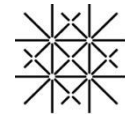




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Effects of pedestrians on behaviour of *Turdus merula*

Master thesis

by

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1. Abstract

Human encounters with wildlife during recreational activities increased massively over the last decades. Previously undisturbed habitats are now being visited by humans. Birds possibly perceive human as predators. Hence, they alter their physiology and behaviour during an encounter with humans. The extent of the physiological and behavioural reactions and their possible negative consequences are quite complex and not well known yet.

This study investigated the short-term effects of a low-threshold anthropogenic disturbance on the behaviour of breeding common blackbirds (*Turdus merula*). Common blackbirds, equipped with PAM-loggers, were disturbed experimentally by pedestrians walking along the hedge they were breeding in. The PAM-loggers measured acceleration in the z-axis with a frequency of 6.25 Hz. The acceleration data was correlated to observations of the birds' behaviour. The three different behaviour types flight, activity and inactivity could be determined. The amounts of each behaviour before, during and after a disturbance event were then compared.

Pedestrians did evoke a sex- and status-dependent change in behaviour of breeding common blackbirds. Incubating female birds increased their flight behaviour, whereas feeding females decreased their activity and were more inactive in response to the disturbance. Feeding male birds showed only a slight increase in flights. These results can be explained by the sex- and status- specific tasks during the reproduction period. A change in behaviour was still visible after the disturbance event. Especially the incubating females increased their amount of inactivity during the 30 minutes after the disturbance event substantially, suggesting that low-threshold disturbances might also have long-term or even fitness consequences.

A combination with the data from the Vhf-transmitters, conducted at the same time, will give some more insight into the temporal and spatial pattern of the reaction of those common blackbirds and might allowing to draw some general conclusions about the impact of pedestrians on common blackbirds.

Key words: Human disturbance, low-threshold disturbance, PAM-loggers, acceleration, behaviour determination

2. Introduction

A disturbance is defined as a physiological and behavioural reaction of an animal to a stressor (Landys et al., 2006; Walker et al., 2005). The animal perceives a stressor via its senses and evaluates the input to induce an accurate stress response. First, adrenaline increases in the blood within seconds. At the same time the hypothalamo-pituitary-adrenal axis (HPA-axis) is activated, and with a delay of about 3 minutes, corticosterone is released from the adrenal cortex (Romero, 2004). Both hormones prepare the organism to overcome a threatful situation. Adrenaline prepares the body for a fight-or-flight reaction by a variety of metabolic changes, as for example an increase of blood flow to the muscles, and it triggers a first behavioural reaction (Wingfield et al., 1998). Corticosterone induces immediate reactions via non-genomic membrane receptors, but also delayed reactions via genomic receptors. It binds at the DNA within the nucleus and affects the transcription and protein synthesis evoking changes lasting for hours and days (Romero, 2004; Sapolsky et al., 2000). Metabolically corticosterone helps to provide the organism with energy necessary for the stress reaction. It promotes the catabolism of protein and the resynthesis of glucose. At the same time, corticosterone has suppressive effects on the immune system, growth and reproduction. By this suppressive effects, energy is spared and redirected to actions to overcome the life-threatening situation (Sapolsky et al., 2000). Finally, corticosterone has effects on the behaviour. If plasma concentration rises during a stressful event, the birds interrupt their actual behaviour and fly away (Jenni-Eiermann, 2014). Such short-term stress responses help to overcome and survive a life-threatening situation. However, when a stressor persists and chronic high levels of corticosterone appear, the bird might experience negative long-term effects which can affect the immune functions or growth (Bolduc and Guillemette, 2003; Sapolsky et al., 2000). During repeated disturbances an animal can lose time to perform other activities such as foraging (Lima and Dill, 1990). Bötsch et al., 2017 could also show that birds in repeatedly disturbed areas have a lower breeding density and that in those areas the species diversity was lower, too. Hence, repeated disturbance might lead to a nest abandonment which in turn might lead to reduced individual fitness (Vitousek et al., 2014) and eventually to a population decrease (Johnson et al., 1992). However, it is difficult to judge whether a specific stressor leads to a reduced fitness of an individual or population. Whether a stressor triggers only a short-term reaction or leads to a long-term effect depends on a multiple of factors (Figure 1 – 1).

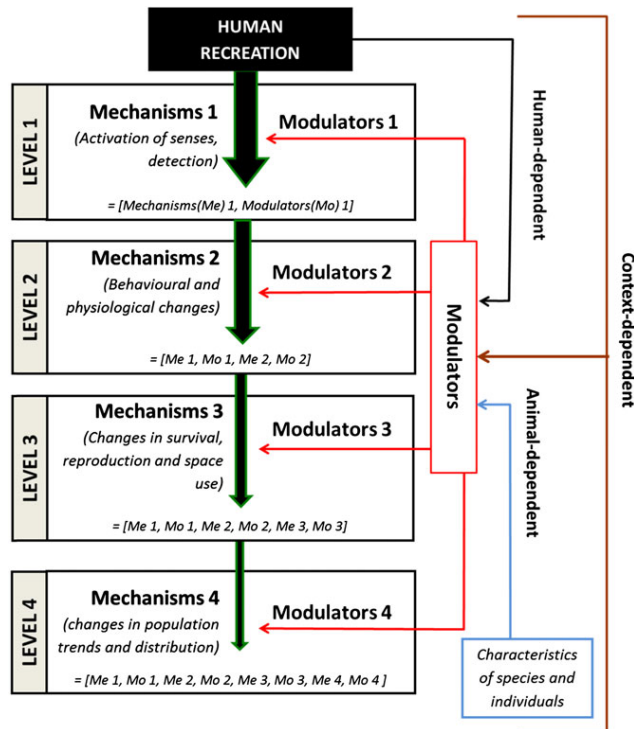


Figure 1 – 1: Conceptual model showing the different levels in the process of interaction between recreationist and wildlife. The reaction to a stressor of animals can be modulated by factors depending on the nature of the stressor (human-dependent), on the characteristics of the individual (animal-dependent) and on the spatio-temporal context (context-dependent).
From: Tablado and Jenni, 2017

First of all, it depends on the nature of the stressor whether it is a chronic stressor like the exposure to toxic substances or whether it is a short disturbance like the sight of a predator. Moreover, the reaction to a stressor is modulated by animal dependent characteristics such as species, sex, body condition or its antipredatory strategy of an individual. Finally, the reaction depends on the spatio-temporal context in which the disturbance takes places. Thus, environmental conditions such as food availability, temperature or habitat might modulate the reaction to a stressor. Therefore, the same stressor can lead to either a short-term reaction or to a long-term reaction depending on the above mentioned modulating factors which itself are dependent on each other as well (Tablado and Jenni, 2017). For example, an acute and short disturbance which has only little effect on adults can lead in young animals to severe long-term effects (Almasi et al., 2015).

Anthropogenic disturbances

The effect of deleterious anthropogenic disturbance like habitat destruction, hunting or car traffic is mostly evident (Andersen et al., 1996; Peris and Pescador, 2004; Reijnen et al., 1995). However, it is difficult to know the effect of low-threshold disturbances. Low-threshold disturbances are for example human encounters with wildlife during outdoor and recreational activities. Humans disturb the wildlife in many different ways, but are generally seen as potential predators by the bird (Beale and Monaghan, 2004). Such low-threshold disturbances increased massively over the last decades. There have been several studies about the increase in encounters between human and wildlife during outdoor activities, for example studies about encounters with free-riding skiers, snowboarders (Arlettaz et al., 2007), joggers and mountain bikers (Gander and Ingold, 1997), or persons with dogs (Banks and Bryant, 2007). Many of those outdoor activities are performed in sensible habitats and in previously undisturbed habitats, such as the underwater world by scuba divers or the airspace with the help of drones (Bolduc and Guillemette, 2003). Therefore, for many species, especially in a densely populated country as Switzerland, it is difficult if not impossible to find refuge areas. For Capercaillies for example, it was shown that outdoor activities severely impact and decrease their home range (Thiel et al., 2008). Therefore, disturbances from encounters with humans have a big impact on an animals' life, especially for vulnerable or endangered species (Czech et al., 2000).

Aim of the study

The aim of the study was to investigate the short-term reaction of common blackbirds (*Turdus merula*) after a human encounter.

More precisely, the behaviour of common blackbirds breeding in hedges was measured with a PAM-logger before, during and after an experimental disturbance (Yoda et al., 1999). Hedges away from paths were chosen and the blackbirds were disturbed experimentally by walking along the hedge and talking normally. The disturbance experiment was repeated 6 times alternating in the morning and in the evening on 6 continuous days. Then the behaviour of a bird during the disturbance was compared with the behaviour of the same bird 30 minutes before and 30 minutes after the disturbance.

The questions were:

1. Is determination of a bird's behaviour possible with PAM-loggers measuring acceleration?
2. Do humans walking along a hedge and talking normally evoke a change in the behaviour of common blackbirds?

3. Material and Methods

Study area and species

The study was conducted in the surroundings of Lake Sempach, Switzerland, from March to July 2017. The area is characterized by small to midsize towns and agriculture.

The experiments were performed in hedges, because hedges are a habitat clearly to overview and allowing observations from the distance. It is also easier to follow birds with VHF-transmitters in such an open habitat than in forests, for example. In hedges, there are less disturbing or false signals being echoed from trees. Finally, the probability to capture and recapture birds in hedges is quite high, in contrast to forests.

The study was conducted in hedges without a path along the hedge. Hence, birds breeding in these hedges usually had no encounters with pedestrians passing by. We defined these hedges as “undisturbed”, although there were some anthropogenic influences from agriculture activities like harvesting, mowing or manuring, as well as influences from livestock grazing next to the hedges. The aim of the study was to investigate the effect of human encounters on the behaviour of common blackbirds (*Turdus merula*) breeding in hedges. To avoid possible environmental factors, as a different plant composition of the hedge, undisturbed hedges away from paths were chosen and breeding birds were disturbed experimentally. Another reason for the experimental approach was that the personality of the birds living in an already disturbed environment might vary from the personality of the birds living in an undisturbed environment.

The common blackbird was chosen as model species because it is known to breed in hedges (Svensson, 2011), especially if thorn and fruit scrub are available. Second, common blackbirds have a suitable size to carry the combination of PAM-loggers and VHF-transmitter. Third, common blackbirds have an abundant presence in agriculture area.

In preparation to capture, all suitable hedges were controlled for nesting or, later in spring, for breeding common blackbirds, and their behaviour and flight paths were observed. This allowed to learn about their status (nest building, incubating, feeding) and facilitated capture.

Catching and tagging

A total of 25 common blackbirds were captured with mist nets at 14 different hedges. Experiments were conducted with 21 birds (10 males and 11 females). Four birds were not suited for experiments because it turned out that they were not breeding in the hedge, but in gardens or forests nearby. One female could not be recaptured, because she gave up her territory in the hedge after her nest got predated. Hence, 20 recaptured birds (10 males, 10 females) breeding in 12 different hedges were left.

After sexing, weighing and ringing each bird was equipped with a radio transmitter (Biotrack Ltd, PIP Ag379, 25 VHF, 0.48 g, lifetime: 28 days) combined with two agglutinated PAM-Loggers (each 1.45 g). The PAM-loggers recorded acceleration in the z-axis with a frequency of 6.25 Hz (6.25 data points per second), and acceleration could continuously be measured at almost 8 consecutive days (storage capacity for one logger: 3d 21h). The whole package had a weight of 3.38 g, which is less than 5% of the bird's body mass (mean: 92 g range: 82 - 109 g). The package was attached to the bird's back with a leg-loop Harness (1470 mm) designed by the Swiss ornithological institute. The package does not affect the birds behaviour (Hill et al., 1999a; Naef-Daenzer et al., 2001).

The data stored on the loggers were downloaded after recapturing the birds (20 birds = 40 loggers). One logger did not record acceleration and therefore the experiments of this (female) bird were excluded from the analysis. Hence, 38 loggers from 10 males and 9 females could be used for analysis.

Experimental design

Each experiment consisted of three parts: before, during and after a disturbance event. For each part, a separate telemetry protocol was made. The start and end times of those protocols were later used for the analysis of the PAM-loggers. For the protocols of the before and after disturbance event (mostly 30 minutes each) the bird's position was recorded as following: Two persons were standing in a rectangular angle to each other, observing the hedge from the distance and recording every 10 seconds the bird's position using telemetry. Measurement of both persons were synchronized by a metronome beat and recorded on a voice recorder.

