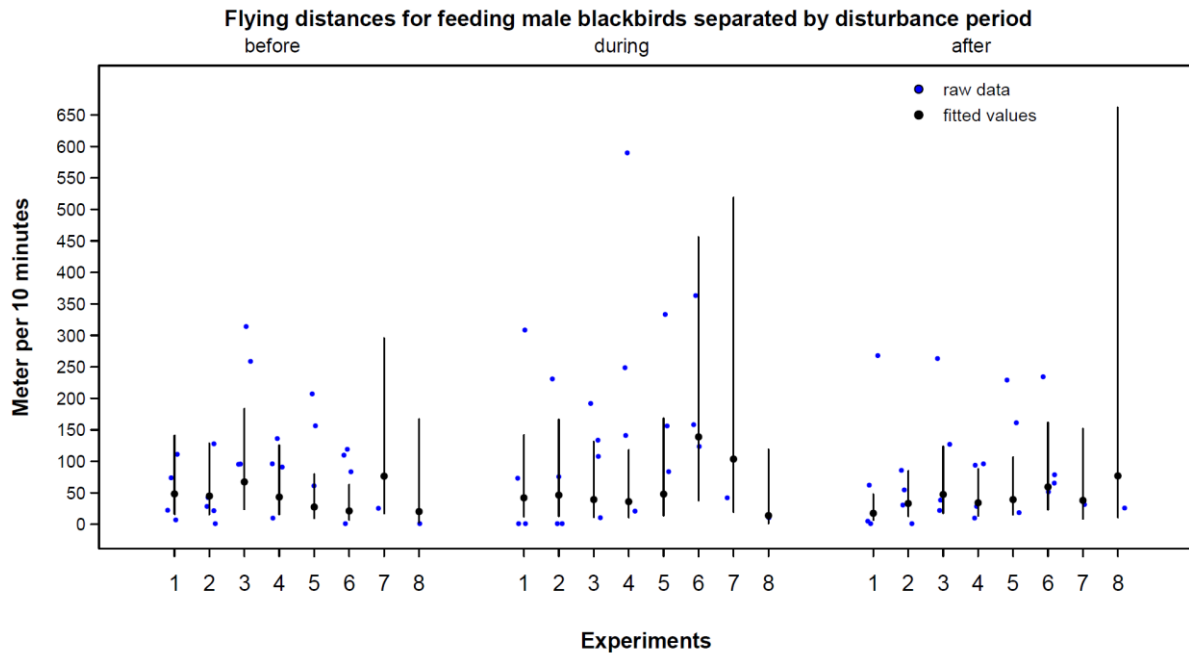


Fig. 5 Flying distances in meter per 10 minutes (\pm 95% CrI), for feeding males before, during and after disturbance, separated by experiments with raw data in colour.

