# Impact of Human Recreational Activities on Forest Birds

---

**Dissertation**

zur

**Erlangung der naturwissenschaftlichen Doktorwürde**
**(Dr. sc. nat.)**

vorgelegt der

**Mathematisch-naturwissenschaftlichen Fakultät**

der

**Universität Zürich**

von

**Yves Bötsch**

von

**Wängi TG**

**Promotionskommission**

Prof. Dr. Lukas Jenni (Vorsitz und Leitung der Dissertation)

Prof. Dr. Lukas F. Keller

Dr. Alain Jacot

**Zürich, 2018**

# TABLE OF CONTENTS

# SUMMARY

Outdoor recreation has increased in popularity through development in infrastructure and transportation, as well as an enormous diversity and specialisation of clothing and gear. Although no harm is intended by recreationists and in some cases actually the opposite (i.e. ecotourism) is the goal, recreation has negative consequences for wild species. Thus, a great amount of research is being done by concerned researchers to try to understand the magnitude of the negative impact of human disturbance.

However, these studies usually have two main caveats. First, they fail in disentangling direct effects of human presence from effects of habitat modifications (e.g. trails or roads) linked to outdoor recreation. Secondly, many studies are done in areas where human disturbances have been occurring already for a long period of time, which may lead to wildlife already being “adapted” (either behaviourally or through pre-selection of individuals inhabiting those areas) to these disturbances, and thus obscure the complete magnitude of the human disturbance impact.

In this thesis we aimed to deal with these two problems through a combination of well-thought comparative and experimental studies. We focused on forested habitats, because forests are a widespread habitat worldwide and frequently used for recreational activities.

In the **first chapter** we were interested in separating the direct human effect from the potential indirect effect of habitat change through recreational trails. Therefore we selected four different forests with a similar network of trails, strongly differing in their human frequentation. Two of them were heavily frequented by humans for recreation whereas the other two were rarely used for human recreation. We used a paired point count design to census the breeding birds in these four forests, with a point count close to a trail and a paired adjacent count further away from the same trail to test how the effect of

the trail varied across forests depending on the amount of visitors. We also investigated how the effect of the trails/human disturbance is modulated by the characteristics of the species. Birds in heavily frequented forests avoided trail proximity; there was a difference in bird abundance of 13% between the close and the far point count, whereas there was no difference between paired point counts in unfrequented forests. Similarly species richness dropped by 12% between the close and its paired far point count in heavily frequented forests, whereas there was no difference in unfrequented forests. Looking at the nesting guilds in unfrequented forests revealed a tendency for ground nesters to prefer trail proximity, whereas there was no trail effect on cavity and open-cup nesters. In heavily frequented forests, cavity nesters as well as open-cup nesters avoided trail proximity, whereas ground nesters showed no effect. These findings imply, besides some species-specific differences, that the direct impact of humans using the trails is the stronger driver for bird composition compared to the indirect impact of habitat changes through trail construction.

In **chapter two** we examined whether birds in highly frequented forests are truly responding less to humans than in forests which are hardly frequented by humans. For that we focused on the antipredatory response, more specifically on flight initiation distance (FID), which is the distance at which a bird flushes from an approaching human. We measured FID in both heavily and rarely frequented forests during the same time of the year for nine forest-bird species. FIDs of most species were larger in the unfrequented forest compared to FID in the frequented forests. This could be explained by birds learning that humans are not a threat and tolerating human presence (habituation) or by human presence acting as a selection factor on personality, with the result that only the most tolerant individuals stay, whereas the shy individuals leave the area.

In the **third chapter** we focused on the least frequented forest to experimentally investigate how the presence of humans during the early spring actually affects territory selection of birds. Therefore, we split forest plots into two halves (split-plots). In one half we walked through the forest without trails, mimicking people hiking, during March to mid-April, and compared the later breeding bird communities between these split-plots and the un-frequented ones. Forest-bird abundance as well as species richness were both reduced by 15% in human frequented plots compared to control plots. This result shows that human presence directly affects a bird's decision where to settle, independently of vegetation characteristics.

Finally, in **chapter four** we studied the potential trans-generational effects of the experimental recreation (preceding chapter) on the individuals that settled, through examining maternal antibody deposition into the eggs of two breeding tit species (Great tits *Parus major* and blue tits *Cyanistes caeruleus*). We measured the amount of total antibodies in six days old tit nestlings (at that age they still rely mainly on maternal antibodies) and compared nestlings hatched in experimentally disturbed split-plots with hatchlings from unfrequented controls. We found a negative effect of the experimental human presence on maternal antibody deposition for great tits, but not for blue tits. Great tits breeding in disturbed split-plots deposited fewer maternal antibodies into their eggs compared to great tits breeding in control split-plots. This disturbance impact was dependent on the vegetation density; with a higher shrub cover lowering the disturbance impact on maternal antibody deposition. For great tits, the amount of maternal antibodies had a positive effect on hatching success and chick weight, both independent of human presence. For blue tits, these results could not be confirmed, instead we found that the presence of great tits was the stronger driver than the experimental disturbance. This study showed, that even low intensities of human recreation (as ours) can stress breeding birds so much, that an immunosuppressive reaction was measurable via maternal antibody deposition, and a trans-generational effect could be confirmed.

Human presence in forests drives breeding bird densities and species richness and, depending on the intensity and duration of recreational activities, could have long term consequences for the avifauna. As these human impacts on wildlife will certainly increase in the future, effective conservation measures are needed. Such measures necessarily include protected wildlife areas with reduced or prohibited access for humans. Outdoor recreational activities should be well guided, mainly through a clever trail-network, bypassing rare species' home ranges and/or habitats, for their conservation. Through such smart conservation measures most outdoor recreationists will not be limited in their activities, but it would allow both, wildlife and recreationists to persist side by side.

**Author's contribution:**

Yves Bötsch's contributions to each chapter include:

- Authored general introduction
- Chapter 1: Study design and planning, data collection of first year, supervision of Bachelor student Daniel Scherl (data collection during second year), data analyses and publication (main author)
- Chapter 2: Study design, part of data collection during the first year, supervision of Selina Gugelmann (data collection during second year, Semester work), data analyses and publication (main author)
- Chapter 3: Study design and planning, data collection, analyses and publication (main author)
- Chapter 4: Study design, blood sample collection, laboratory work, data analyses and publication (main author)
- Authored general discussion

# ZUSAMMENFASSUNG

Freizeitaktivitäten in der Natur haben in den letzten Jahrzehnten an Popularität gewonnen. Durch moderne Infrastrukturen sowie spezialisierte Ausrüstung wurden viele Aktivitäten für die breite Öffentlichkeit zugänglich gemacht. Obwohl die meisten Erholungssuchenden der Natur nicht schaden wollen, ja sich sogar an ihr erfreuen, können ihre Aktivitäten negative Folgen für Wildtiere haben. Damit man den Einfluss der Freizeitaktivitäten messen und verstehen kann, wird weltweit viel Forschung betrieben. In diesen Studien gibt es zwei problematische Punkte: Erstens können die meisten Studien direkte Effekte durch die Präsenz von Menschen nicht von Habitatveränderungseffekten durch die Infrastruktur (z.B. Wege) trennen. Zweitens werden viele Studien in Gebieten durchgeführt, in welchen schon seit langer Zeit Freizeitaktivitäten stattfinden und die lokale Tierwelt sich bereits an diese Aktivitäten gewöhnt haben könnte (angepasstes Verhalten oder Selektion von störungstoleranten Individuen), was dazu führen kann, dass die Grössenordnung des Einflusses der Freizeitaktivitäten unterschätzt wird.