During a disturbance event, two persons walked along one side of the hedge in a steady pace. One of them tracked the bird with telemetry (Figure 3 – 1, D1 & T2), while a third person tracked the bird from the distance (T1). This person was standing in a rectangular angle in relation to the disturbers. The bird's position was recorded every ten seconds through a walky talkie. Observations of the bird's movement were also noted.

All individuals were disturbed six times, alternatively in the morning and in the evening around the same time on six continuous days or if necessary on up to eight days.

After completion of the experiment, a survey of the floral composition of every hedge was made.

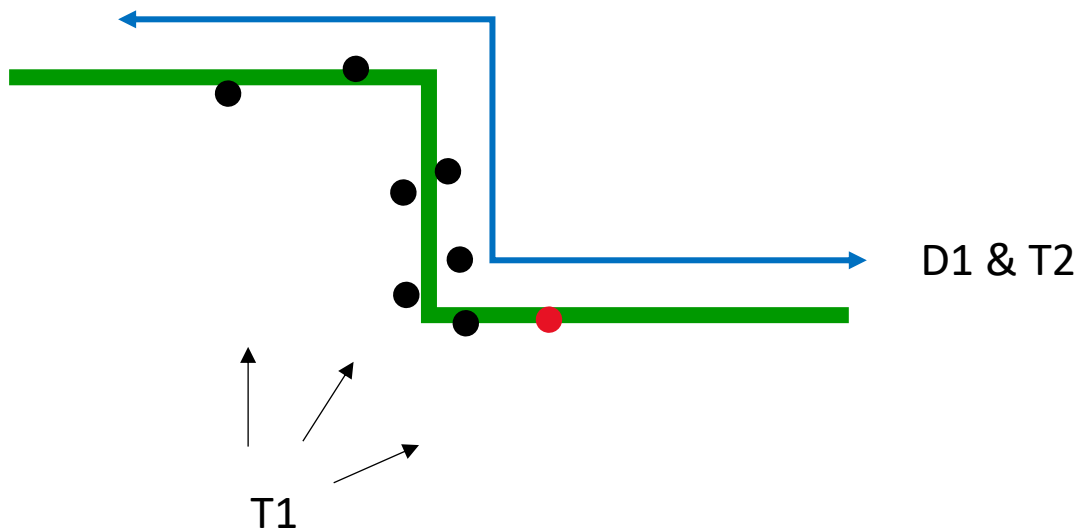


Figure 3 – 1 Draft of experimental design. Green: hedge, points: the bird's position, red point: bird's position at start of the experiment, black points: possible position of the bird during the experiment, blue arrow: route of the disturbers, T1: Person 1 with telemetry in rectangular angle to the disturbers, T2: person 2 with telemetry walking along the hedge, D1: disturber 1 walking along hedge with T2.

Behaviour determination

Data processing was conducted using R 3.4.1. (R Development Core Team, 2008). Each logger was read out separately, due to the big amount of data (2 098 650 data points, 16 Mb per logger). Loggers were measuring total acceleration in a range between -3 g and 3 g (- 29.4 m/s² and 29.4 m/s²). The acceleration signal consists of two parts: a static and a dynamic component.

The static component is the incline of the accelerometer in relation to earths gravitation field (Shepard, 2008), which depends on the position of the accelerometer on the body (Wilson et al., 2006). The static component ranges from 1g to -1g and it sums always to 1 when acceleration is measured in all three axes (Wilson, 2008). The dynamic component of acceleration indicates the change in velocity during locomotion. To determine different locomotion modes (behavioural patterns), the dynamic component needs to be separated from the static component. To achieve this, the static component needs to be subtracted from total acceleration over a rolling window of 2 seconds, as recommended by Wilson et al. (2006). For each data point the static component was estimated by calculating the mean over a window of 6 data points before and after the particular data point. This mean was then subtracted from the total acceleration recorded at this data point, leaving only the dynamic component of the acceleration signal for each data point (Figure 3 – 2). Negative as well as positive values of g represent an increase in dynamic acceleration, therefore it was operated with absolute values (Shepard, 2008) (Figure 3 – 3).

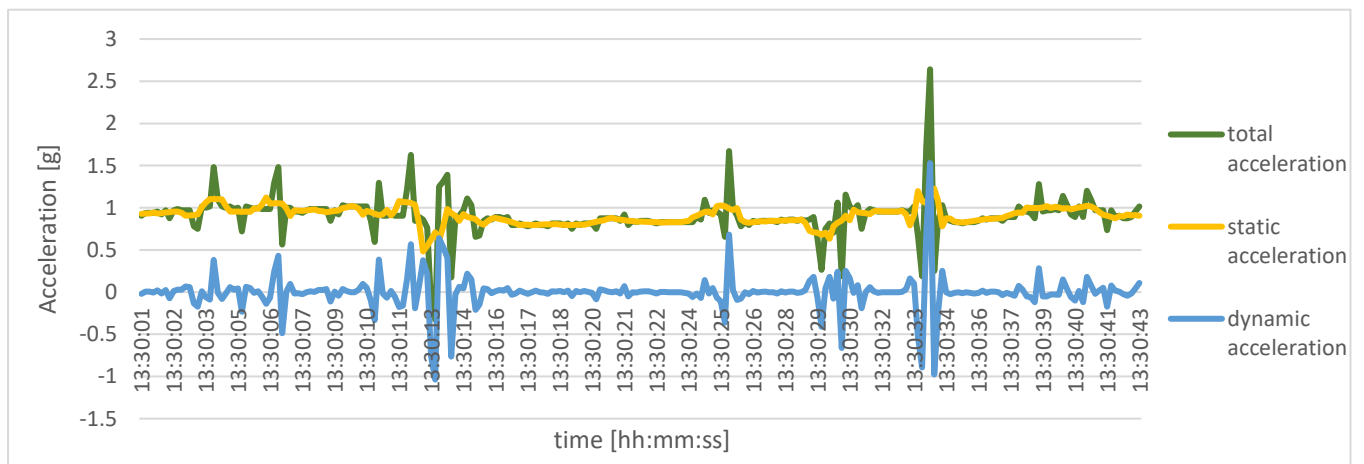


Figure 3 – 2 Example of total acceleration (green) separated in its static (yellow) and dynamic (blue) component over 42 seconds.

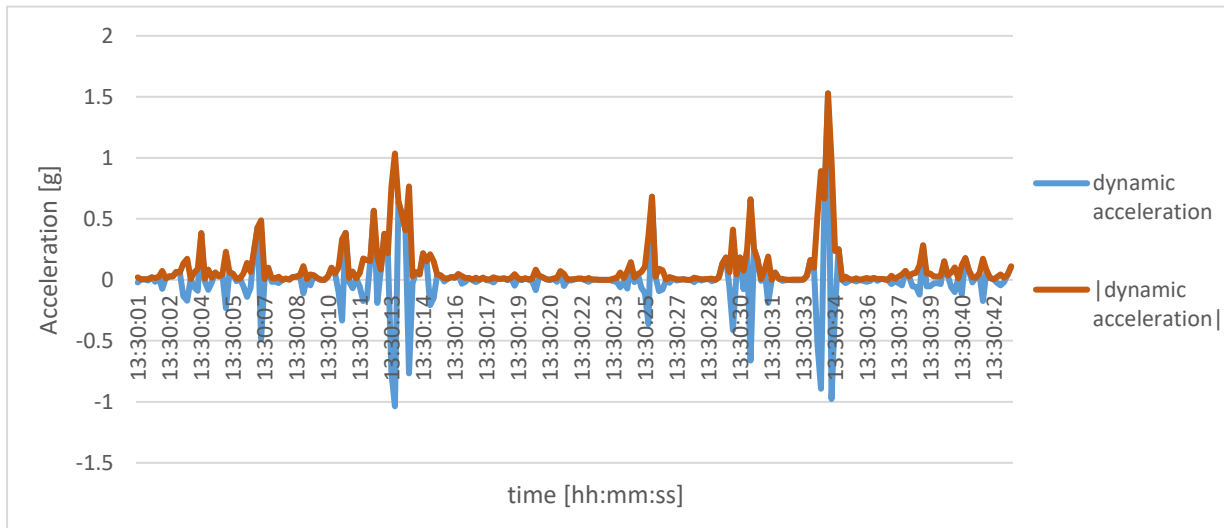


Figure 3 – 3 Example of the dynamic component of acceleration (blue) and its absolute values (dark red) over 42 seconds.

For validation, birds equipped with PAM-loggers were observed from afar and notes were made of the accurate time and behaviour. These observations allowed assigning the accelerometer data to certain behaviours. Three behavioural patterns could be distinguished: flight, activity like foraging, hopping, picking and inactivity.

Iterative patterns in oscillation of the dynamic component allowed distinguishing flights and inactivity by deriving specific thresholds on different parameters. Parameters were amplitude, the maximum value of the signal, and variance, the average of the squared differences from the mean. The threshold qualifications were implemented around a bout of 2 second for each data point. A bout therefore contains 6 data points before and after the data point in question. Thresholds for each bout were defined as follow:

- specific number of peaks with certain amplitude
- specific distance between peaks of the certain amplitude
- specific variance over a certain value.

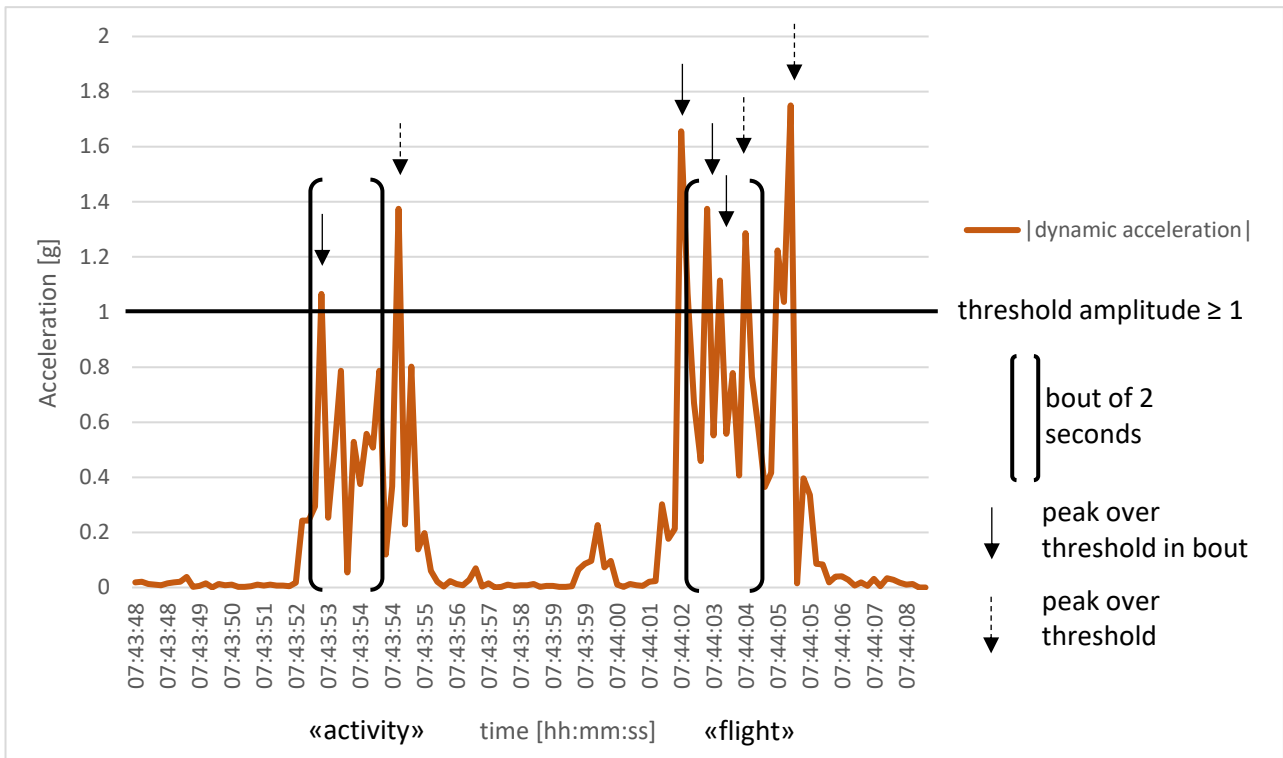


Figure 3 – 4 Example of “activity” and “flight”, defined according to height of absolute amplitude within a bout of 2 seconds. The threshold in amplitude for “flight” is indicated with a black line. Parenthesis: bout of 2 seconds, arrow: peaks with threshold ≥ 1 . “Activity” is characterized by up to 2 peaks higher than 1 in a bout and “flight” by more than 3 peaks higher than 1 in a bout.