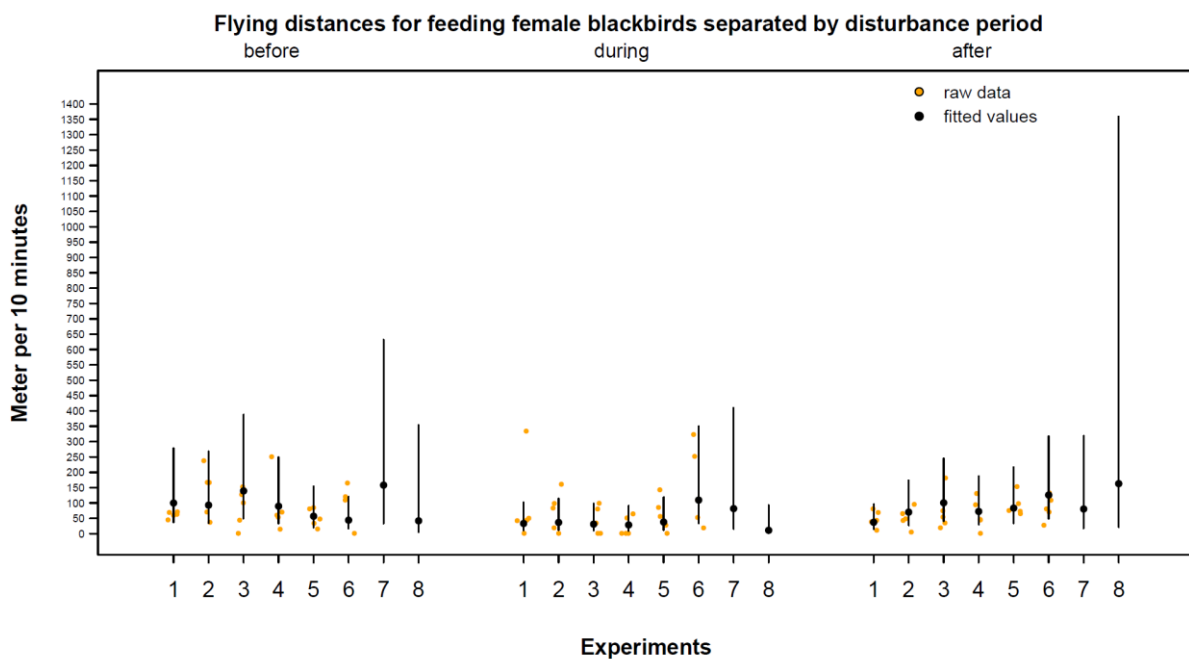


Fig. 6 Flying distances in meter per 10 minutes (\pm 95% CrI), for feeding females before, during and after disturbance, separated by experiments with raw data in colour.

Table 3 Model estimates (\pm 95% CrI) of the effects tested in the LMEs investigating the influence of specified predictors on flying distance including the experiments. The corresponding level of each factor is given in parentheses after the variable name. The missing factor levels (Sex1 = Males, Disturbance0 = Before Disturbance, Statusfeeding) are the ones used as reference categories in the models. Disturbance1 = During Disturbance, Disturbance2 = After Disturbance, Sex2 = Females.

Dependent variable	Number of events in 10 Minutes
Intercept	3.907 (2.812; 4.937)
Experiment2	-0.068 (-0.932; 0.768)
Experiment3	0.334 (-0.514; 1.213)
Experiment4	-0.107 (-0.933; 0.714)
Experiment5	-0.563 (-1.421; 0.275)
Experiment6	-0.824 (-1.716; 0.020)
Experiment7	0.440 (-0.847; 1.725)
Experiment8	-0.926 (-2.765; 1.224)
Sex2	0.718 (-0.361; 1.770)
Disturbance1	-0.159 (-1.235; 0.923)
Disturbance2	-1.005 (-2.011; -0.039)
Statusincubating	-1.543 (-2.881; -0.035)
Statusunknown	-0.391 (-1.418; 0.690)
Temp_sc	-0.046 (-0.316; 0.203)
Sun_diff_sc	-0.086 (-0.253; 0.093)
Predation_sc	0.009 (-0.137; 0.158)
Width_sc	0.055 (-0.155; 0.263)
Tree_count_sc	0.476 (0.253; 0.713)
Disturbance1 \times Statusincubating	0.612 (-0.600; 1.872)
Disturbance2 \times Statusincubating	0.464 (-0.667; 1.501)
Disturbance1 \times Statusunknown	1.077 (0.169; 1.946)
Disturbance2 \times Statusunknown	0.525 (-0.208; 1.255)
Sex2 \times Disturbance1	-0.944 (-1.876; 0.003)
Sex2 \times Disturbance2	0.040 (-0.794; 0.845)
Experiment2 \times Disturbance1	0.164 (-1.003; 1.343)
Experiment3 \times Disturbance1	-0.401 (-1.618; 0.747)
Experiment4 \times Disturbance1	-0.037 (-1.224; 1.124)
Experiment5 \times Disturbance1	0.673 (-0.552; 1.914)
Experiment6 \times Disturbance1	2.026 (0.786; 3.254)
Experiment7 \times Disturbance1	0.452 (-1.273; 2.318)
Experiment8 \times Disturbance1	-0.194 (-3.163; 2.486)
Experiment2 \times Disturbance2	0.695 (-0.539; 1.887)
Experiment3 \times Disturbance2	0.630 (-0.552; 1.836)
Experiment4 \times Disturbance2	0.747 (-0.406; 1.947)
Experiment5 \times Disturbance2	1.367 (0.062; 2.597)
Experiment6 \times Disturbance2	2.051 (0.806; 3.257)
Experiment7 \times Disturbance2	0.312 (-1.516; 2.269)
Experiment8 \times Disturbance2	2.385 (-0.571; 5.187)

Distribution = Norm; link function = natural logarithm; random factors = experiment, ringnr, and disturbance/ringnr

6 Discussion

In this study we investigated how the movement of a bird changed during a disturbance event. To that aim, we monitored the movement of breeding blackbirds before, during and after a disturbance event with radio-transmitters and quantified their flying distances. We showed that disturbance by human encounters changed the flying distances and movement events in a sex-specific way and depended on the status of the bird, i.e. whether a bird was incubating, feeding or of unknown status.