Das Ziel dieser Arbeit war, diese beiden Schwierigkeiten mit gut geplanten, vergleichenden sowie experimentellen Studien zu umgehen. Wälder sind ein weit verbreitetes Habitat in Europa und ein beliebter Ort für verschiedenste Freizeitaktivitäten, weshalb wir unseren Forschungsschwerpunkt auf diesen Habitat-typ legten.

Im **ersten Kapitel** wollten wir den direkten Effekt der menschlichen Präsenz mit dem indirekten Effekt der Habitatveränderung durch Wege vergleichen. Dazu wählten wir vier verschiedene Wälder mit einem ähnlichen Wanderwegenetz, aber einer stark unterschiedlichen Frequentierung aus. Zwei davon werden selten begangen, während die anderen beiden Wälder in Stadtnähe sehr oft für Freizeitaktivitäten benutzt werden. Wir führten in diesen Wäldern paarweise Punkt-Stopp-Zählungen durch. Eine Zählung fand nah und eine weiter entfernt von einem Wanderweg statt, um zu testen, wie sich

Habitatveränderungen durch Wege und menschliche Präsenz auf die Vogelwelt auswirken. Des Weiteren untersuchten wir, wie sich die Effekte Weg und Begehungsintensität auf unterschiedliche Artgruppen auswirkten. Die Vögel mieden die wegnahen Punkte in Wäldern, welche oft begangen werden (Abundanz um 13% reduziert im Gegensatz zu den weiter entfernten Flächen), wogegen in selten begangenen Wäldern kein Unterschied zwischen wegnahen und wegfernen Punkten festgestellt wurde. Einen ähnlichen negativen Effekt (-12%) zeigte sich auch für die Artenzahl in oft begangenen Wäldern. In wenig begangenen Wäldern konnten wir eine leichte Präferenz von Bodenbrütern für wegnahe Punkte feststellen; hingegen zeigten Höhlenbrüter sowie Offenbrüter keinen Unterschied zwischen wegnahen und wegfernen Punkten (Abundanz und Artenzahl). In den oft begangenen Wäldern wurden die wegnahen Punkte vor allem von Höhlenbrütern und Offenbrütern gemieden, wo hingegen Bodenbrüter keinen Effekt zeigten. Diese Resultate zeigen, dass neben gewissen Artgruppen spezifischen Effekten, die menschliche Präsenz der stärkere Treiber gegenüber weginduzierten Habitatveränderungen darstellt.

Im **zweiten Kapitel** testeten wir, ob Vögel in häufig begangenen Wäldern tatsächlich weniger stark auf Menschen reagieren im Vergleich zu Vögeln aus selten begangenen Wäldern und somit den Effekt der Störung verwaschen. Wir haben dazu unser Augenmerk auf die Fluchtdistanz gelegt, d.h. die Distanz, bei welcher ein Vogel von einem sich annähernden Menschen flüchtet. Wir haben Fluchtdistanzen von neun Vogelarten zur gleichen Jahreszeit in häufig begangenen und selten begangenen Wäldern gemessen. Die Fluchtdistanzen der meisten Vogelarten waren im selten begangenen Wald grösser als in den häufig begangenen Wäldern. Möglicherweise entstehen die Fluchtdistanz-Differenzen zwischen häufig begangenen und wenig begangenen Wäldern durch eine erlernte Toleranz gegenüber Menschen (Habituation) oder durch eine Selektion von Individuen, die die Anwesenheit von Menschen tolerieren, und eine Abwanderung von menschen-intoleranten Individuen bewirkt (Individualität).

Im **dritten Kapitel** untersuchten wir mit einem experimentellen Ansatz den direkten Einfluss von Wanderern auf das Ansiedlungsverhalten von Waldvögeln. Dazu wanderten wir 2-3 Mal täglich während der Ansiedlungsphase der Brutvögel (März bis Mitte April) durch Waldflächen ohne Wegenetz und verglichen danach die Brutvogel Gemeinschaften zwischen diesen begangenen Flächen und unbegangenen Kontrollflächen. Die Abundanz der Waldvögel sowie ihr Artenreichtum waren auf den begangenen Flächen beide um 15% geringer als auf den nicht begangenen Kontrollflächen. Dies zeigt, dass menschliche Präsenz unabhängig von der Vegetationsstruktur das Ansiedlungsverhalten von Waldvögeln direkt beeinflusst.

Dies leitet direkt über zu **Kapitel vier** wo wir den möglichen Effekt der experimentellen Störungen (siehe vorangehendes Kapitel) auf die Übertragung von maternalen Antikörpern in die Eier untersuchten. Dazu haben wir die Antikörpertiter von sechs Tage alten Blau- und Kohlmeisen-Nestlingen gemessen, da ihre Antikörper in diesem Alter noch hauptsächlich von der Mutter stammen. Wir verglichen die Titer der in den von uns begangenen Flächen geschlüpften Küken mit denen von Küken aus den unbegangenen Kontrollflächen. Kohlmeisen-Nestlinge, welche in experimentell gestörten Flächen schlüpften, hatten tiefere maternale Antikörpertiter als Jungmeisen, welche in ungestörten Flächen schlüpften. Dieser Effekt war aber abhängig von der Vegetationsdichte; dichtere Vegetation reduzierte den Störungseinfluss auf die maternalen Antikörpertiter.  Generell stellten wir fest, dass der Antikörpertiter bei Kohlmeisen mit der Schlupfrate sowie mit dem Gewicht der Jungmeisen positiv korrelierte. Bei den Blaumeisen konnten wir, ausser der Korrelation zwischen den Antikörpertitern und dem Körpergewicht der Jungmeisen, keinen der gefunden Effekte nachweisen. Bei den Blaumeisen schien es, dass die Anwesenheit von Kohlmeisen der stärkere beeinflussende

Faktor darstellte als unsere Störung. Die geringe Intensität an experimenteller menschlicher Aktivität störte die Kohlmeisen während der Eiablage offenbar so stark, dass deren erhöhter Stresshormonspiegel (Corticosteron) seine immunosuppressive Funktion ausüben konnte, und wir diese via maternale Antikörpertiter in den Nestlingen feststellen und somit einen inter-generationen Effekt aufzeigen konnten.

Die Anwesenheit von Menschen in Wäldern beeinflusst also die Abundanz der Brutvögel sowie deren Artenzahl und kann in Abhängigkeit von der Intensität und Dauer von Freizeitaktivitäten mögliche Langzeitfolgen haben. Die Ausweisung von Schutzgebieten mit eingeschränktem oder unterbundenem Zugang für Besucher scheint daher eine angebrachte Naturschutzmassnahme zu sein. Damit seltene Arten oder Lebensraumtypen erhalten werden können, sollten Freizeitaktivitäten in der Natur mit durchdachten Wegführungen gelenkt werden. Durch solche Massnahmen können die Ansprüche von Wildtieren und von Erholungssuchenden gleichermassen erfüllt und ein einvernehmliches Miteinander garantiert werden.