- The following specific thresholds were derived to assign the behaviour “flight” to a data point:
- 3 or more peaks in the bout must have an amplitude equal or higher than 1 (Figure 3 – 4)
 - the distance between data points with an amplitude equal or higher than 1 must be smaller or equal than 4 data points
 - variance must be higher or equal to 0.5 over the bout (Figure 3 – 5).

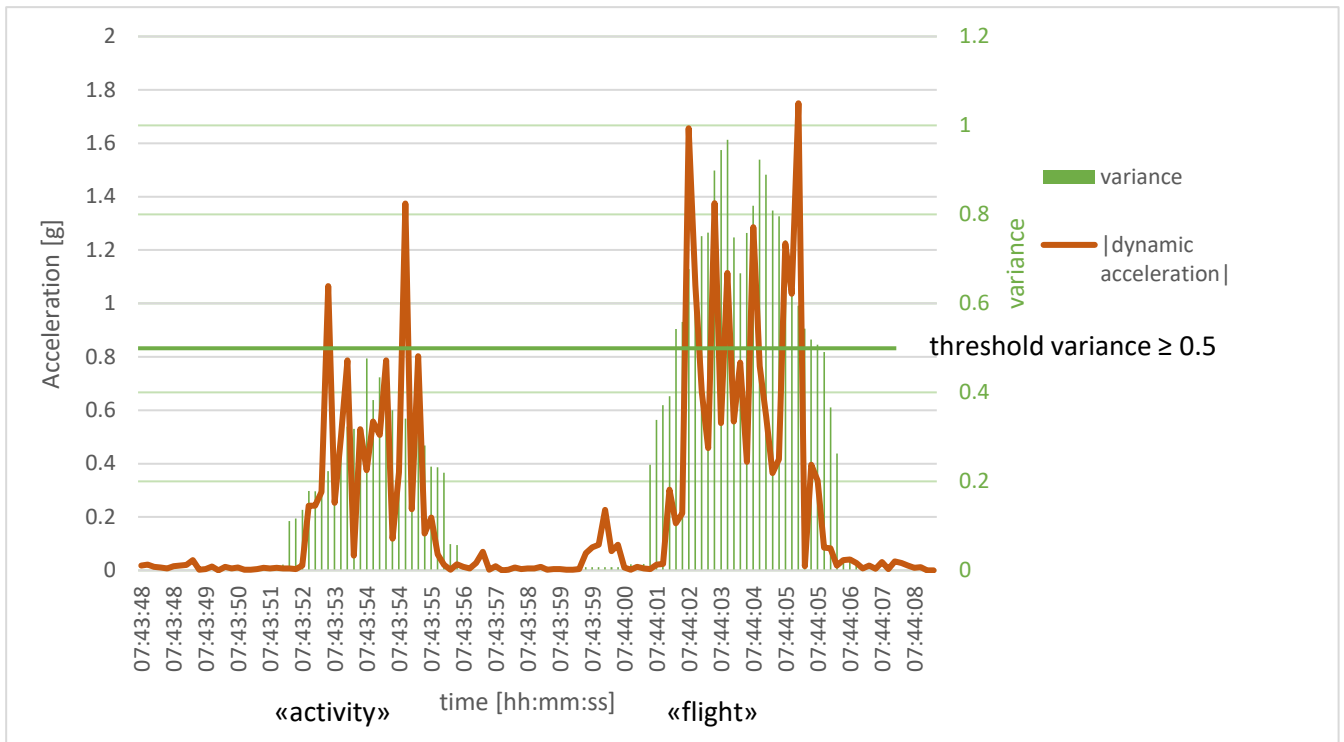


Figure 3 – 5 Example of absolute dynamic parameter with the parameter variance (green) illustrated. “Activity” is characterized by variance lower than 0.5 and “flight” by variance higher than 0.5.

In the next step, all the data points that fulfilled the above terms were arranged in groups, by aligning all consecutive data points in one group. These groups are the possible flight events 1. Starting from each median of the possible flight events 1, extended start- and endpoints, where the variance became lower than 0.25, were defined. Thereby, more data points were assigned to the behaviour “flight”. This made each possible flight event slightly longer (= flight events 2; Figure 3 – 6). Then, a comparison of plots from assigned flight events 1 to observed flight patterns by observation showed that the duration of observed flights is longer. Different thresholds were tested by comparing plots with assigned flight events and observed flights. First, it was assumed that 4 peaks per bout should have an amplitude over 0.75. However, it turned out that 3 peaks with an amplitude higher or equal to 1 are more accurate. For more details, see validation of behaviour determination.

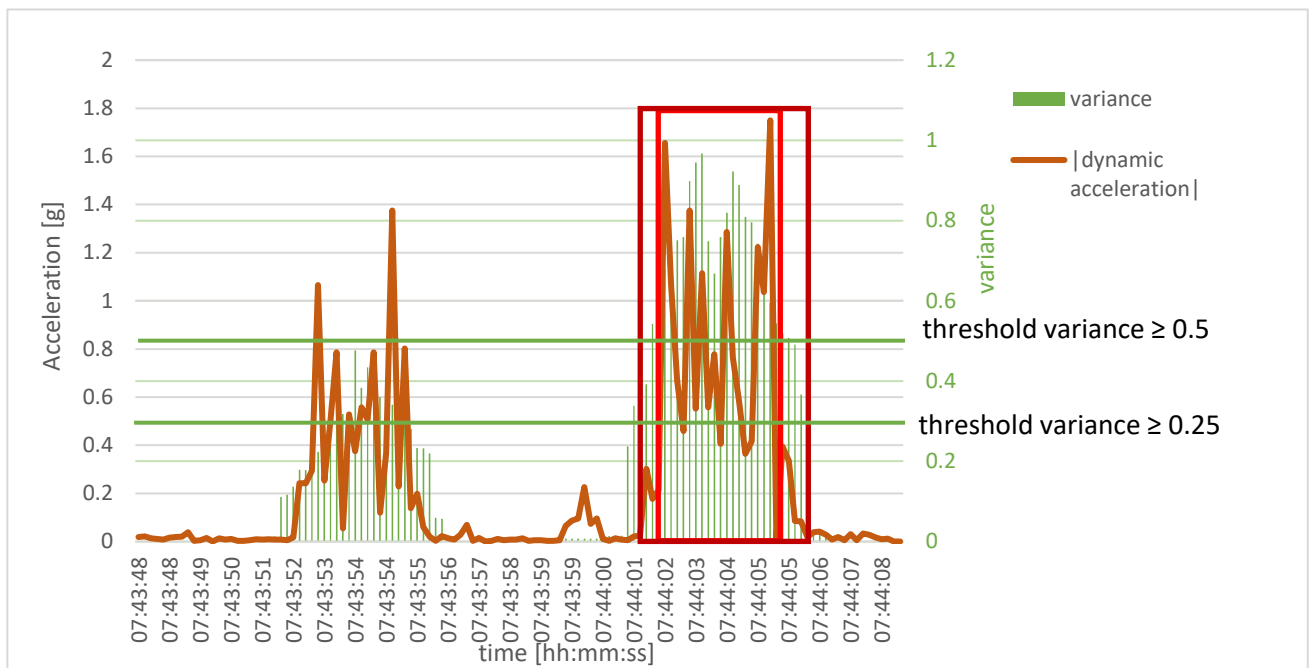


Figure 3 – 6 Difference of duration of flights when start- and end-points were defined by variance ≥ 0.5 (possible flight events 1, red window) and when start and end-point were defined by variance ≥ 0.25 (flight events 2, dark red window).

To assign inactive behaviour to a data point, the following specific thresholds were defined:

- 10 or more peaks in the bout must have an amplitude smaller or equal than 0.25
- the variance must be smaller or equal than 0.01.

All the data points that fulfilled these terms were grouped in the same way as the flight events. The first and the last data point of a group were taken directly as a start- and end-point. The inactivity events assigned according to the above-mentioned criteria were plotted and compared to known resting periods to adjust the thresholds.

All the remaining data points were assigned to the behaviour “activity”.

In the end, each of the over 2 million data points from one logger had one of the three behaviours assigned.

This was done for all loggers that were active during an experiment (34 in total).

Problems and Validation of behaviour determination

The attempt to define active behaviours like short flights from branch to branch or hopping during foraging more precisely did not succeed due to different reasons. First, it was difficult to accurately define those behaviours. A very short flight can be very similar to a long hop. Also, there was a lack of precise observations of those behaviours, therefore they could not be validated with the plotted acceleration data. Hence, the available observations did not allow detecting a specific pattern of short flights in the plotted data – in contrast to “flights”. Therefore, all foraging, hopping, picking, flapping and other active behaviours were taken together and assigned to the pattern “activity” without further distinction.

The behaviour determination was validated by comparing the assigned behaviours with the known behaviour from periods when the birds were observed. Those observations originated mainly from one individual which did not breed in the hedge, but in a nearby front yard. Further observations originated from two other birds which could easily be observed outside the disturbance experiments. Finally, some observations were from a common blackbird equipped with an acceleration logger in the aviary of the Swiss ornithological institute. However, no flight observations were made for this bird, because the observations were made on a cold and wet day when the bird was most of the time inactive or little active.

Four different threshold definitions for flights were compared. The definitions were varying in the amplitude and number of the peaks but always for a bout of 2 seconds.

Definition 1: 4 peaks with an amplitude ≥ 0.75

Definition 2: 3 peaks with an amplitude ≥ 0.9

Definition 3: 3 peaks with an amplitude ≥ 1

Definition 4: 3 peaks with an amplitude ≥ 1.1

For all four definitions it was controlled whether an observed flight was characterized as flight or as activity and vice versa (total of about 130 observations). First, definition 1 was compared to definition 2 showing that definition 2 was more accurate than definition 1 (overall performance of 76 % to 80 %). Then, definition 2 was compared with definition 3 and 4, to see whether a higher amplitude would be more accurate. Definition 3 did best with an overall performance of 89 % compared to 80 % (Definition 2) and 88 % (Definition 4), respectively. Definition 3 assigned 90 % of the observed flight and 88 % of the observed active (including hopping and picking) behaviour correctly. 83 % of all defined flights events were observed flights and 93 % of defined activity was observed active behaviour. For more details see attachment.

Quantification of behaviour

For quantification, the percentage of each behaviour during each part of the experiment was calculated. ‘Before disturbance’ was defined by start of the telemetry protocol before the disturbance until start of the telemetry protocol during the disturbance, ‘During disturbance’ by start and end of the telemetry protocol during the disturbance event and ‘After disturbance’ by the time points from the end of the actual disturbance event until the end of the telemetry protocol after the disturbance. Numbers of data points assigned to a specific behaviour were divided by total number of data points during this part. Results were ranging between 0 and 1. This was done for each experiment part and each behaviour. For example:

$$\text{Flights (before)} = \frac{\#datapoints_{flights}(\text{before})}{\#datapoints_{total}(\text{before})}$$

Fitting Models

Each model had one outcome variable: flight, activity or inactivity which is numeric. The data points are dependent from each other because the logger recorded acceleration continuously. Hence proportion of each behaviour are not count data. So, neither a Poisson nor a binomial distribution, but a Gaussian (= Normal) distribution was used. A logit transformation was used to achieve normal distribution. Given that in logit function 0 and 1 are infinite, all the 0 and 1 values needed to be replaced before transformation. 1 was replaced by subtracting half of the difference between 1 and the highest value (0.99904) from 1 (1 -> 0.99952). 0 was replaced by adding half of the smallest value (0.00072) to 0 (0 -> 0.00036). The observations are also not independent but grouped (repeated measurements for same birds, and some individuals were from the same hedge). For these reasons the linear mixed-effects model from the lme4 package in R 3.4.1. was applied (Bates et al., 2018; R Development Core Team, 2008). As a next step the model assumptions were checked. The assumptions for a linear mixed-effect model are that the residuals are independent and identically distributed (Korner-Nievergelt et al., 2015). There was no serious violation of the model assumptions found (Figure 3 – 7). The first model only considered an interaction between disturbance and status. This was discarded in favour of a model with an additional interaction between disturbance and sex, because female and male birds seemed to react differently to a human encounter. A model with a three-way interaction was also considered, but this model was deficient. This was most likely because of insufficient data for such a complicated model and therefore it was discarded. In all models all the fixed factors measured during the experiment were considered, and no factor was removed.