Blackbirds of unknown status showed the strongest change in behaviour. During the disturbance event they increased their flying distances compared to the non-disturbed periods directly before and after and they showed a strong tendency to increase numbers of movement events (Fig. 3 & 4, Table 2). Our findings are comparable to those of Tarjuelo et al. (2015) who found that Little bustards *Tetrax tetrax* spent more time flying during higher rates of human activity. Ugolini (2018) found that percentage of flights of male blackbirds with unknown status increased during human disturbance but not for females. Increased flying distances and movement due to disturbance is directly associated with elevated energy consumption. Energy expenditure for flying is two times higher than for stop-over (Alerstam & Hedenström 1998). Therefore, disturbed wildlife could suffer negative effects from recreationists thru elevated metabolic rate.

Contrary to our expectations we did not find a clear long lasting effect. We had speculated that after the disturbance period either food intake (more movement) might increase for compensation or that vigilance (less movement) increases as found in other studies (Tarjuelo et al. 2015). We only found a trend that females with unknown status remained at the same flying distances than during disturbance (Fig. 3) while this tendency was not present for movement events (Fig. 4). This might indicate that females with unknown status use sites further away after disturbance than before disturbance. However, despite this trend for unknown females our interpretation is very vague with this small sample size (5 individuals). Therefore, further studies are strongly recommended, considering single individuals might show contrary reaction, even if they have same sex and status, but may differ significantly in body condition thru environmental factors (Stillman & Goss-Custard 2002).

Feeding blackbirds showed a sex-specific reaction to disturbance. There was a tendency that females reduced flying distances during the disturbance period. This could be due to enhanced vigilance or to avoid attraction in order to protect the nest (Sauer 1991). Conversely, feeding males moved more during disturbance, which could be interpreted as escape behaviour, a reaction often described when a bird is approached. These findings coincide with data from PAM-Loggers from the same individuals (Ugolini 2018). Both sexes change their behaviour suggesting that pedestrians walking along the hedge were perceived as a threat, a potential predator (Burger & Gochfeld 1991, Fernandez et al. 2013). This change in behaviour might have consequences for the nestlings. Parents have less time to feed the nestlings which might – on a long-term scale when repeated disturbances occur – lead to a

reduced body mass of the nestlings. Reduced body mass means less survival chance (Naef-Daenzer et al. 2001). Furthermore, experiencing frequent anthropogenic disturbance also affect nestlings by elevated baseline corticosterone levels, and increased corticosterone stress response and a lower body mass (Almasi et al. 2015). However, whether altering movement behaviour has an effect on the nestlings or not, could not be clarified in this study. Further studies are needed to investigate potential carry-over effects of changed behaviour of the parents raised by human encounters on the breeding success.

In general, incubating females moved little (Fig. 3 & 4, Table 2). Hill et al. (1999) found that females spent most of the time heating the nestlings during the first few days. Consequently, movement distance was very low. We showed that the decrease of movement events of incubating birds (females) in general (Fig. 4, Table 2) compared to the decrease of flying distance of incubating birds (Fig. 3, Table 2) differ less to the other two status. This result is in line with the findings found for feeding females that behave cryptically (Refugee-Seeking-Behaviour) when perceiving a threat (Arlinghaus et al. 2016).

The finding that the incubating females move for shorter distances let speculate that the disturbance might have a negative impact on the reproductive output. However, further studies are needed which investigate the consequences of recreational encounter on female behaviour pattern (for e.g. feeding rate, quality of food) and its carry-over effects on breeding success.