# GENERAL INTRODUCTION

## Pressure on nature

Human impacts on habitats and wildlife increase unrestrictedly, as the world population is growing steadily (Gerland *et al.* 2014). Natural habitats not only are affected by the mere living space needed for the human population along with the need for food-producing cultivated area. Also human recreation activities commonly occur in nature. New recreational activities (e.g. stand-up paddling) with its infrastructure are developed as well as vast amounts of specialized clothing and gear. Therefore outdoor recreation entails a large economic sector, still booming nowadays (Balmford *et al.* 2009). The vast majority of outdoor recreationists are not interested in directly enjoying nature (e.g. fauna and flora observations), but in outdoor sport-activities, from the most popular hiking/jogging to more specialized activities like paragliding, downhill cycling or rock climbing. More and more previously pristine and unfrequented habitats, from steep rock faces to white water, become used by humans.

Being outdoors has been shown to positively affect human health and well-being (Martinez-Juarez *et al.* 2015). Even the willingness to spend money for conservation is positively affected by former experience with nature (Zaradic, Pergams & Kareiva 2009). Therefore “allowing” humans to get in contact with nature has positive consequences for both humans and nature conservation. Nevertheless, human outdoor activities affect wildlife and direct wildlife observations and photography, known as ecotourism and “non-consumptive” activity (Wilkes 1977; Goodwin 1996), also impact wildlife (Müllner, Linsenmair & Wikelski 2004). We also cannot deny research(er) related effects on wildlife/natural habitats (Götmark 1992). In the following paragraphs I will point out the effects of outdoor recreation on wildlife as well as demonstrate activity and habitat dependent modulators of wildlife reactions.

## Effects of outdoor activities

### Direct effects

Outdoor-activities can impact wildlife immediately, as humans are often perceived by animals as predators (Frid & Dill 2002); therefore animals flush or hide. Besides consumptive activities like fishing and hunting, also collisions with cars can directly be lethal (Clevenger, Chruszcz & Gunson 2003).

Frightened animals can show a behavioural reaction and/or may trigger a physiological one, non-detectable from the outside (Müller *et al.* 2006; Thiel *et al.* 2008; Almasi *et al.* 2015; Arlettaz *et al.* 2015). These direct impacts can have drastic effects for animals, as they lose energy through escaping from the threat, or via increased physiological demands, as for example an activation of the HPA-axis (Hypothalamic Pituitary Adrenal) and/or the cardiac system (Romero, Soma & Wingfield 1998; Sapolsky, Romero & Munck 2000; Nephew, Kahn & Romero 2003; Romero 2004). Such physiological reactions can negatively affect the animal's survival, as for example chronically elevated levels of stress hormones (corticosterone or cortisol) negatively affect an individual's immune system (Saino *et al.* 2003; French *et al.* 2010).

Human presence can also alter the animal's spatial and/or temporal space use (Ciucci *et al.* 1997; Olson, Squibb & Gilbert 1998) or even cause the desertion (local extinction) of a given area (Boyle & Samson 1985; Garber & Burger 1995). Moreover the individual's reproductive output and later also the offspring's survival can be directly affected through human presence (Safina & Burger 1983, but see also **Seasonality and habitat** below).

### Indirect effects

Many outdoor activities rely on some kind of infrastructure (e.g. ski lift), with trails and roads being the most common ones (from now on referred to as trails). The construction of trails entails a dramatic change in vegetation, soil surface and altered water balance (Benninger-Truax, Vankat & Schaefer 1992; Trombulak & Frissell 2000). Besides the direct change (reduction) in habitat, an additional important factor joins in, namely fragmentation. Habitats not only get smaller through trail construction but become also more and more fragmented, separating wildlife populations and reducing gene-flow (Saunders, Hobbs & Margules 1991; Reed, Johnson-Barnard & Baker 1996; Forman & Alexander 1998; Trzcinski, Fahrig & Merriam 1999; Bregman, Sekercioglu & Tobias 2014). Additionally trails can facilitate access of predators, which consequently increases predation risk and lowers habitat suitability for the local species/individuals (Miller, Knight & Miller 1998).

Therefore outdoor activities often affect wildlife indirectly, e.g. via changing the habitat. Depending on disturbance intensity, indirect effects on wildlife become detectable only after a certain period of time (Steven, Pickering & Castley 2011; Monz, Pickering & Hadwen 2013), but are then long-lasting, compared to some direct/short-time effects.

### Factors modulating the effects of human disturbance

The severity of human recreation impacts can be modulated through several factors, which are described in the three following paragraphs.

### Type of leisure activity

Not all types of recreational activities have the same impact on wildlife. The predictability of a given activity plays an important role; activities with a predictable direction are perceived as less severe than un-predictably directed activities (predicted directions refer mostly to on-trail activities, whereas un-predictable to off-trail, see Miller, Knight & Miller 2001; Coppes & Braunisch 2013). In addition, also the speed and/or noise of a given activity have been shown to determine its severity, where faster/louder activities are perceived as more dangerous (Burger 1981; Arroyo & Razin 2006; Lethlean *et al.* 2017). Apart from recreational activity types, the number of recreationists (group size) in general affects the impact, with larger groups having a stronger impact (Geist *et al.* 2005; Remacha, Pérez-Tris & Delgado 2011). Finally, recreationists accompanied by dogs are perceived as more dangerous than recreationists without dogs (Miller, Knight & Miller 2001; Langston *et al.* 2007; Young *et al.* 2011; Waldstein Parsons *et al.* 2016). Even the colour of the clothing worn by the recreationist affects the threat severity (Gutzwiller & Marcum 1997; Putman *et al.* 2017).

### Species characteristics

There are several species-specific characteristics which have been shown to affect the "disturbance tolerance" of an animal, e.g. nesting site, diet or body size (Blumstein *et al.* 2003; Kangas *et al.* 2010; Samia *et al.* 2015). Apart from species-specific sensitivities towards recreational activities, individual differences (e.g. sex, age or body condition) may influence human impact too. Age for example can be attributed to experience, and more experienced individuals either react stronger (sensitization) or less (habituation) towards a recreationist (but see Bejder *et al.* 2009). Animals can get used to a certain level of disturbance, but not all species, populations or individuals are able to habituate in the same way - some do habituate while others do not (Nisbet 2000; Walker, Dee Boersma & Wingfield 2006; Baudains & Lloyd 2007; Bonier, Martin & Wingfield 2007; Bejder *et al.* 2009; Rodríguez-Prieto *et al.* 2009; Samia *et al.* 2015; Vincze *et al.* 2016). This phenomenon can be seen when individuals of a certain species manage to live in human dominated urban landscapes, e.g. cities, and then fully adapt to these "artificial" environments (e.g. regardless of increased noise levels or unsuitable urban food resources (Meyrier *et al.* 2017)). Certain individuals of a given species are better capable of circumventing such new environmental hurdles, than others. These different types of individuals are called personalities or are sometimes clustered into different reaction norms (Wilson 1998; Sih, Bell & Johnson 2004; Mathot *et al.* 2012; Sih *et al.* 2015; Nicolaus *et al.* 2016; Arroyo, Mougeot & Bretagnolle 2017), and have been attributed to affect the habituation potential (Evans, Boudreau & Hyman 2010; Rebolo-Ifrán *et al.* 2015; Cavalli *et al.* 2016; Vincze *et al.* 2016). Within urban areas (e.g. cities) one type of personality (bold, aggressive) is overrepresented compared to the homogenous distribution of personalities in a natural (rural) population (Evans, Boudreau & Hyman 2010; Miranda *et al.* 2013; Sprau & Dingemanse 2017).