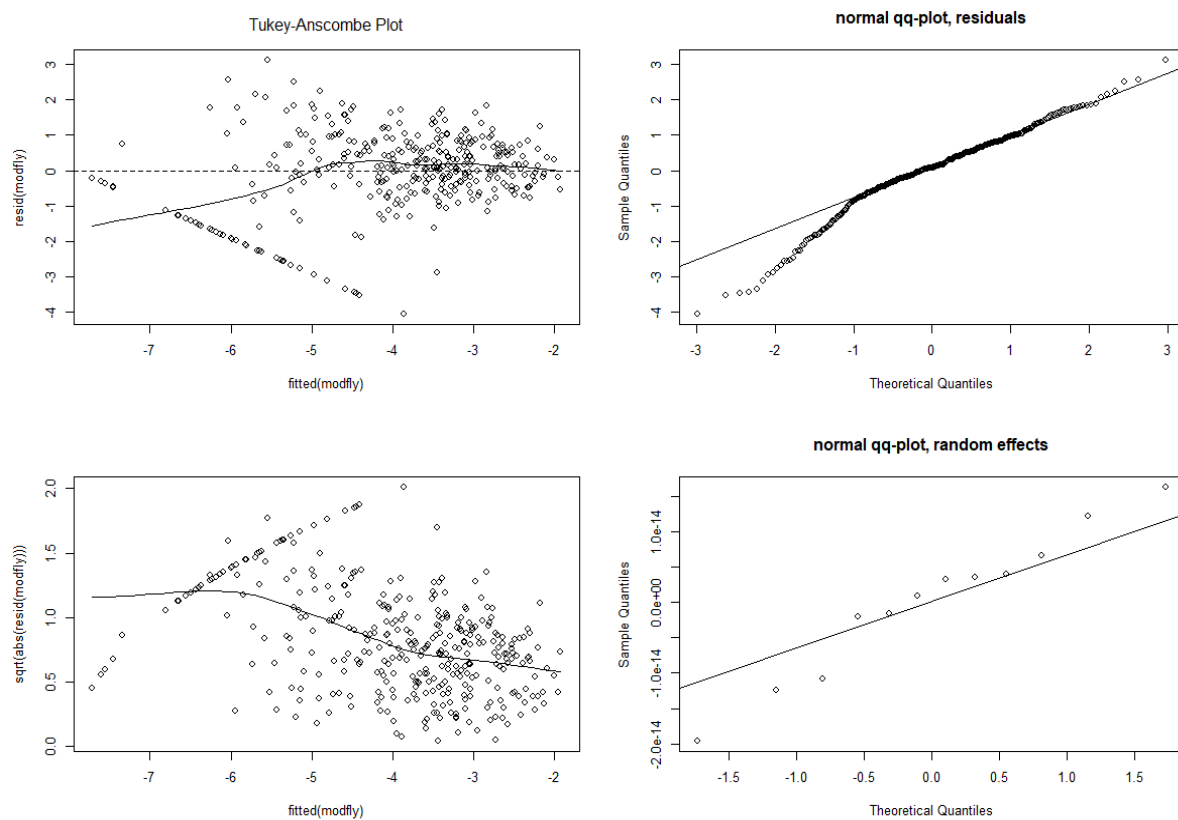


Figure 3 – 7 Diagnostic residuals and random effect plots to assess model assumptions of the model with flight as outcome. Upper left: residuals versus fitted values. Upper right: Normal QQ plot of the residuals. Lower left: square-root of the absolute values of the residuals versus fitted values. Lower right: Normal QQ plot of the random effect (location).

Statistical analysis

The amount of flight, activity and inactivity was modelled in three separate linear mixed-effects models for the main result. Disturbance (3 levels; before, during, after), sex (2 levels; male, female), status (3 levels; unknown, incubating, feeding), time (2 levels; morning, evening), Julian date (continuous), temperature (continuous) and width of the hedge (continuous) were considered as fixed factors. Additionally, the model included an interaction between disturbance and status and an interaction between disturbance and sex. All continuous variables were z transformed (mean = 0 and SD = 1) to facilitate convergence of the models (Korner-Nievergelt et al., 2015). Hedge (= location), ring number (= individual) and experiment number were included as random factors to account for repeated measure of the same hedge and of the same individuals, as well as to account for between-experiment variance. As another random factor, weather (3 levels; sunny, cloudy, rainy) was included in the models.

Illustration of the model:

$$\hat{y}_i = \beta_0 + b_{\text{expnr } i} + b_{\text{Individual } i} + b_{\text{location } l} + b_{\text{weather } l} + \beta_{1l} (\text{disturbance} = \text{during}) + \beta_{2l} (\text{disturbance} = \text{after}) + \beta_{3l} (\text{sex} = \text{male}) + \beta_{4l} (\text{status} = \text{feeding}) + \beta_{5l} (\text{status} = \text{unknown}) + \beta_6 \text{jdate.z} + \beta_7l (\text{time} = \text{morning}) + \beta_8 \text{temp.z} + \beta_9 \text{width.z} + \beta_{9l} (\text{disturbance} = \text{during})l(\text{status} = \text{feeding}) + \beta_{10l} (\text{disturbance} = \text{after})l(\text{disturbance} = \text{feeding}) + \beta_{11l} (\text{disturbance} = \text{during})l(\text{status} = \text{unknown}) + \beta_{12l} (\text{disturbance} = \text{after})l(\text{status} = \text{unknown}) + \beta_{13l} (\text{disturbance} = \text{during})l(\text{sex} = \text{male}) + \beta_{14l} (\text{disturbance} = \text{after})l(\text{sex} = \text{male})$$

$$Y_i \sim \text{Norm}(\hat{y}_i, \sigma^2)$$

$$b_{\text{expnr}} \sim \text{Norm}(0, \sigma_b^2)$$

$$b_{\text{Individual } l} \sim \text{Norm}(0, \sigma_b^2)$$

$$b_{\text{location}} \sim \text{Norm}(0, \sigma_b^2)$$

$$b_{\text{weather}} \sim \text{Norm}(0, \sigma_b^2)$$

Since the interest was in the fixed effects, the maximum likelihood (ML) model was used instead of the restricted maximum likelihood estimation (REML). For analysis a Bayesian approach was used (Korner-Nievergelt et al., 2015). To obtain the posterior distribution, a Monte Carlo simulation of 5000 values from the joint posterior distribution of the model parameters were made. Therefore, the function `sim` was used from the R-package `arm` which assumes an improper prior distribution (Gelman et al., 2016). The fitted mean values from the joint posterior distributions of the model parameters were used as estimates. As lower and upper limits of the 95 % credible interval (CrI), the 2.5 % and 97.5 % quantiles from the posterior distribution were used (for more details see tables in the attachment).

Interpretation

For quantitative interpretation, the results from the model output (via 'summary') was manually added to calculate the mean of specific groups as indicated in the formula and was then transformed back and noted in percentage for easier interpretation. For example, to calculate the difference in the percentage of flights between feeding males before and during a disturbance, all terms belonging to each of those groups were added. A male bird during feeding before disturbance (=mfb) had the following percentage of flight behaviour:

$\hat{Y}_{mfb} = \beta_0 + \beta_{3l} (\text{sex} = \text{male}) + \beta_{4l} (\text{status} = \text{feeding}) = -4.76 + -0.46 + 1.44 = -3.78$ or, back transformed in percentage 2.23%.

Compared to a male bird during feeding during disturbance (=mfd):

$\hat{Y}_{mfd} = \beta_0 + \beta_{3l} (\text{sex} = \text{male}) + \beta_{4l} (\text{status} = \text{feeding}) + \beta_{1l} (\text{disturbance} = \text{during}) + \beta_{9l} (\text{disturbance} = \text{during})|(\text{status} = \text{feeding}) + \beta_{13l} (\text{disturbance} = \text{during})|(\text{sex} = \text{male}) = -4.76 + -0.46 + 1.44 + 0.84 + -1.67 + 1.24 = -3.37$ or back transformed in percentage 3.32%.

Hence, the feeding male bird had about 1% more flight behaviour before than during disturbance.

Habituation/Sensitization model

A second set of three linear mixed-effects models was applied to investigate whether the birds showed a habituation or a sensitization during the course of the six experiments. Flight, activity or inactivity was the dependent variable. Disturbance, sex, status, time, Julian date, temperature, width of the hedge and as additional explanatory variable, experiment number were considered as fixed factors. Location and individual were included as a nested random factor and weather as second random factor. The model included the three-way interactions disturbance x status x experiment number and disturbance x sex x experiment number, as well as all two-way interactions from those combinations. The same Bayesian approach was used as for the main results.

Ethical aspects

The study was conducted under the ethical guidelines of the Canton Lucerne. All persons involved in bird handling have an accurate ringing licence.

4. Results

Descriptive statistics

In total 19 birds from 12 different hedges were used for analysis: 9 females from 8 different hedges and 10 males from 9 different hedges. 4 of the males were feeding chicks, the other 6 males had an unknown status. For the females, 2 had an unknown status, 2 were incubating and the other 5 were feeding chicks. In summary, there were 2 incubating birds, 9 feeding birds and 8 birds with an unknown status (Table 4 – 1). In common blackbirds, only the females incubate the eggs. This is the reason why none of the males had the status incubating. During the first few days, the female still spends quite a lot of time heating the nestling, hence the male is providing most of the food. Later on, both sexes will contribute to feeding the nestling (Hill et al., 1999b).

Percentage of flight behaviour ranged from 0.036 % to 28.13 % (mean = 4.30 %, SD = 0.04), percentage of active behaviour from 0.036 % to 70.24 % (mean = 20.02 %, SD = 0.14) and percentage of inactive behaviour from 24.60 % to 99.95 % (mean = 75.69 %, SD = 0.16).

Experiments took place from Julian day 107 (17.4.2017) to 191 (10.7.2017). During this time, temperature ranged between estimated -1 ° Celsius and 31° Celsius (mean = 16 °C, SD = 7 °C). From totally 354 experiments, 194 took place during sunny, 129 during cloudy, and 31 during rainy weather.

The shortest disturbance event took 4 minutes and the longest 48 minutes (mean = 25 min, SD = 10 min).

Hedge width varied from 4.65 meter to 12.17 meters (mean = 7.18 m, SD = 1.65 m).

Table 4 – 1 List of the sample sizes separated per status and sex.

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

Flights

A linear mixed-effects model with flight as dependent variable, disturbance, sex, status, Julian date, time, temperature, width of the hedge, the interaction terms disturbance x status, disturbance x sex as fixed factors and location, individual and experiment number and weather as random factor was performed. The model showed distinct effects of the interaction terms disturbance (during) x status (feeding), disturbance (during) x status (unknown) and disturbance (during) x sex (male). The effect size of the following fixed effects was small: Julian date, time of day, temperature and width of the hedge and of the interaction terms disturbance (after) x status (feeding), disturbance (after) x status (unknown) and disturbance (after) x sex (male). The main effects of terms that were also involved in an interaction term were not interpreted further, because of the different intercept (Korner-Nievergelt et al., 2015). The standard deviation for the random effects was the lowest between hedges and highest between individuals (Table 4 – 2).

Table 4 – 2 Estimates and standard error of effects for the fixed factors, interactions and standard deviations for the random effects from the linear mixed-effect model with the dependent variable “flights” (logit transformed).

Intercept is given for incubating female birds before disturbance in the afternoon.

Parameter	Estimate	Std. Error
<u>Fixed effects</u>		
Intercept	- 4.76	0.82
disturbance (during)	0.84	0.44
disturbance (after)	- 0.80	0.44
sex (male)	- 0.46	0.62
status (feeding)	1.44	0.97
status (unknown)	0.66	1.04
Julian date (z transformed)	0.38	0.32
time (morning)	0.08	0.22
temperature (z transformed)	- 0.26	0.18
hedge width (z transformed)	0.33	0.35
disturbance (during) x status (feeding)	- 1.67	0.52
disturbance (after) x status (feeding)	0.60	0.52
disturbance (during) x status (unknown)	- 1.12	0.57
disturbance (after) x status (unknown)	0.41	0.57
disturbance (during) x sex (male)	1.24	0.35
disturbance (after) x sex (male)	0.29	0.35
<u>Random effects</u>		
	SD	
experiment number	0.41	
individual	1.01	
location	< 0.001	
weather	0.03	
Residual	1.47	

The percentage of “flights” of all behaviour is illustrated per status, sex and disturbance in Figure 4 – 1.