Our second aim was to find out whether birds that were not accustomed to human encounters get habituated or whether they become sensitized. Our sample size was too small to draw conclusions, but the data show some interesting trends. The flying distances for the after disturbance period increased in experiment 5 and 6 and also for the during disturbance period in experiment 6 (Fig 5. males, Fig. 6 females and Table 3), both indicating a sensitization to human encounters over a couple of days. Studies in high predation areas found the contrary, a lower FID. Thus, they feature habituation as main effect (Atwell et al. 2012, Rodriguez-Prieto et al. 2009). Hence, it might be possible that birds living in a nearly undisturbed area as the blackbirds in our study do either sensitize to disturbance or they have a different personality than birds living in highly frequented areas. Our approach to measure flying distances for the same individual with information on status and sex repeatedly during consecutive days might enhance information precision. Further studies focusing on flying distances for birds with different status and sex have to show whether the observed trends prove to be correct or results belong to shy individuals (personalities), as mentioned by other studies (Bötsch et al. 2018a).

An unexpected result was that the numbers of trees had a pronounced positive effect on movement distances for either flying distances or movement events (Table 2). During our field study, the berries of the ripple ivy *Hedera helix* was a substantial food source for blackbirds (Glutz & Bauer 1988). Hence, when available, blackbirds took advantage and flew from canopy to canopy thereby covering bigger distances than blackbirds moving in a hedgerow (own observation). Furthermore, it is

conceivable that predation risk is lower when movement is done by tree hopping, rather than in the understory of the hedgerow. This effect of number of trees on flying distances was independent on disturbance event. Despite findings evaluated the effect of vegetation on escape behaviour of birds (Fernández-Juricic & Tellería 2000, Fernández-Juricic et al. 2001), suggestions minimizing influence of disturbance, are lacking.

For our research question, we developed an applicable field method using radio telemetry. In order obtaining high resolution of movement patterns we choose ten seconds as appropriate sample unit for flying distances. This enables recording of repeated fast, short flights. Due to zero inflation (many 10 seconds periods without data) we were faced by choosing either data transformation methods or zero inflation models. Due to widely-used LMEs for drawing conclusions, we decided to summarise flying distances and movement events to ten minutes intervals. This allowed us to answer our main research questions accurately and to compare them with data from PAM-Loggers gathered in a parallel study (Ugolini 2018).

In conclusion, we observed sex- and status-specific responses of blackbirds to human encounters disrupting their feeding behaviour. This result suggests that a negative effect on fitness parameters on the parents and/or the nestlings might be possible. Moreover, these negative effects might be enhanced in areas with high numbers of recreational activities, because the blackbirds did not seem to habituate to human encounters, but on contrary, to sensitize. Therefore, visitor guidance and prevention of path construction and reduction of road network in semi-natural habitats would reduce human encounters most efficiently.

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8 Ethics Statement

We had the permits to tag blackbirds for the canton of Luzern. Through manipulation no animals were harmed, although reflecting a short time disturbance event. These short time disturbance events do not differ from a potential outdoor recreationist walking along hedgerows.