### Spatio-temporal context: Seasonality and habitat

Depending on the season (breeding, migration or overwintering), disturbance events can have additional far reaching consequences. When parents, for example, are hindered from feeding, their chicks will face a reduced survival, which then could have an effect up to the population level (Robert & Ralph 1975; Glądalski *et al.* 2016). During wintertime, animals flushed out of their den, face additional losses of energy, firstly due to flushing, and secondly via reduced protection from the harsh environment. This increased energy loss could lower survival (Arlettaz *et al.* 2015). When animals on migration are disturbed at stopover sites they could be forced to continue their journey without enough restored energy reserves, which lowers their survival (Pfister, Harrington & Lavine 1992). Therefore human impacts at one location can have carry-over effects on the population at an other location or in a different season (mostly for migrating species).

Besides season also the time of day when the activity takes place, influences its impact (e.g. nocturnal versus diurnal species; Tablado & Jenni 2017). Finally, also the type of habitat where a recreational activity is taking place, affects its impact. Denser vegetation shields animals from the passing recreationists (Thiel *et al.* 2007; but see also

Whittingham *et al.* 2004), whereas the disturbance impact reaches further in more open, less vegetated habitats.

## Study aims

Former studies looking at human recreation impacts on wildlife were mostly comparative, and in many cases study sites had been exposed to recreation for a long time. This usually creates the following two problems: firstly there is the problem of disentangling direct from indirect effects, as they often act in combination, making it hard (or sometimes impossible) to determine the driving mechanisms. Secondly, areas already used for recreation for a while face the problem that the most sensitive species or individuals (i.e. personalities) might already have disappeared from the most heavily frequented areas (i.e. spatial rearrangement), or might have habituated to human presence, leading to animals already being “adapted” to human recreation. This can obscure the magnitude of human recreation impacts on wildlife and lead to erroneous conclusions. Therefore we used a set of well-designed comparative and experimental studies, to counteract these difficulties. We focused our studies on forest birds, as forests are a widely distributed habitat and often used for recreational activities. Birds in general are suitable for studying human recreational impacts, as they are highly mobile, quite easy to detect and census, and they show a relatively high species richness. Additionally, during breeding, most bird species are territorial and have a fixed nesting site, which facilitates catching adults and allows gathering brood data easily.

(Chapter 1) Firstly we wanted to disentangle the direct effects of humans from the indirect effects of the trails via habitat change. Therefore we compared bird communities at different distances from trails in several forests with a wide variety of human use. We used a paired point count study design, where one point count was placed close to the trail and the second far away from the trail, to examine both human-presence and trail impact on bird communities. Moreover we investigated whether this human and/or trail impact was modulated by species specific traits.

(Chapter 2) Within the same forests, varying in human frequentation, we measured bird species-specific tolerances towards human approach using flight initiation distances (FID) in order to investigate whether birds in heavily frequented forests are already “adapted” and therefore responding less to recreation. We were examining whether FIDs of nine common forest bird species differed between forests depending on the levels of recreational use. Therefore we measured FIDs in heavily frequented forests and compared them with measures taken in an unfrequented forest.

To exclude the possibility to examine a “human-adapted” bird community, we finally focused on the least-disturbed forest and conducted two experimental studies. (Chapter 3) In the first we measured the direct impact of recreational activities on forest birds during a possibly sensitive time period, without changing the surrounding habitat. We disturbed forest plots during early-breeding season period and compared abundance and species richness of the birds which finally settled in the experimental plots with those of undisturbed control plots.

(Chapter 4) Secondly, we examined whether there are carry-over effects of the impact of human disturbance during the early-breeding season on offspring through maternal antibody deposition in the eggs during the disturbance period. A higher amount of maternal antibodies has been previously attributed to an increased survival, as the chicks fully rely on these maternal antibodies to withstand infections during the first days of their life (Pihlaja, Siitari & Alatalo 2006).

The findings of this thesis hopefully contribute to our understanding about the impact of human disturbance on wildlife and its conservation implications, in order to help us protect wildlife while allowing recreationists to appreciate nature.

# CHAPTER 1

## Effect of recreational trails on forest birds: does human presence matter?

Yves Bötsch, Zulima Tablado, Daniel Scherl, Roland Graf and Lukas Jenni

Submitted to **Biodiversity and Conservation**

Illustration credit: Yves Bötsch

# Effect of recreational trails on forest birds: does human presence matter?

Yves Bötsch[1, 2], Zulima Tablado[1], Daniel Scherl[1, 3], Roland Graf[3] and Lukas Jenni[1]

[1]Swiss Ornithological Institute, Seerose 1, CH-6204 Sempach, Switzerland

[2]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, CH-8057 Zurich, Switzerland

[3]ZHAW Zurich University of Applied Sciences, Institute of Natural Resource Sciences, Grüental, CH-8820 Wädenswil, Switzerland

## ABSTRACT

Outdoor recreational activities are increasing worldwide and occur especially close to cities at high frequency. Forests are a natural environment often used for these activities (e.g. jogging, hiking, dog walking, mountain biking, and horse riding). The pure presence of people in forests can disturb wildlife, which may perceive humans as predators. Many of these activities rely on trails, which intersect an otherwise continuous habitat and hence impact wildlife's habitat. The aim of this study was to separate the effect of the change in vegetation and habitat structure through trails, from the effect of mere human presence using these trails, on forest bird communities. Therefore we compared the effect of recreational trails on birds in two forests frequently used by recreationists with that in two rarely visited forests. In each forest, we did paired-point counts to investigate the differences between the avian community close (50m) and far (120m) from trails, while accounting for possible habitat differences. In the disturbed, high recreation level forests we found a reduction in the density of birds (-13%) and species richness (-12%) at points close to trails when compared to those further away, whereas such an effect was not detectable within the low recreation level forests. Additionally we found that the effect of human presence varied depending on the characteristics of the species. These findings suggest that the mere presence of humans impoverishes the forest bird community along trails and affects different species differently.

**Key words:** Human disturbance, recreation ecology, recreational activity, avian diversity, nesting guild

# INTRODUCTION

Nature-based recreational activities have increased enormously in the last decades (Boyle & Samson 1985; Steven, Pickering & Castley 2011; Monz, Pickering & Hadwen 2013; Steven & Castley 2013; Hammitt, Cole & Monz 2015). This trend is raising concerns of researchers and conservationists about the potential impact of human recreation on wild animals. Humans may be perceived by wildlife as predators (Frid & Dill 2002). Thus, when exposed to human presence, animals may react with important changes in their behaviour and physiology (e.g. increased vigilance, flight, release of stress hormones; (Ikuta & Blumstein 2003; Beale & Monaghan 2004a; b; Tablado & Jenni 2017)), which in turn might have consequences for the fitness and dynamics of animal populations.

Many studies have therefore aimed at assessing the effects of outdoor recreational activities on wildlife. One way of approaching this issue has been to investigate the effects of recreational trails on bird abundance and species composition. However, the results of these studies are not always consistent, with some studies finding an effect of trails while others do not (Gutzwiller *et al.* 1998; Miller, Knight & Miller 1998; Deluca & King 2014; Thompson 2015). One reason for this disparity could be the difficulty to disentangle the direct effect of human presence from the indirect effect of habitat modification caused by the installation of trails and roads, which entails a less dense vegetation or even the clearance of it in most habitats (Miller, Knight & Miller 1998; Miller & Hobbs 2000; Smith-Castro & Rodewald 2010; Butler *et al.* 2012; Morelli *et al.* 2015).