Incubating female birds increased their amount of flights by about 1 %, from 0.85 % (95 % CrI = 0.16 % – 4.42 %) before disturbance to 1.94 % (95 % CrI = 0.38 % – 10.03 %) during disturbance. Thereby, they were more than doubling (+ 128 %) their flights. In contrast, there was a decrease of – 124 % from 0.85 % (95 % CrI = 0.16 % – 4.42 %) before disturbance to 0.38 % (95 % CrI = 0.07 % – 2.06 %) after disturbance.

Feeding common blackbirds showed a reversed pattern for males and females. Males increased their amount of flights by about 1 %. Before disturbance, 2.24 % (95 % CrI = 0.68 % – 7.15 %) of the time was assigned to flight behaviour compared to 3.32 % (95 % CrI = 1.00 % – 10.16 %) during the disturbance (+ 48 %). After disturbance, feeding males still had a slightly higher amount of flights, with 2.43 % (95 % CrI = 0.75 % – 7.70 %), compared to before disturbance (+ 8 %).

In contrast, feeding female birds decreased their amount of flights on average by about 2 % during disturbance. Before disturbance, 3.50 % (95 % CrI = 1.13 % – 10.69 %) of the time was assigned to flight behaviour, compared to 1.54 % (95 % CrI = 0.50 % – 4.83 %) during the disturbance, which is less than half (- 127 %). After the disturbance event, feeding female birds still had a decreased amount of flights, with a percentage of 2.87 % (95 % CrI = 0.95 % – 8.68 %), compared to before disturbance (- 22 %).

Males of unknown status increased flights by about 2 % during disturbance from 1.04 % (95 % CrI = 0.34 % – 3.11 %) before to 2.66 % (95 % CrI = 0.87 % – 7.88 %) during disturbance. This is an increase of 156 %. After the disturbance event, males with unknown status had a slightly smaller amount of flights (- 11 %) than before disturbance with 0.94 % (95 % CrI = 0.31 % – 2.84 %).

The two female birds of unknown status decreased their amounts of flights from 1.64 % (95 % CrI = 0.41 % – 6.40 %) before disturbance, to 1.23 % (95 % CrI = 0.30 % – 4.78 %) during disturbance (- 33 %) and to 1.11 % (95 % CrI = 0.27 % – 4.41 %) after disturbance (- 48 %).

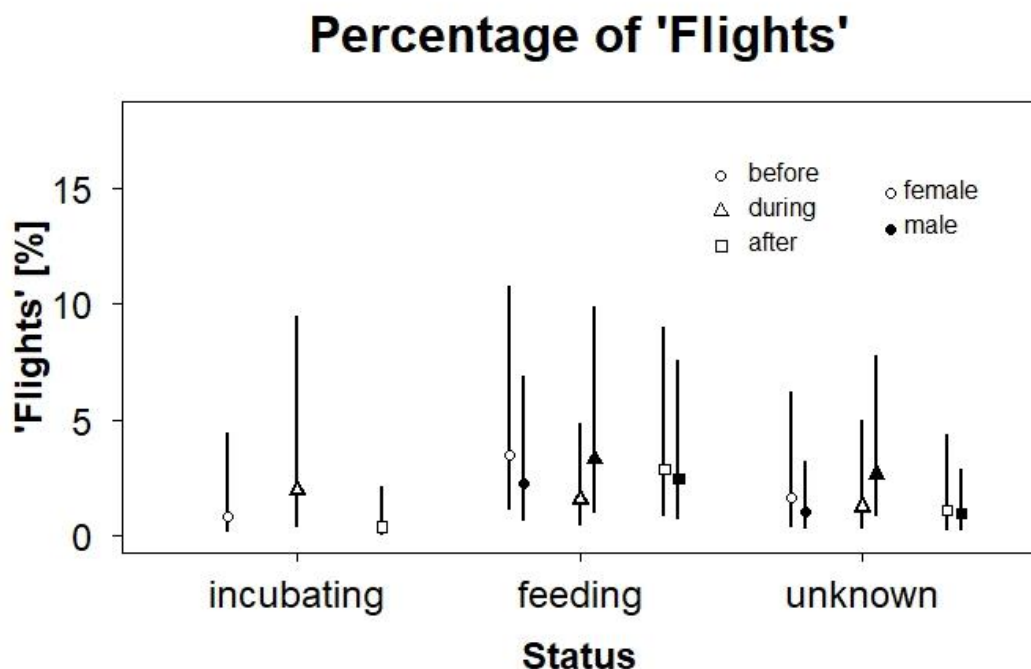


Figure 4 – 1 Percentage of the behaviour “flights” of all behaviours, for incubating, feeding and birds with unknown status before, during and after disturbance, separated for male and female birds.

Estimated means with 95 % Credible intervals.

Incubating females n = 2, feeding females n = 5, feeding males n = 4, unknown females n = 2, unknown males n = 6

Activity

A linear mixed-effects model with activity as dependent variable and the same fixed and random factors as above was performed. The model showed again distinct effects of the interaction terms disturbance (during) x status (feeding), disturbance (during) x status (unknown) and disturbance (during) x sex (male). The effect size of the following fixed effects was small: Julian date, time of day, temperature and width of the hedge and of the interaction terms disturbance (after) x status (feeding), disturbance (after) x status (unknown) and disturbance (after) x sex (male). The standard deviations for the random effects for experiment number and location were similar and quite low and very small for individual (Table 4 – 3).

Table 4 – 3 Estimates and standard error of effects for the fixed factors and interactions and standard deviations for the random effects from the linear mixed-effect model with the dependent variable “activity” (logit transformed).

Intercept is given for incubating female birds before disturbance in the afternoon.

Parameter	Estimate	Std. Error
<u>Fixed effects</u>		
Intercept	- 2.37	0.48
disturbance (during)	- 0.11	0.39
disturbance (after)	- 0.42	0.39
sex (male)	- 0.05	0.36
status (feeding)	1.21	0.55
status (unknown)	0.12	0.60
Julian date (z transformed)	0.11	0.19
time (morning)	0.11	0.18
temperature (z transformed)	- 0.05	0.15
hedge width (z transformed)	0.19	0.18
disturbance (during) x status (feeding)	- 0.93	0.46
disturbance (after) x status (feeding)	0.39	0.46
disturbance (during) x status (unknown)	- 0.71	0.50
disturbance (after) x status (unknown)	0.35	0.50
disturbance (during) x sex (male)	0.85	0.31
disturbance (after) x sex (male)	0.09	0.31
<u>Random effects</u>		
	SD	
experiment number	0.23	
individual	0.23	
location	< 0.001	
weather	0.03	
Residual	1.14	

The percentage of “activity” of all behaviour per status, sex and disturbance is illustrated in Figure 4 - 2.

Incubating female birds decreased their amount of activity by about 1 %, from 8.54 % (95 % CrI = 3.47 % – 19.71 %) before disturbance to 7.71 % (95 % CrI = 3.12 % – 17.73 %) during disturbance (- 11 %). After the disturbance event, incubating females decreased the amount of activity even more (- 48 % from before) to a percentage of 5.78 % (95 % CrI = 2.29 % – 13.77 %).

Feeding common blackbirds showed the same pattern in their activity for males and females. Males reacted less strongly and decreased their active behaviour by about 3 %. Before disturbance, 23.01 % (95 % CrI = 12.73 % – 37.22 %) of the time was assigned to active behaviour, compared to 19.88 % (95 % CrI = 10.87 % – 33.06 %) during the disturbance. This is a decrease of 16 % of activity. With 24.05 % (95 % CrI = 13.39 % – 38.77 %) after the disturbance, feeding males had 1 % more activity as before disturbance (+ 5 %).

Feeding female birds decreased their amount of activity by about 14 % from 23.85 % (95 % CrI = 13.50 % – 38.84 %) before to 9.96 % (95 % CrI = 5.18 % – 18.14 %) during disturbance. Hence activity was reduced by more than 139 %. With 23.34 % (95 % CrI = 12.96 % – 37.79 %) after the disturbance feeding females had almost the same amount of activity as before disturbance (- 2 %).

Male birds of unknown status did not seem to change their amount of activity because of the disturbance. The percentage of activity was 9.17 % (95 % CrI = 4.88 % – 16.49 %) before disturbance, 9.42 % (95 % CrI = 5.08 % – 16.65 %) during disturbance and 9.32 % (95 % CrI = 5.01 % – 16.80 %) after disturbance.

The two female unknown birds decreased their activity by about 5 % during disturbance, similar as feeding female birds. Before disturbance 9.57 % (95 % CrI = 4.47 % – 19.74 %) of the time was assigned to active behaviour, compared to 4.43 % (95 % CrI = 2.04 % – 9.55 %) during disturbance. This is again less than half of the activity shown before disturbance (-116 %). With 8.99 % (95 % CrI = 4.28 % – 18.67 %) after the disturbance unknown females had almost the same amount of activity as before disturbance (- 6 %).

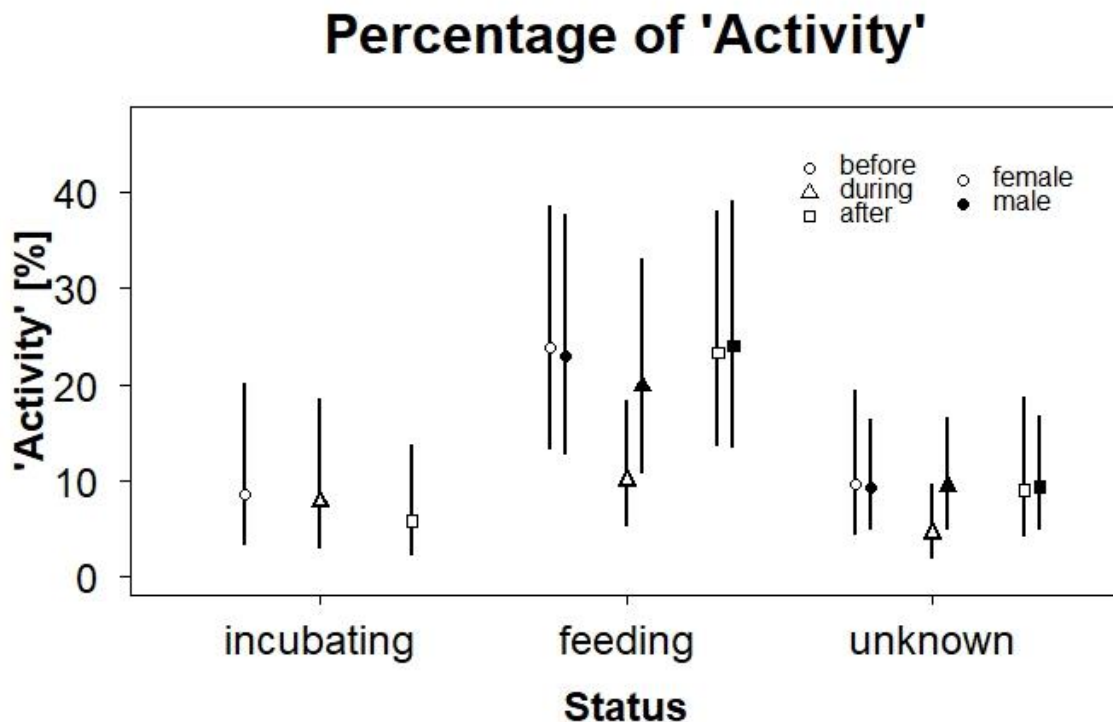


Figure 4 – 2 Percentage of the behaviour “activity” of all behaviours, for incubating, feeding and birds with unknown status, before, during and after disturbance, separated for male and female birds. Estimated means with 95 % credible intervals. For sample size see Figure 4 – 1.

Inactivity

A linear mixed-effects model with inactivity as dependent variable and the same fixed and random factors as above was performed. The model showed distinct effects of the interaction terms disturbance (during) x status (feeding) and disturbance (during) x sex (male). There was little effect of Julian date, time of day, temperature and width of the hedge and of the interaction terms disturbance (during) x status (unknown), disturbance (after) x status (feeding), disturbance (after) x status (unknown) and disturbance (after) x sex (male). The standard deviations for the random effects experiment number and location were similar and quite low and very small for the random effect individual (Table 4 – 4).

Table 4 – 4 Estimates and standard error of effects for the fixed factors and interactions and standard deviations for the random effects from the linear mixed-effect model with the dependent variable “inactivity” (logit transformed).

Intercept is given for incubating female birds before disturbance in the afternoon.