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10 Appendix

Study side

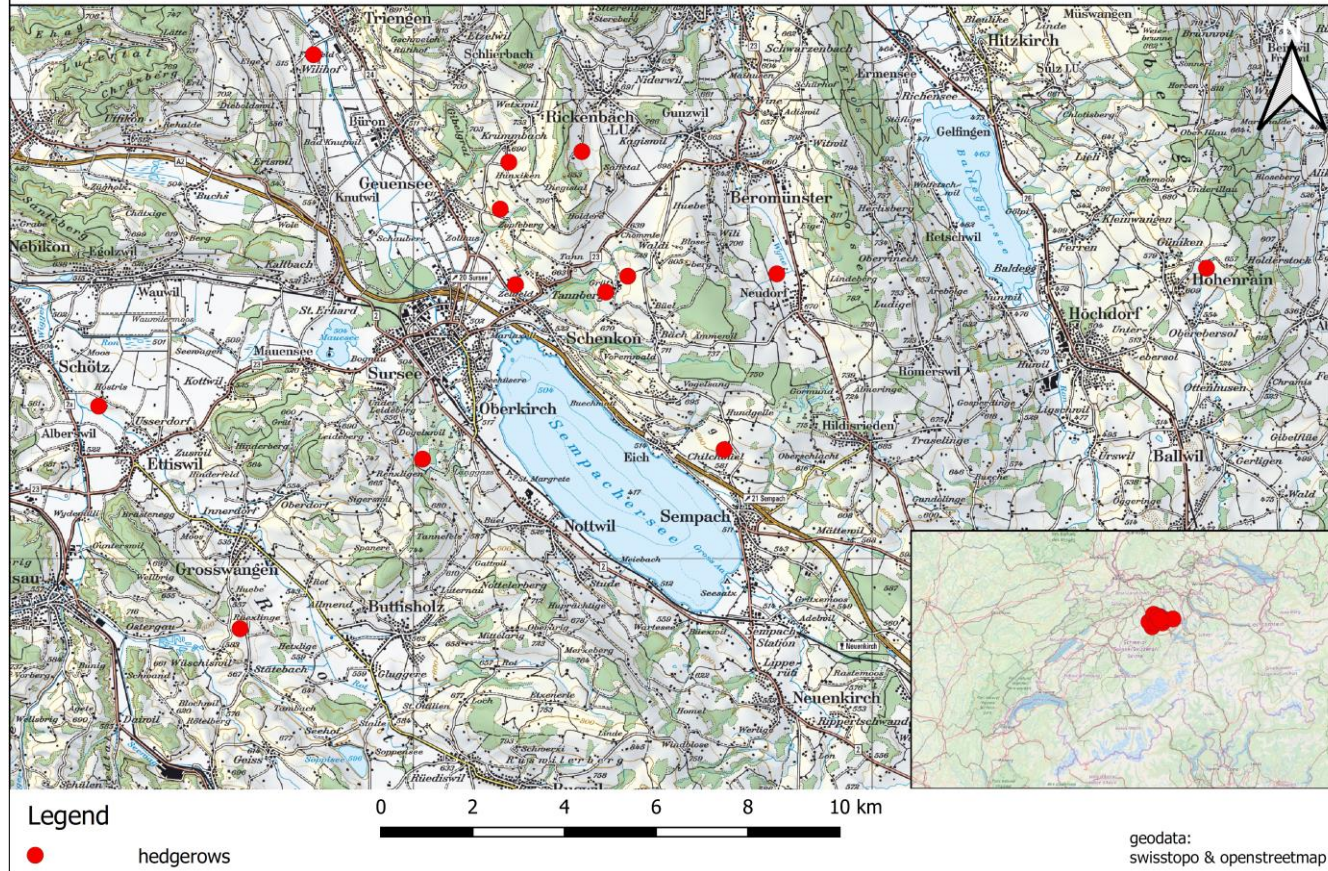


Fig. S1 Hedgerows in the surroundings of Lake of Sempach, Switzerland

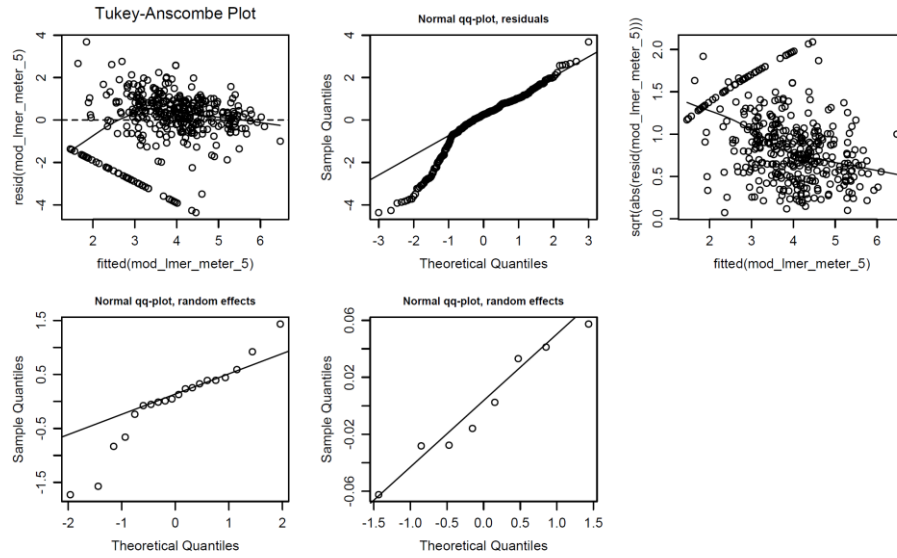


Fig. S2 Diagnostic residuals and random effects plots for flying distances. Upper left: residuals versus fitted values. Upper middle: Normal QQ plot of the residuals. Upper right: square-root of the absolute values of the residuals versus fitted values. Lower left: Normal QQ plot of the random effect (ringnr). Lower right: Normal QQ plot of the random effect (experiments).