In order to disentangle the effects of human presence from habitat modifications through trails we examined how breeding–bird communities changed with distance to trails that were similar in size and structure, but were in forests with widely different levels of recreation. We predicted that the differences between bird communities close and far from trails will be higher in forests experiencing high recreational levels than in forests experiencing low recreational levels. That is, in high-recreation forests we expected lower densities and richness of breeding birds close to the trails than further away, while this difference would not exist or be much lower in low-recreation forests. Additionally, we expected to find inter-specific differences in the impact of trails according to species characteristics, since habitat clearance and/or human presence are likely to affect bird species differently according to their nesting-guild, foraging-guild and sensitivity to humans (Blumstein *et al.* 2003; Langston *et al.* 2007; Mallord *et al.* 2007; Kangas *et al.* 2010; Thompson 2015).

## MATERIALS AND METHODS

### Study sites

We selected four different forests. Two of them (Allschwilerwald (47°32’N, 7°32’E) and Sihlwald (47°15’N, 8°33’E), in Switzerland) were close (< 2 km) to cities with more than 150,000 inhabitants, and heavily used by humans for recreation. The other two forests (Forêt de Chaux (47°05’N, 05°40’E) in France, and Laufenwald (47°26’N, 7°26’E), in Switzerland) were less frequently used (> 8 km from towns with less than 25,000 inhabitants). This classification of the forests into high and low levels of recreation through the proximity to cities was confirmed by own observations during fieldwork. In the Forêt de Chaux and Laufenwald we observed, on average, no more than one human passage per day, while there were 15-25 and 5-15 visitors per hour in the Allschwilerwald and the Sihlwald, respectively. Most recreationists were walking (with or without dogs), and a few were biking. All forests were broad-leafed, with pedunculate oaks (*Quercus robur*) and/or European beech (*Fagus sylvatica*) as the dominating tree species and some admixed European hornbeam (*Carpinus betulus*), sycamore maple (*Acer pseudoplatanus*), European ash (*Fraxinus excelsior*) and scarcely some conifer trees (*Picea abies*, *Abies alba, Pinus sylvestris, Pseudotsuga menziesii*). The four study sites contained a well-developed network of gravel roads and trails (hereafter called trails) which were freely accessible to the public for recreation (e.g. walking, biking), but where cars and motorbikes were prohibited, except for foresters.

### Point count surveys

To assess the avian community near and far from trails we used classical point count surveys (Bibby *et al.* 2000) in a paired design (Fig. 1). We counted birds at 37 pairs of points within forests with a high recreational level (Allschwilerwald 8 pairs and Sihlwald 29 pairs), and at 25 pairs of points in forests with a low recreational level (Forêt de Chaux

12 pairs and Laufenwald 13 pairs). Within each pair, we placed one point close (at 50 m) to a trail and the other point further away at an average distance of 120 m (range 70 - 160 m from the trail depending on the spatial configuration). The location of the points was chosen from aerial photos, with the criterion of placing both points of a pair within a homogenous forest patch.

During each point count a single observer recorded all birds heard or seen within 50 m during six minutes. To estimate the number of territories within 50 m we used only observations of birds showing territorial behaviour (e.g. singing). We used range finders (Nikon Prostaff 7 monocular or Zeiss Victory 10x45 T* RF) to check whether observations fell inside or outside the 50 m radius. Points were censused twice in the Allschwilerwald and Sihlwald in 2013 (first round 30 May - 18 June, second round 26 June - 17 July), and three times in all four forests in 2015 (first round 18 March - 18 April, second round 18 April - 31 Mai, third round 11 May - 17 June). In 2015 we could only monitor 14 of the 29 pairs of points in the Sihlwald, due to time constraints. All point counts were done by only two observers: Y.B. in 2013 and D.S. in 2015. To account for possible researcher-related effects, the order in which points within a pair were censused changed from census round to census round. Also the order in which the pairs within a forest were censused changed from round to round to eliminate a potential effect of time of day. Point count surveys were only done in the early morning, starting right after sunrise (i.e. between 05:21 and 09:45 Central European Time (CET), (Bibby *et al.* 2000)). This means that most census work was done before the bulk of recreationists arrived (R. Schmidt unpublished data).

### Vegetation surveys

In both years we recorded the vegetation to account for differences in habitat composition among points. Surveys were done at five different locations around each point (one at the point-count spot itself and four at locations 25 m away from it into the four main cardinal directions; Fig. 1). At each location, we estimated *ground* vegetation *cover* (%) on a 2x2 m area, *shrub cover* (%) on a 3x3 m area (i.e. vegetation with diameter at breast height (dbh) of less than 5 cm, otherwise counted as trees) and *canopy cover* (%) by looking straight up and assessing the proportion of canopy against the sky in the visual field of the observer (same observers as for the point counts). Additionally we counted the trees on an 8x8 m area per species (*beech*, *oak* and *conifers*), including standing dead trees (*deadwood*). The vegetation surveys were conducted after the point-count censuses, when the vegetation was fully developed (end of May until September). For each vegetation variable, we averaged the vegetation measures among the five locations within each point before analysis.

### Statistical analysis

In order to examine whether the avian community differed between points close to or far from trails, we used two generalized linear mixed models (GLMM), with the number of either breeding-bird territories (*Number of territories*) or breeding-bird species (*Species richness*) per point count as the dependent variable (both following a Poisson distribution). As explanatory variables we included *distance* to the trail (categorical: far vs. close), level of recreation (*disturbance*; categorical: high- vs. low level of recreation), vegetation characteristics (*ground cover*, *shrub cover*, *canopy cover*, mean number of *beech-, oak*-, *conifer*-trees*,* and dead-trees (*deadwood*)), and accounted for the seasonal and daily variation in singing-activity by including the linear and quadratic terms of the Julian date (*Jdate* and $Jdate^2$), and the time (in minutes) elapsed since sunrise ($\Delta$ *Sunrise*). Vegetation variables did not show strong correlations among each other (Pearson correlation coefficient < 0.6) and were therefore all included in the models. We included the interactive effect between *distance* and *disturbance* to test for the impact of recreation on the differences between close and far points. To control for potential differences in singing activity depending on recreation intensity (Gutzwiller *et al.* 1994; Frid & Dill 2002), we also incorporated the interaction between Δ *Sunrise* and *disturbance*. A preliminary analysis, including also trail-type, revealed, that there was no difference in effect of gravel roads versus trails (Online Resource Fig. S1). Therefore we removed trail-type as variable from further analyses. As random factors we included *year*, which accounted for both the inter-annual differences in bird community and observer effect (observer changed with year), *round* (to control for correlations among counts within the same census period), and *point_ID* nested within *pair_ID,* which in turn was nested within *Site,* to account for spatial autocorrelation (Table 1).