Parameter	Estimate	Std. Error
<u>Fixed effects</u>		
Intercept	2.24	0.56
disturbance (during)	- 0.10	0.42
disturbance (after)	0.43	0.43
sex (male)	0.06	0.41
status (feeding)	- 1.30	0.64
status (unknown)	- 0.20	0.70
Julian date (z transformed)	- 0.19	0.21
time (morning)	- 0.11	0.16
temperature (z transformed)	0.10	0.13
hedge width (z transformed)	- 0.22	0.21
disturbance (during) x status (feeding)	1.10	0.51
disturbance (after) x status (feeding)	- 0.39	0.51
disturbance (during) x status (unknown)	0.74	0.55
disturbance (after) x status (unknown)	- 0.38	0.55
disturbance (during) x sex (male)	- 0.96	0.34
disturbance (after) x sex (male)	- 0.09	0.34
<u>Random effects</u>		
	SD	
experiment number	0.26	
individual	0.32	
location	< 0.001	
weather	0.02	
Residual	1.15	

The percentage of “inactivity” of all behaviour per status, sex and disturbance is illustrated in Figure 4 – 3.

Incubating female birds decreased their amount of inactivity by about 1 %, from 90.20 % (95 % CrI = 76.42 % – 96.46 %) before disturbance to 89.26 % (95 % CrI = 73.29 % – 96.00 %) during disturbance. After the disturbance event, incubating females slightly increased their amount of inactivity to 93.43 % (95 % CrI = 83.11 % – 97.61 %).

Feeding male birds did nearly not react in their amount of inactivity to disturbance. The percentage of inactive behaviour was 71.81 % (95 % CrI = 54.63 % – 84.76 %) before disturbance, 72.64 % (95 % CrI = 55.44 % – 85.13 %) during disturbance and 70.78 % (95 % CrI = 53.47 % – 84.11 %) after disturbance.

Feeding female birds increased their amount of inactivity by about 15 % during disturbance. Before disturbance the percentage of inactivity was 71.21 % (95 % CrI = 53.55 % – 84.03 %), compared to 87.06 % (95 % CrI = 75.86 % – 93.51 %) during disturbance. Hence, feeding female birds increased their activity by 22 %. After the disturbance, feeding females had with 72.28 % (95 % CrI = 54.55 % – 84.73 %) almost the same amount of inactivity as before disturbance.

Male birds of unknown status decreased their amount of inactivity by 3.5 % during disturbance. Before disturbance 89.02 % (95 % CrI = 79.57 % – 94.42 %) of the time was assigned to inactive behaviour, compared to 85.46 % (95 % CrI = 73.96 % – 92.29 %) during disturbance. This is a decrease of 4 % in inactive behaviour. With 88.69 % (95 % CrI = 78.82 % – 94.26 %) of the time after the disturbance assigned to inactive behaviour, unknown males had almost the same amount of inactivity than before.

The two female unknown birds increased their amount of inactivity by about 5 %, which is not as much as the feeding female. Before disturbance, their amount of inactivity was 88.73 % (95 % CrI = 76.35 % – 94.90 %), compared to 93.71 % (95 % CrI = 85.90 % – 97.31 %) during disturbance. With 89.37 % (95 % CrI = 77.88 % – 95.35 %) after disturbance unknown females had almost the same amount of inactivity as before disturbance.

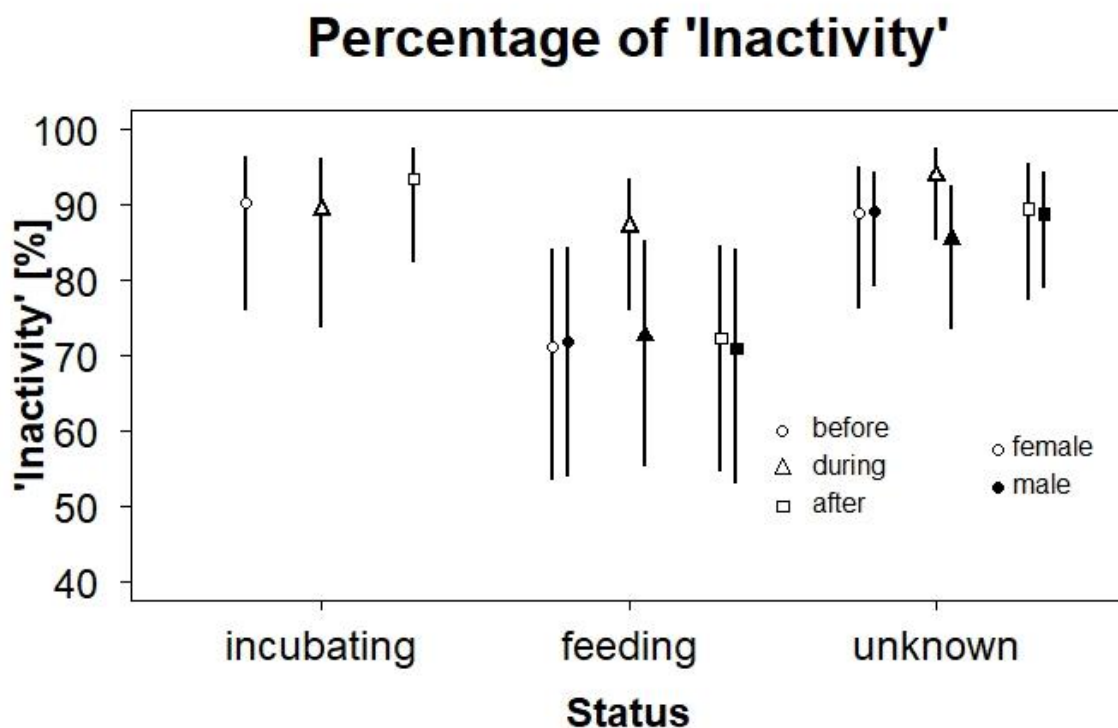


Figure 4 – 3 Percentage of behaviour the “inactivity” of all behaviours, for incubating, feeding and birds with unknown status, before, during and after disturbance, separated for male and female birds. Estimated means with 95 % credible intervals. For sample size see Figure 4 – 1.

Habituation/Sensitization

Linear mixed-effects models were performed, with flights, activity or inactivity as dependent variable, the fixed factors experiment number, disturbance, sex, status, Julian date, time, temperature, width of the hedge, the interaction terms disturbance x status x experiment number and disturbance x sex x experiment number and location and individual as well as weather as random factors.

The results were not statistically analysed. The estimated means with the credible intervals for the 3 experimental events were plotted, separated by the six experiments, for each behaviour, status and sex. The results did not show a visible trend. Therefore, only the example for feeding males is shown (Figure 4 – 4). For a better visualization, the quotients of during disturbance/before disturbance and after disturbance/before disturbance were made. No clear effects of repeated disturbance events could be seen (Figure 4 – 5)

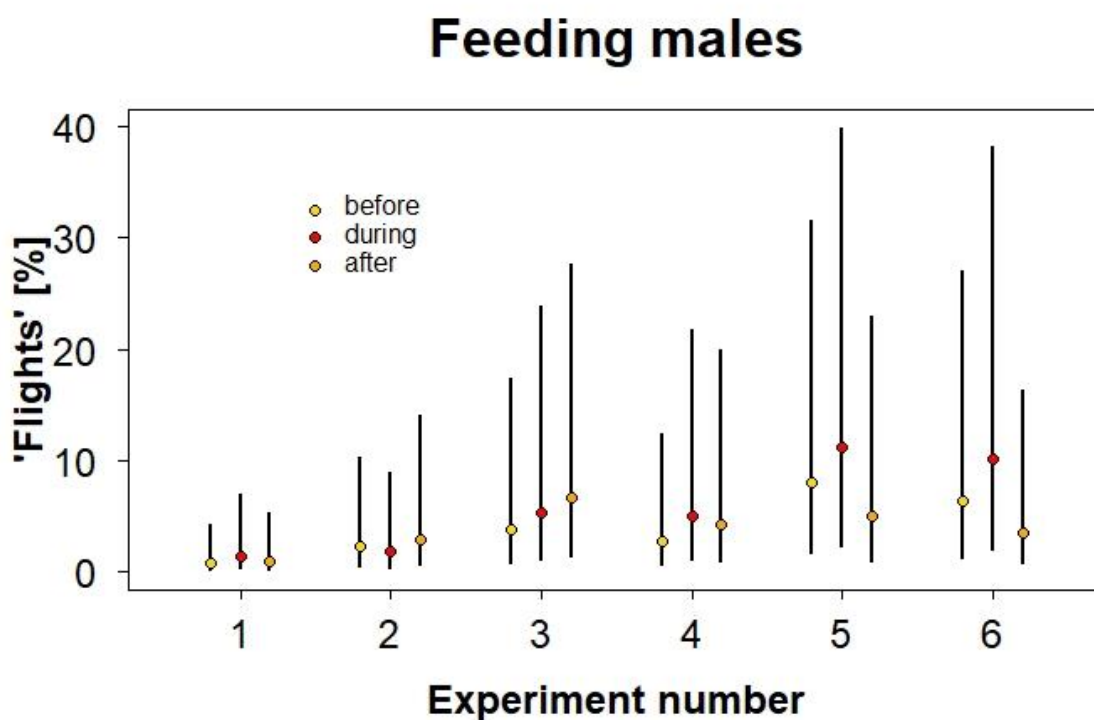


Figure 4 – 4 Percentage of the behaviour “flight” of all behaviours, of feeding male birds for before, during and after disturbance for each of the six experiments. Estimated means with 95 % credible intervals. n = 4

Feeding males

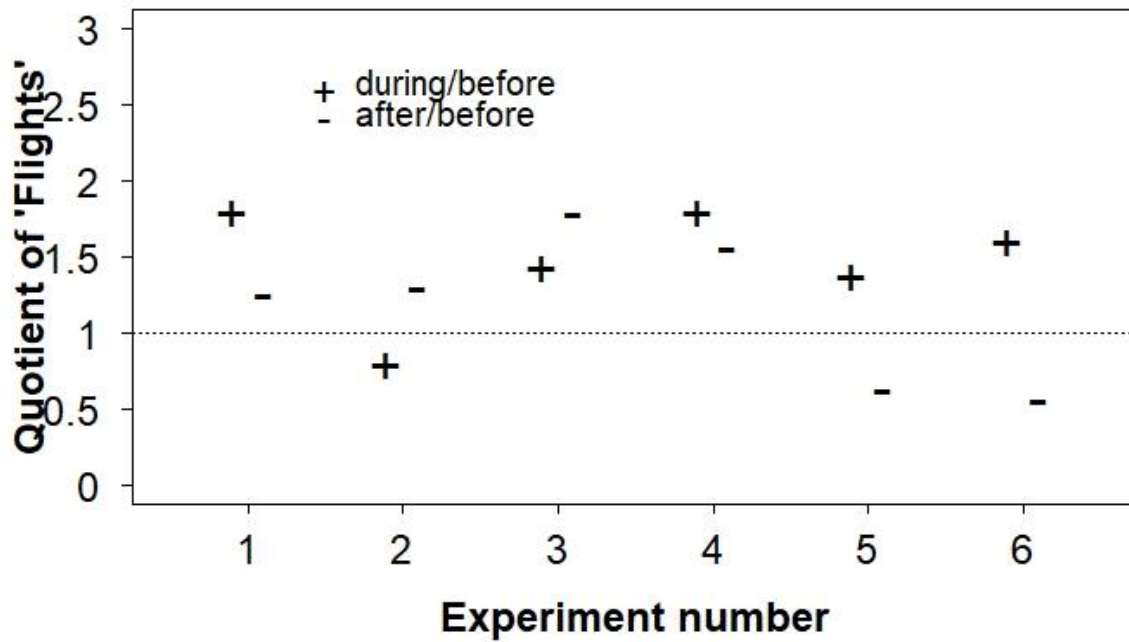


Figure 4 – 5 Percentage of the behaviour “flight” of all behaviours, for feeding male birds for each of the six experiments.

+ = Quotient of percentage of flights during divided by percentage of flights before disturbance

- = Quotient of percentage of flights after divided by percentage of flights before disturbance.

5. Discussion

This study examined the effects of an anthropogenic disturbance on the short-term behavioural reaction of common blackbirds. The behaviours flights, activity and inactivity were defined from the acceleration data of PAM-loggers. The low threshold disturbance, experimentally investigated by humans walking along a hedge and talking normally, did evoke a change in behaviour of blackbirds breeding in this hedge. The change was dependent on the status and sex of the bird.