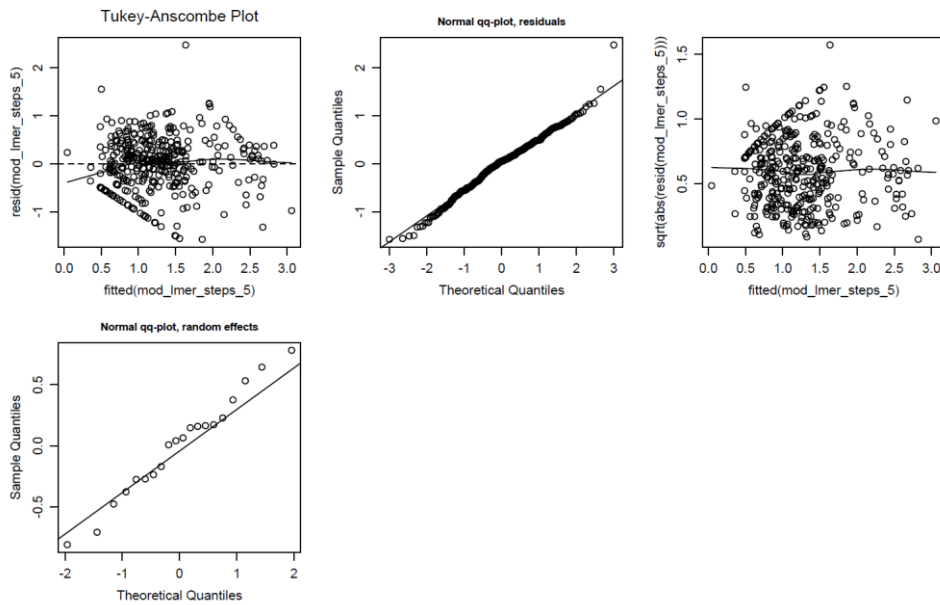


Fig. S3 Diagnostic residuals and random effects plots for movement events. Upper left: residuals versus fitted values. Upper middle: Normal QQ plot of the residuals. Upper right: square-root of the absolute values of the residuals versus fitted values. Lower left: Normal QQ plot of the random effect (ringnr).

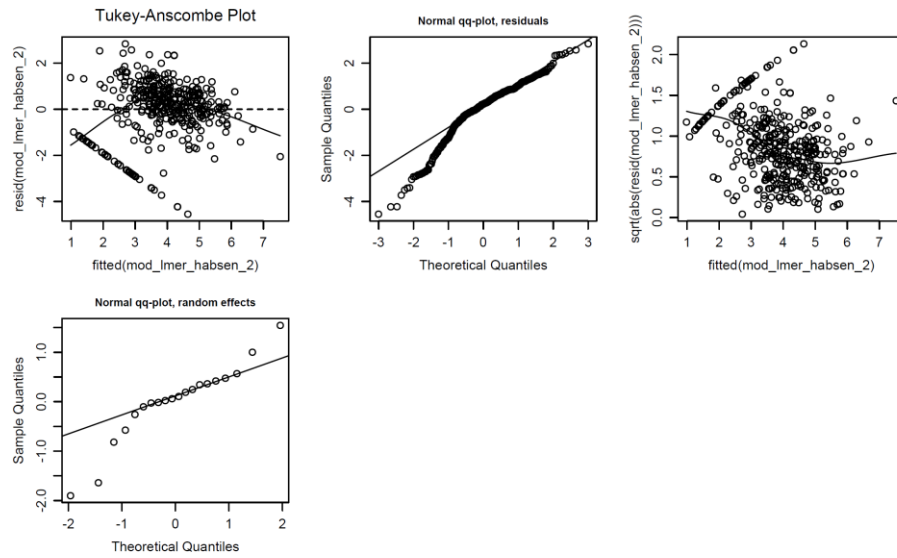


Fig. S4 Diagnostic residuals and random effects plots for flying distances including experiments as predictor. Upper left: residuals versus fitted values. Upper middle: Normal QQ plot of the residuals. Upper right: square-root of the absolute values of the residuals versus fitted values. Lower left: Normal QQ plot of the random effect (ringnr).