In order to explore differences in response to trails according to species properties, we performed three additional GLMMs. These had a similar structure as the previous ones but additionally included either a three-level factor describing *nesting-guild* (cavity, ground or open-cup nesters according to Perrins and Cramp (1998)), a two-level factor describing *foraging-guild* (ground vs. above-ground according to Perrins and Cramp (1998)) or a two-level factor describing the *sensitivity* towards humans, respectively, as well as their two-way and three-way interactions with *distance* and *disturbance*. In order to define sensitivity towards humans we used the species' mean flight initiation distance (FID) (low sensitivity = FID lower than the median FID for all our species vs. high sensitivity = FID equal or larger than the median FID; FID data from Møller (2008) and Díaz et al. (2013) for non-urban areas; see Online Resource Table S1). We acknowledge that FID may be modulated by many factors (Tablado & Jenni 2017), but is still a reasonable and widely available proxy for sensitivity to human disturbance (Blumstein *et al.* 2003).

All analyses were conducted in R version 3.3.0 (Ihaka & Gentleman 1996; R Core Team 2016) using the glmer function from the R-package lme-4 (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 & Su 2015)), simulating 10,000 random samples of the joint posterior distribution of the model parameters (Online Resource Fig. S2). Additionally, we computed the pairwise differences (with 95% CrI) of the number of territories and species between close and far points (Figs. 2 and 3) using the highest probability density interval-function (HPDInterval-function from the R-package coda; (Plummer *et al.* 2006)). 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).

## RESULTS

In forests with a high level of recreation the number of territories at points close to trails was 12.9 % lower than at paired points further away (7.2 versus 8.3 territories on average), while in forests with a low level of recreation no difference between points close to and far from trails was noticeable (7.9 versus 7.8 on average) (Fig. 2a, Table 1). Similarly, we found a reduction of 12.0 % for species richness (5.7 species versus 6.5 on average) at points close to trails compared to far points in forests with a high level of recreation, which was not observed in forests with low levels of recreation (6.4 species in both on average) (Fig. 2b, Table 1). Additionally, we found a quadratic effect of Julian date on the number of territories. That is, records of breeding-bird territories were more numerous in the middle of the season compared to early or late spring, which reflects the general singing phenology of breeding birds. Furthermore, the number of oaks positively affected the number of territories and species richness, while the number of beeches negatively affected the number of territories (Table 1).

Cavity nesters (and to a certain extent also open-cup nesters) had lower numbers of territories and species close to trails compared to paired points further away in forests with high levels of recreation (Figs. 3a and b, Online Resource Table S2 and Figs. S2a and b). This effect was not observed in forests with low levels of recreation, where proximity to trails seems to only slightly decrease cavity nester presence (Figs. 3a and b, Online Resource Table S2 and Figs. S2a and b). Ground-nesting birds, on the other hand, showed higher numbers of territories and species close to trails than far from them in forests with low levels of recreation (Figs. 3a and b, Online Resource Table S2 and Figs. S2a and b). However, this positive effect of trails was not observed in forests with high levels of recreation. The foraging-guild specific analysis revealed no differences in number of territories or species between close and far points in forests with low levels of recreation, whereas in forests with a high level of recreation, above-ground foragers showed a reduction in number of territories and species close to trails compared to further away (Figs. 3c and d, Online Resource Table S3 and Figs. S2c and d). Concerning sensitivity to humans, we found that in forests with high levels of recreation both high- and low- sensitivity species showed lower numbers of territories, and to a certain extent also of species, close to versus far from trails. In forests with a low level of recreation, however, the tendency of lower numbers of territories and species close to trails was less important and only observed in highly sensitive species (Figs. 3e and f, Online Resource Table S4 and Figs. S2e and f).

## DISCUSSION

In this study, we were able to disentangle the effect of human presence from that of trail-associated habitat modifications by investigating the response of the avian community to trails with different levels of recreation. We showed that the disturbance caused by recreation activities (mostly walking) reduced forest bird density and richness by 12 - 13% and that this effect was not merely due to the habitat modification associated with the presence of trails. This agrees with an experimental study with humans walking off-trail in a forest in France where it was observed that humans *per se*, without habitat modification, negatively impact the bird community (Bötsch et al. unpubl. data). Our findings are also comparable to those of Ware et al. (2015) who found that traffic-noise alone, without real roads, was enough to cause a reduction in bird density.

Habitat modifications resulting from trail construction may have a positive or negative effect depending on bird species (Morelli *et al.* 2014). We found a positive influence of trails on the number of ground nesting birds (Figs. 3a and b for low-recreation forests), although this positive effect disappeared with disturbance in forests with a high level of recreation. This could be explained by the fact that forest clearing for trail construction allows the development of a rich understory at the edges, which in turn can serve as refuge and breeding-site/nest cover for ground nesters (Virkkala 1987; Trzcinski, Fahrig & Merriam 1999; Šálek, Svobodová & Zasadil 2010). Conversely, for cavity nesters there was a tendency, although small, to fewer territories and species close to trails even in forests with low levels of recreation. This could be due to the clearing of old, large trees (which provide natural cavities) during trail construction and also later for visitor safety reasons. The effect of trails per se is also in agreement with previous studies in tropical forests, where trail construction has been suggested to impact bird communities negatively (Andrén 1994; Laurance, Stouffer & Laurence 2004; Laurance, Goosem & Laurance 2009). The importance of habitat in driving avian community is further confirmed in our analyses by the overall positive effect of oaks on both the number of territories and species richness, which coincides with previous studies which show that oaks are determinants of forest biodiversity (Caprio, Ellena & Rolando 2009).

The impact of recreational trails also varied according to other species characteristics, such as, foraging guild and sensitivity to humans. Surprisingly, we did not find a strong effect of recreational trails on ground foragers as we expected after Thompson (2015). This could be due to the overall low number of ground foragers found in these forests or the higher availability of food along the trail edge for certain species (Šálek, Svobodová & Zasadil 2010; Batáry *et al.* 2014). Highly sensitive species (large FID) seem to avoid areas close to trails even in forests with low levels of recreation, while low-sensitivity species seem to only be negatively affected by trail presence in highly frequented forests. Therefore sensitivity, approximated by FID, as we did, could be used to help designing future conservation measures through management of tourist numbers and access (Blumstein *et al.* 2003, 2005; Fernández-Juricic *et al.* 2005; Koch & Paton 2014).

In conclusion, by comparing the response of the bird community to trails in high-recreation versus low-recreation forests, we observed that human presence *per se* causes important disturbance to birds in recreational areas and that the overall effect of recreational trails depends not only on recreation intensity but also on species characteristics. Moreover, the fact that we found a negative effect of recreationists on the avifauna of forests which have been used for recreation for decades suggests that habituation to humans has not been able to outweigh the negative impact of human disturbance. Our findings have also some additional implications. Firstly, census and monitoring schemes which are often done from roads and trails (Hanowski & Niemi 1995; Sutter, Devis & Duncan 2000; Sauer *et al.* 2013) should take into account the species-specific responses to habitat alterations and the level of recreation on trails in order to interpret the census results adequately. Secondly, our results provide further evidence that the impact of recreation could be reduced by limiting the access of visitors to certain areas (core wilderness areas) and encouraging visitors to stay on trails elsewhere (Miller, Knight & Miller 2001; Reed & Merenlender 2008; Coppes & Braunisch 2013). Enough undisturbed wildlife habitat (quiet zones) away from trails not only benefits birds, but also mammals (Taylor & Knight 2003; George & Crooks 2006; Reed & Merenlender 2008). Finally, if new recreational trails or roads have to be constructed a well-designed plan is crucial, which incorporates habitat and spatial requirements of the different species (e.g. sensitivity to humans or fragmentation; Andrén 1994; Reed et al. 1996; Forman and Alexander 1998; Rodríguez-Prieto et al. 2014), considers renaturation of unused trails (e.g. harvesting roads) and takes into account the possibility that new trails facilitate access of new predators (Miller & Hobbs 2000). In summary, this study supports that trails and roads can profoundly affect bird community composition and abundance, not only by modifying habitat along trails, but mainly through their use by recreationists.