Behaviour determination with PAM-Loggers

The use of PAM-loggers to track the behavioural reaction of birds during a period of about 6 days requires methodological validations. There are several methods how to define behaviours from acceleration data (Halsey et al., 2009; Laich et al., 2009; Watanabe et al., 2005; Yoda et al., 2001) depending on the animal and the logger specification. First, the axis measuring acceleration needs to be chosen. Acceleration measurement is possible in x-axis, y-axis, z-axis or in any combination of the three axes. To determine major behavioural categories, measuring acceleration in one axis is sufficient, because the signal coding for these categories is distinct and – using only one axis - reduced the storage capacity. The z-axis was chosen, because it proved to reliably detect flight and active behaviour (Laich et al., 2009). Second, the frequency of acceleration needs to be chosen. To be able to distinguish different behaviours changing within seconds, a high frequency is necessary which in turn might limit the storage capacity of the logger. Therefore, a minimum frequency had to be found still enabling the distinction of different behaviours. A previous pilot study testing different frequencies showed that measuring acceleration with a frequency of 6.25 Hz in z-axis was exact enough for the framework of this study and it kept the data points at their minimum.

For further field seasons, it has to be discussed if the loggers could only be activated during a restricted time of day, instead of continuously measuring acceleration. This would require less storage capacity, and acceleration could then also be measured and stored in the x- and y-axis, enabling to calculate the overall dynamic body acceleration (=ODBA). ODBA can be used as an estimate for energy expenditure (Godfrey, 2003; Elliott et al., 2013; Green et al., 2009; Halsey, 2011; Qasem et al., 2012) and would allow considering fitness consequences of a disturbance (Riddington et al., 1996).

For behaviour determination, known behaviours gathered during observations in free-ranging common blackbirds and in a blackbird kept in an aviary were compared with the plotted data during the same time. Clear patterns for the behaviour flights and inactivity were revealed and specific thresholds could be defined to determine those behaviours. This approach was successful, with an overall performance of 89 %. Results from the analysis also confirmed the definitions for the behaviours. As expected, incubating female birds had the least amount of flights, because they were sitting on the nests most of the time, whereas feeding and foraging birds had the highest percentage of active behaviour.

The definitions are most likely applicable for other common blackbirds that carry loggers with the same specifications. However, these definitions would have to be adapted for other bird species or other logger specifications. Generally, this work can be used as an example for future projects in this field.

As discussed in the material and methods part, it was not possible to determine more than the three behaviours: flights, activity and inactivity. However, it might be possible to define more behaviours, if more precise and accurate observations can be made from the behaviours in question. This can be challenging for active behaviours, because the common blackbird forages in dense vegetation such as bushes or crop fields, invisible for the observer. Video recordings with a time tag of the birds' behaviour during open observations might help to gather more accurate data. For determination of highly precise or more variable behaviours such as picking or chick-feeding a more complex technique such as spectral analysis or Fourier transformation is required (Laich et al., 2009; Watanabe et al., 2005).

Effect of disturbance on behaviour

The aim of the study was to investigate whether common blackbirds react to a low threshold disturbance. In general, the common blackbirds' behaviour was affected, and they did change their behaviour in response to the low threshold disturbance. Interestingly the change was status- and sex-dependent. Feeding birds seemed to be affected most, and females more than males. Feeding females showed much more inactive and less active behaviours (activity and flights) because of the disturbance. Feeding males showed more flights and only little increase in inactive behaviour. Incubating females seemed to still be affected up to 30 minutes after the disturbance.

Whether such a rather brief change in behaviour negatively affects the birds' fitness cannot be answered with our experimental design. Generally, a stress response helps to overcome a threatening situation, and as long as the birds gets enough food in a refuge area and quickly returns to normal behaviour after the disturbance, the negative impact is small (Burger and Gochfeld, 1998). However, repeated disturbances might reduce foraging or feeding activity and increases energy expenditure because of more energy consuming behaviours (flights, hopping, flapping) (Fernández and Azkona, 1993). Consequently, repeated disturbance might reduce body mass of the parents and/or the nestlings. For example, barn owl nestlings have a reduced body mass in areas with numerous anthropogenic encounters (Almasi et al., 2015). In great tits, a reduced body mass of fledglings is known to reduce survival probability (Lindén et al., 1992; Naef-Daenzer Beat et al., 2001). It was also found that juvenile hoatzins which were stressed from ecotourism had a reduced body mass and might therefore have a lower survival rate (Müllner et al., 2004). The fact that the change in behaviour could still be observed up to 30 minutes after the disturbance events suggests that the common blackbirds also had possible negative effects from short disturbance on fitness parameters.

Incubating females

The pedestrians caused a doubling of flight behaviour at the expense of active behaviour in incubating female birds. In the 30 minutes after the pedestrians have passed, the incubating females reduced their amount of flights and activity, thus showing a clear increase in their amount of inactivity.

Overall, incubating females had a low amount of flight behaviour (Figure 5 – 1). This is biological reasonable. During incubation, females spend most of their time on the nest, warming the eggs, leaving them only from time to time to search for food.

The increased amount of flight of incubating females during the disturbance might be explained as a reaction to save their own lives, because humans seem to be perceived as possible predators (Beale and Monaghan, 2004). Another explanation might be that incubating common blackbirds wanted to lure the disturber away from the nest. High activity around the nest might attract possible predators and increase the predation risk (Skutch, 2008). Therefore, minimizing the activity around the nest by flying away lowers this risk (Conway and Martin, 2000). Whether some individuals choose this strategy or whether escape flights are context dependent cannot be answered with our study because of the small sample size.

After disturbance the incubating females showed a higher amount of inactivity.

Incubating female common blackbirds have to find a trade-off between warming and protecting their offspring and getting enough food (Conway and Martin, 2000). It might be possible that the incubating females wanted to catch up the time the eggs were not warmed during the disturbance. Measurement of the stress hormones and plasma metabolites might give more insight about how much the incubating females were still stressed from the encounter with the pedestrians.

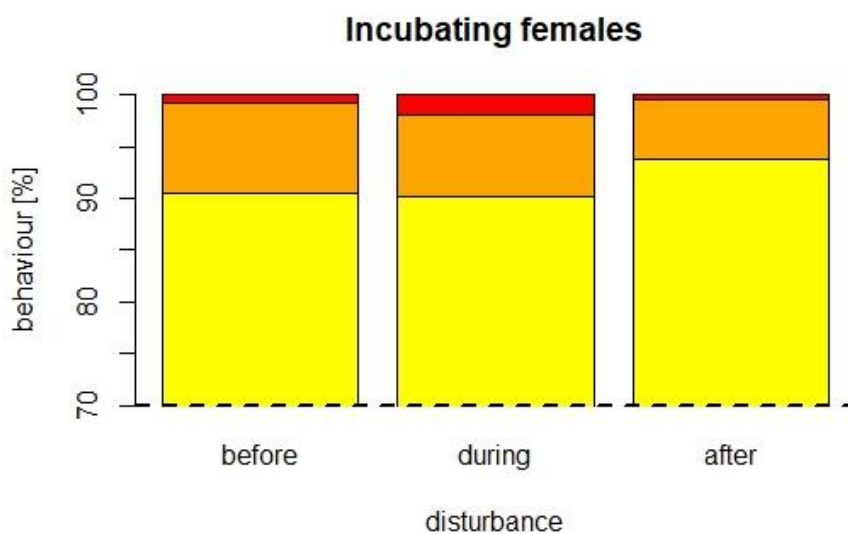


Figure 5 – 1 Percentage of all three behaviours for incubating female birds before, during and after the disturbance.

Yellow: percentage of “inactivity”, orange: percentage of “activity” and red: percentage of “flights”

Feeding birds

Feeding common blackbirds showed a high amount of activity and generally more flights than incubating females. Both sexes of blackbirds do feed their nestlings, but - as expected from feeding literature data (Hill et al., 1999) - females were observed to stay longer on the nest warming the nestling, whereas the males did only feed the nestling.

Both feeding females and feeding males were disturbed by encounters with pedestrians. On average, the feeding males reacted to the disturbance in reverse to the feeding females. The male feeding birds increased the amount of flights at the expense of activity. In contrast, female feeding birds halved the amount of flights and activity during the disturbance and substantially increased their inactivity

(Figure 5 – 2).

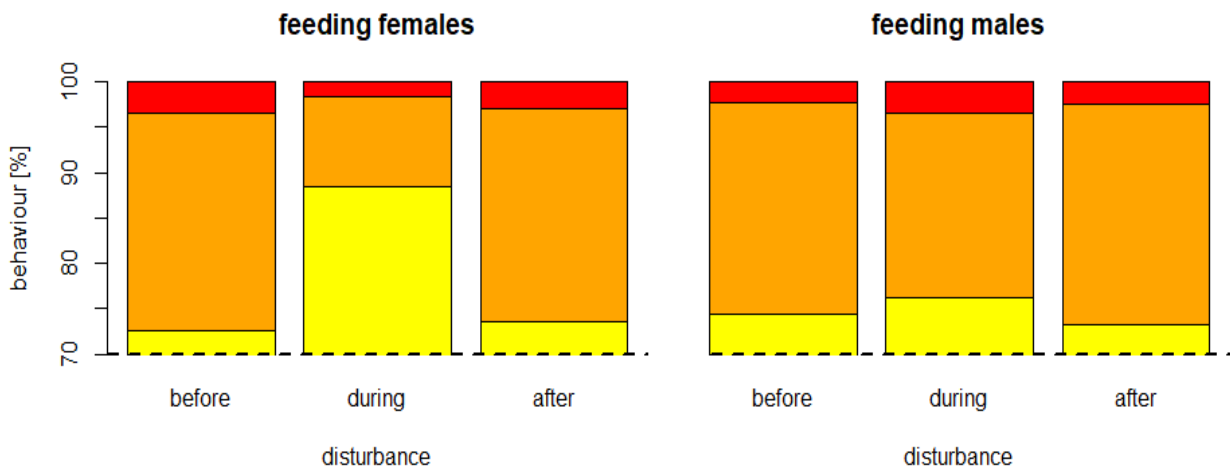


Figure 5 – 2 Percentage of all three behaviours for incubating female and male birds before, during and after disturbance.

Yellow: percentage of “inactivity”, orange: percentage of “activity” and red: percentage of “flights”

The individual data however showed a varying pattern (Figure 5 – 3). Only 1 of the 5 feeding females decreased her amount of flights during the disturbance.

This discrepancy can be explained with the logit transformation which was done to achieve normal distribution for the model. A logit transformation puts more weight to an equal difference between small values than between high values. Therefore, the means are prone to outliers. Hence, interpretations of the means need to be made carefully.

The female which showed least flights during the disturbance (Figure 5 – 3, lower red encircled violet line) behaved differently than the other feeding birds, also in respect to the behaviours activity and inactivity. This female had very young nestlings and the nest was located at the end of the hedge, close to a street. This hedge was included in the study as undisturbed habitat, because there was no path next to it and the street was only at one end close to the hedge. The male from the the same nest was logged at a later time, and experiments were conducted as well. He also decreased his amount of flights during disturbance compared to before and even more to after the disturbance (Figure 5 – 3, upper red encircled green line for feeding birds). The change in the amount of activity and inactivity also differs from the other feeding common blackbirds. The two birds had a more extreme decrease in activity and thus a stronger increase in inactivity than the other individuals. Observations confirmed that this female was staying motionless at or on the nest. One might hypothesize that she did this to not attract the disturber. Such behaviour is known from penguins (Willener et al., 2015), Oystercatchers (Hüppop and Hagen, 1990) and snow grouse (Ingold et al., 1992) which did not leave the nest when humans were approaching. Nevertheless, those animals were disturbed and most probably stressed as heart rate sharply increased during, respectively decreased after, the disturbance (Ingold et al., 1992). Hence, both birds from this hedge reacted differently to the disturbance than the other individuals which could be due to the car traffic from the street. Studies with incubating passerines and grassland species showed that birds breeding close to a road have a reduced breeding density. Hence, nesting sites close to a street seem to be less attractive for the birds due to the noise of the cars; however, visual stimuli cannot be excluded (Peris and Pescador, 2004; Reijnen et al., 1995). Birds breeding in a non-preferential habitat close to a street might therefore have different behaviour patterns.