## ACKNOWLEDGMENTS

We thank all the foresters or responsible managers, who allowed us to access their woods: Ch. Stauffer and R. Schmidt of the Sihlwald and M. Romanski and J.-L. Dessolin of the Forêt de Chaux. Bruno Baur gave helpful information on the Allschwilerwald. For statistical advice we thank F. Korner-Nievergelt and B. Almasi.

## TABLES

**Table 1** Model estimates (± 95% CrI) of the effects tested in the GLMMs investigating the impact of recreational trails on the overall number of territories and species richness. The corresponding level of each factor is given in parentheses after the variable name. The missing factor levels are the ones used as reference categories in the models

| Dependent variable | Number of territories | | Species richness | |
|---|---|---|---|---|
| Intercept | 2.070 | (1.604; 2.516) | 1.856 | (1.568; 2.147) |
| Distance (far) | -0.012 | (-0.116; 0.090) | -0.003 | (-0.124; 0.121) |
| Disturbance (high) | -0.092 | (-0.216; 0.035) | -0.116 | (-0.274; 0.039) |
| Juliandate | 0.100 | (0.042; 0.159) | 0.018 | (-0.046; 0.084) |
| Juliandate$^2$ | -0.045 | (-0.086; -0.004) | -0.042 | (-0.088; 0.071) |
| Δ Sunrise | 0.018 | (-0.039; 0.074) | 0.005 | (-0.060; 0.071) |
| Ground cover | 0.009 | (-0.032; 0.051) | 0.007 | (-0.040; 0.056) |
| Shrub cover | 0.019 | (-0.015; 0.054) | 0.025 | (-0.017; 0.065) |
| Canopy cover | -0.005 | (-0.050; 0.041) | -0.006 | (-0.060; 0.049) |
| Beeches | -0.050 | (-0.092; -0.008) | -0.047 | (-0.096; 0.001) |
| Oaks | 0.042 | (0.004; 0.081) | 0.047 | (0.003; 0.091) |
| Conifers | -0.026 | (-0.071; 0.019) | -0.023 | (-0.075; 0.029) |
| Deadwood | -0.014 | (-0.053; 0.025) | -0.003 | (-0.046; 0.042) |
| Δ Sunrise × Disturbance (high) | 0.013 | (-0.059; 0.085) | 0.017 | (-0.067; 0.099) |
| Disturbance (high) × Distance (far) | 0.150 | (0.015; 0.285) | 0.130 | (-0.024; 0.286) |

*Distribution = Poisson; link function = natural logarithm; random factors = year, round, and point_ID/pair_ID/Site*

# FIGURES

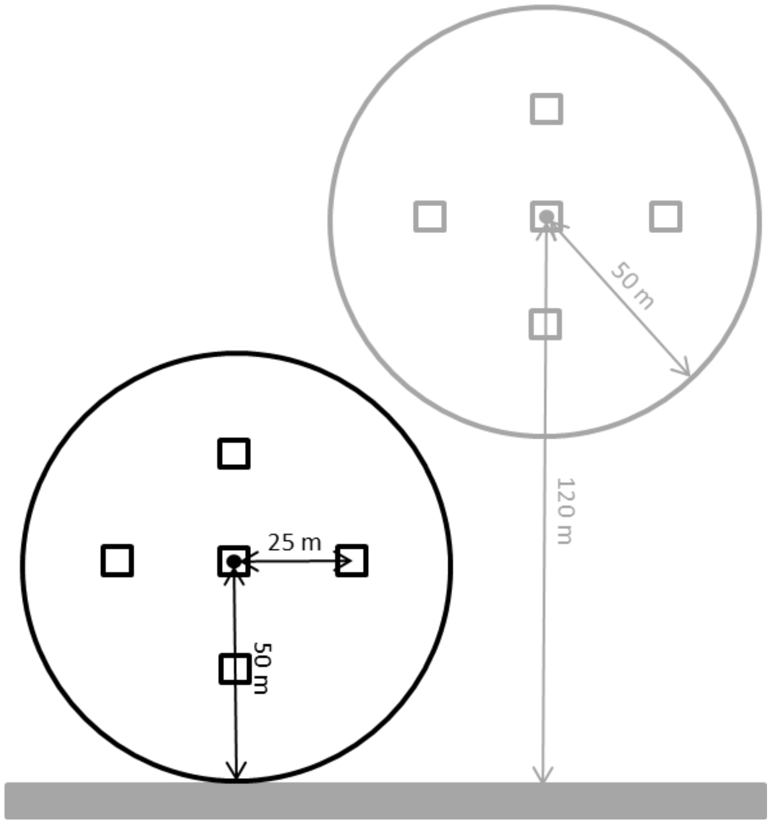

**Fig. 1** Schematic representation of a pair of points for counting birds within a radius of 50m (circles). The grey bar represents a trail. The black and grey circles represent the surveyed area of the point close and far from the trail, respectively. Squares (five in each point count circle) show the locations where the vegetation survey took place. The middle point is the spot from which the bird census (point count) was performed