Percentage of 'Flights'

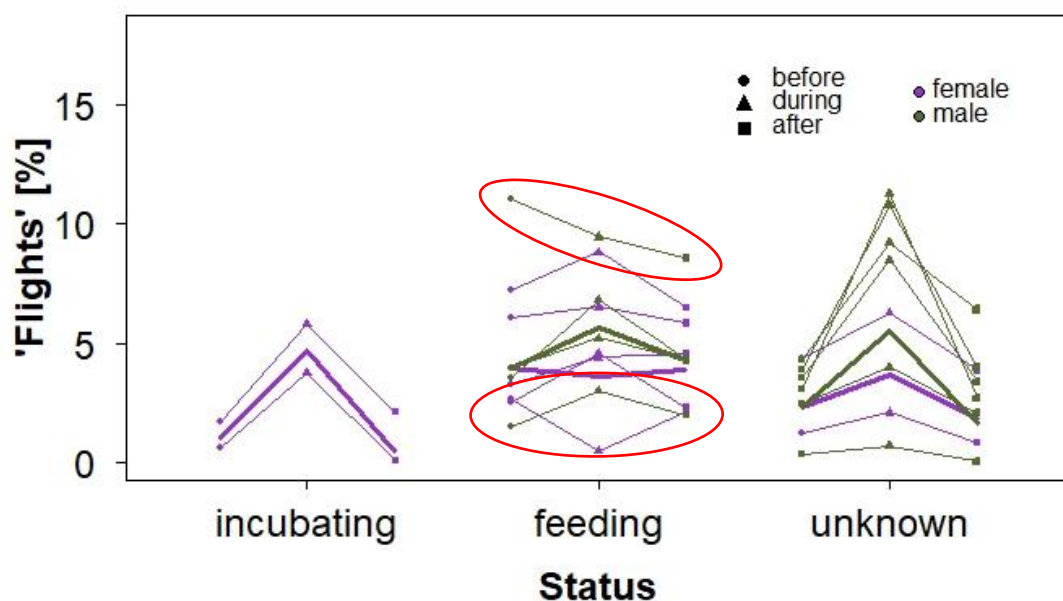


Figure 5 – 3 Percentage of the behaviour “flights” of all behaviour for incubating, feeding and birds with unknown status before, during and after disturbance, separated for males (green lines) and females (purple lines). Each of the fat lines represents the average per status and sex. Incubating females n = 2, feeding females n = 5, feeding males n = 4, unknown females n = 2, unknown males n = 6

No matter whether these two individuals were included in the analysis or not, the feeding females reacted stronger to the disturbance than the feeding males. Sex difference in risk-taking behaviour was also found in other studies. In flocks of sparrows, it was observed that males tend to stay more often at a disturbed patch than females (Breitwisch and Hudak, 1989). In Southern house wrens, females returned earlier to the nest after a disturbance than males (Fernandez et al., 2013). There is no qualitatively consistent effect of sex difference across studies, but females seem to react more sensitive to disturbers (Stankowich, 2008).

In general, feeding birds have to find a trade-off between foraging and survival (Lima and Dill, 1990). If birds see humans as possible predators, they will respond in a similar way as to a predator (Gill et al., 1996). Other studies also found that feeding birds decreased the active behaviour because of a human disturbance as they would do if a predator approached (Burger and Gochfeld, 1998; C. Hillman and Lovari, 1985; Fernández-Juricic and Tellería, 2000; Gill et al., 1996; Stillman and Goss-Custard, 2002). Therefore, they cannot use the full potential of their foraging area and might need to move to a refuge area which might have less or worse food available, or they may interrupt foraging completely during a disturbance.

It is difficult if not impossible to interpret just from the determined behaviours when the bird did change its foraging behaviour or where it was flying. A combination with the data from the VHF-transmitters would enable to answer such questions. It would also become possible to see at which distance the blackbirds are impacted by the disturber (for example flying initiation distance or alert distance). Likewise, the duration of the disturbance event could be defined more precisely, because start and end of the period when a bird actually reacted to the human encounter could be determined. For this study, duration of the disturbance event was defined by start and end of the walk along the hedge. Depending on the length and complexity of the hedge, a bird might have perceived the walking humans and adjusted its behaviour at varying times and consequently the disturbance event might have been shorter than the actual walk along the hedge. In this case, the main disturbance event, especially in long hedges, can be diluted because the disturber needed a certain time to get close to the bird. Hence, effects of the human encounter are most likely even more extreme.

Birds with unknown status

Male birds with unknown status doubled their amount of flights compared to the feeding male, thereby decreasing their amount of inactivity. Female birds with unknown status decreased their amount of flights and more than halved their amount of activity because of the disturbance. The amount of flights further decreased in the 30 minutes after the disturbance.

In other words, the behavioural reaction to the disturbance was similar to feeding birds. Therefore, one might speculate that at least some of the male birds had nestlings to feed.

Habituation/Sensitization

Habituation, in the context of anthropogenic disturbances, is the process which leads to a decreased stress response of an animal to humans as a stressor. Sensitization, its counterpart, is the process which leads to an increase in the stress response of an animal (Blumstein, 2016).

The common blackbirds increased their flight behaviour during the course of the 6 experiments not only during, but also before and after the disturbance event. Hence, habituation or a sensitization to the repeated disturbance could not be observed. The increasing flight behaviour in the course of the 6 days lasting experiment can be explained with a higher feeding rate of the growing nestlings which demand for more food. The reason why the birds did not get habituated or sensitized to the disturber could be that a short disturbance repeated for six days is not enough to evoke a lasting behavioural change. A few studies examined the habituation rate to human disturbance and mainly found great interindividual variation in reactivity to the disturbance (Carrete and Tella, 2010; Ellenberg et al., 2009; Runyan et al., 2004). Most studies measured flight initiation distance (=FID), and habituated birds might not only show a decreased reactivity rate but also a faster recovery rate (Vincze et al., 2016). A study measuring FID in waterbirds found a stable reaction per individual to a disturbance, hence no habituation or sensitization by repeated disturbance could be measured (Seltmann et al., 2012). Also, experiments with rural and urban blackbirds did not find a change in reaction to repeated short human encounters under captive conditions (Miranda Ana Catarina et al., 2013).

Conclusion

In summary was found that a low threshold disturbance evoked a behavioural change in common blackbirds. The reaction differed during the breeding season and was sex dependent. Incubating female birds showed more flight behaviour, whereas feeding females showed less active behaviours and therefore more inactivity in response to the disturbance. Feeding male birds showed only a slight increase in flights. Especially in incubating birds, it was shown that the birds were still impacted during the 30 minutes after the disturbance event.

A stress response is modulated by human-dependent, context-dependent and animal-dependent factors (Figure 1 – 1). Therefore, as many factors as possible were tried to be kept stable, namely the quality of disturbance (human-dependent), by always two persons walking in the same pace along the hedge, and the quality of hedge. However, environmental conditions (temperature, food availability) changed with progressing breeding season, and also the life history stage of the birds changed (incubating to feeding). Neither temperature, time of a day nor Julian date had a large effect on the result in the model. Sex, as animal dependent modulating factor, was besides breeding status the most important factor. This is mainly explained by the status and sex-specific tasks during the reproductive period. Females provide a higher amount of parental care and therefore might also have a higher energy expenditure during the disturbance than males (Fernández and Azkona, 1993). Dickens and Bentley (2014) showed sex specific physiological regulators of breeding status which are likely to play an important role in the stress response, and females had a higher amount of corticotropin releasing hormone which causes indirectly the secretion of corticosterone. Therefore, males and females might differently activate the complex pathway integrating the stress response and the reproductive physiology. Hence, it is recommended to include sex specific behaviours in future analyses of behaviour responses to human disturbances.

In combination with the study about the spatial and temporal pattern of the bird's reaction, this study will give an insight into the effects of pedestrians on the behaviour of common blackbirds and can be used to make predictions about optimal wild life buffer zones (Holmes et al., 1993).

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8. Attachment

Table 8 – 1 Threshold Definition 1 determines 4 peaks with an amplitude ≥ 0.75 within a 2 second bout as flight behaviour.

87 % of observed flights were determined as flights, 69 % of observed activity was determined as activity, 66 % of determined flight were observed flights, 88 % of determined activity was observed activity and overall performance (= correctly determined behaviours) was 76 %.

Definition 1	Activity (observed)	Flights (observed)	Total
Activity (determined)	61	8	69
Flights (determined)	27	52	79
Total	88	60	148

Table 8 – 2 Threshold Definition 2 determines 3 peaks with an amplitude ≥ 0.9 within a 2 second bout as flight behaviour.

87 % of observed flights were determined as flights, 76 % of observed activity was determined as activity, 71 % of determined flight were observed flights, 89 % of determined activity was observed activity and overall performance (= correctly determined behaviours) was 80 %

Definition 2	Activity (observed)	Flights (observed)	Total
Activity (determined)	67	8	75
Flights (determined)	21	52	73
Total	88	60	148

Table 8 – 3 Threshold Definition 3 determines 3 peaks with an amplitude ≥ 1.0 within a 2 second bout as flight behaviour.

90 % of observed flights were determined as flights, 88 % of observed activity was determined as activity, 84 % of determined flight were observed flights, 93 % of determined activity was observed activity and overall performance (= correctly determined behaviours) was 89 %.

Definition 4	Activity (observed)	Flights (observed)	Total
Activity (determined)	68	7	75
Flights (determined)	8	45	53
Total	76	52	128

Table 8 – 4 Threshold Definition 4 determines 3 peaks with an amplitude ≥ 1.1 within a 2 second bout as flight behaviour.

87 % of observed flights were determined as flights, 89 % of observed activity was determined as activity, 85 % of determined flight were observed flights, 91 % of determined activity was observed activity and overall performance was 88 %.

Definition 3	Activity (observed)	Flights (observed)	Total
Activity (determined)	67	5	72
Flights (determined)	9	47	56
Total	76	52	128

Table 8 – 5 Fitted means and 2.5% and 97.5% quantiles for lower and upper limits of 95% credible interval for each group of the linear model with “flights” as dependent variable.

disturbance	status	sex	lower	upper	fitted
before	incubating	female	0.16%	4.42%	0.85%
during	incubating	female	0.38%	10.03%	1.94%
after	incubating	female	0.07%	2.06%	0.38%
before	feeding	female	1.13%	10.69%	3.50%
during	feeding	female	0.50%	4.83%	1.54%
after	feeding	female	0.95%	8.68%	2.87%
before	unknown	female	0.41%	6.40%	1.64%
during	unknown	female	0.30%	4.78%	1.23%
after	unknown	female	0.27%	4.41%	1.11%
before	feeding	male	0.68%	7.15%	2.24%
during	feeding	male	1.00%	10.16%	3.32%
after	feeding	male	0.75%	7.70%	2.43%
before	unknown	male	0.34%	3.11%	1.04%
during	unknown	male	0.87%	7.88%	2.66%
after	unknown	male	0.31%	2.84%	0.94%

Table 8 – 6 Fitted means and 2.5% and 97.5% quantiles for lower and upper limits of 95% credible interval for each group of the model with “activity” as dependent variable.

disturbance	status	sex	lower	upper	fitted
before	incubating	female	3.47%	19.71%	8.54%
during	incubating	female	3.12%	17.73%	7.71%
after	incubating	female	2.29%	13.77%	5.78%
before	feeding	female	13.50%	38.84%	23.85%
during	feeding	female	5.18%	18.14%	9.96%
after	feeding	female	12.96%	37.79%	23.34%
before	unknown	female	4.47%	19.74%	9.57%
during	unknown	female	2.04%	9.55%	4.43%
after	unknown	female	4.28%	18.67%	8.99%
before	feeding	male	12.73%	37.22%	23.01%
during	feeding	male	10.87%	33.06%	19.88%
after	feeding	male	13.39%	38.77%	24.05%
before	unknown	male	4.88%	16.49%	9.17%
during	unknown	male	5.08%	16.65%	9.42%
after	unknown	male	5.01%	16.80%	9.32%

Table 8 – 7 Fitted means and 2.5% and 97.5% quantiles for lower and upper limits of 95% credible interval for each group of the model with “inactivity” as dependent variable.

disturbance	status	sex	lower	upper	fitted
before	incubating	female	76.42%	96.46%	90.20%
during	incubating	female	73.29%	96.00%	89.26%
after	incubating	female	83.11%	97.61%	93.43%
before	feeding	female	53.55%	84.03%	71.21%
during	feeding	female	75.86%	93.51%	87.06%
after	feeding	female	54.55%	84.73%	72.28%
before	unknown	female	76.35%	94.90%	88.73%
during	unknown	female	85.90%	97.31%	93.71%
after	unknown	female	77.88%	95.35%	89.37%
before	feeding	male	54.63%	84.76%	71.81%
during	feeding	male	55.44%	85.13%	72.64%
after	feeding	male	53.47%	84.11%	70.87%
before	unknown	male	79.57%	94.42%	89.02%
during	unknown	male	73.96%	92.29%	85.46%
after	unknown	male	78.82%	94.26%	88.69%