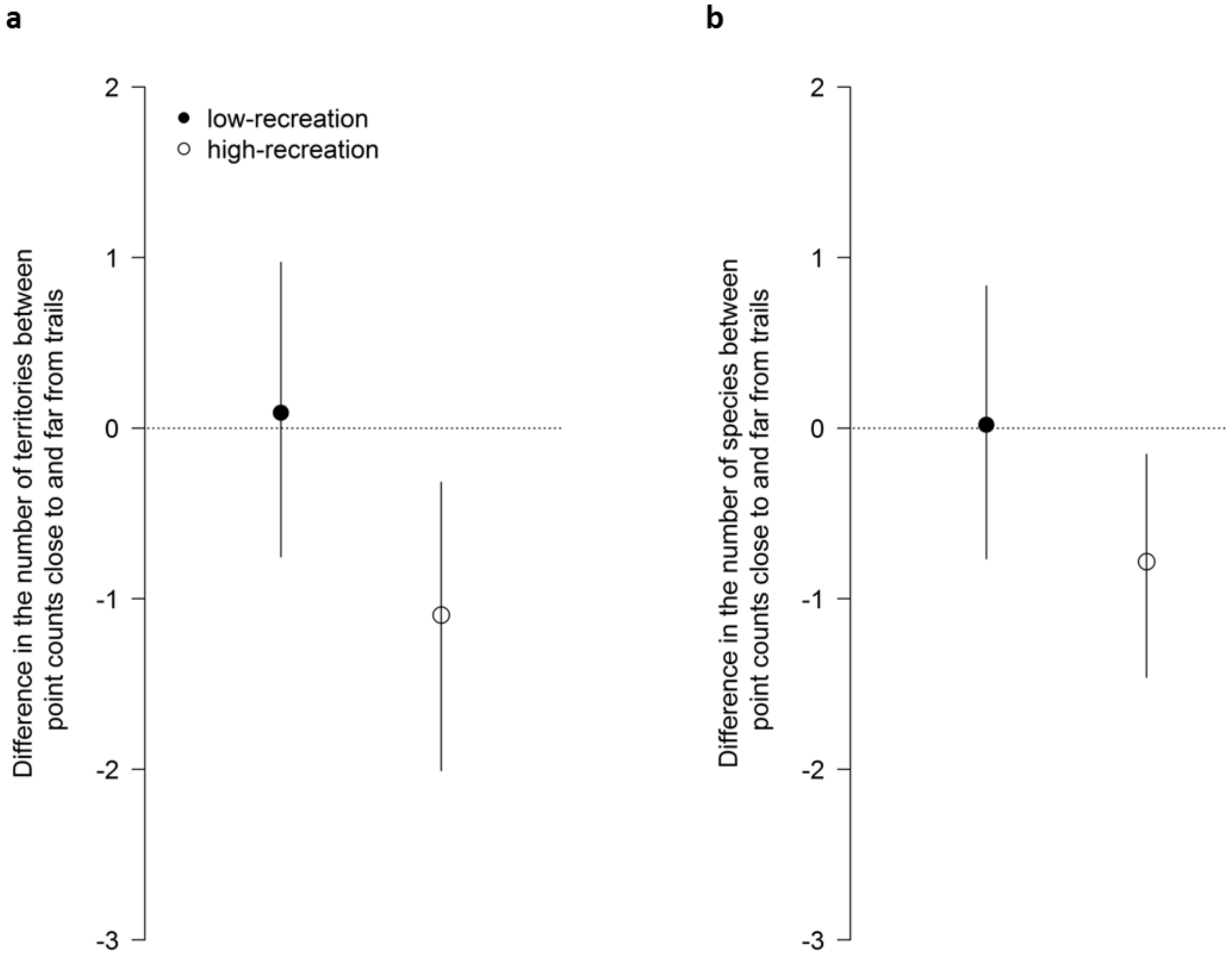

**Fig. 2** Differences (mean ± 95% CrI) in the fitted number of territories (a) and species (b) between paired point-counts close to and far from trails in forests with low- or high- levels of recreation. Negative values indicate more territories or species far from trails while positive values indicate higher number of territories or species closer to trails. The dotted line (zero) represents an equal number of territories or species at both distances from the trail

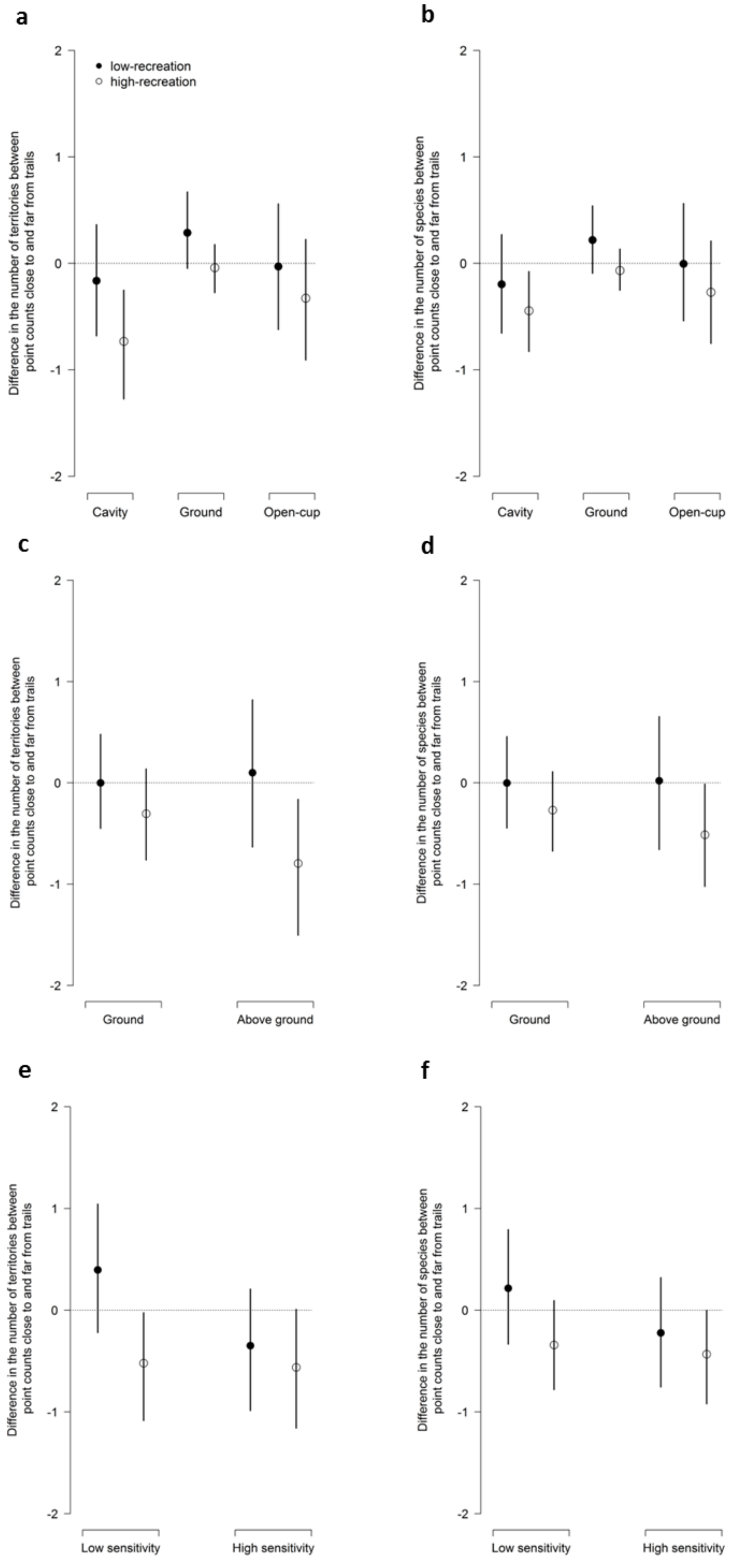

**Fig. 3** Mean differences (± 95% CrI) in the fitted number of territories and species, respectively, between points close and far from trails in forests with high- and low levels of recreation, according to (a, b) nesting-guild, (c, d) foraging-guild, and (e, f) sensitivity towards humans. Negative values indicate more territories or species per guild at far points compared to close points, positive values indicate the opposite, while the dotted line represents an equal number between far and close points

## Online Resource

**Table S1** List of bird species recorded during the censuses in 2013 and 2015, with scientific and English names, corresponding nesting-guild, foraging-guild and classification into two sensitivity groups (according to flight initiation distance (FID): High = FID ≥ median FID, Low = FID < median FID, median FID = 12.85m)

| **Scientific name** | **English name** | **Nesting guild**[1] | **Foraging guild**[1] | **Sensitivity**[2] |
|---|---|---|---|---|
| *Accipiter nisus* | Eurasian Sparrowhawk | Open-cup | Above ground | High |
| *Aegithalos caudatus* | Long-tailed Tit | Open-cup | Above ground | Low |
| *Buteo buteo* | Common Buzzard | Open-cup | Above ground | High |
| *Certhia brachydactyla* | Short-toed Treecreeper | Open-cup | Above ground | Low |
| *Certhia familiaris* | Eurasian Treecreeper | Open-cup | Above ground | Low |
| *Coccothraustes coccotraustes* | Hawfinch | Open-cup | Above ground | High |
| *Columba oenas* | Stock Dove | Cavity | Ground | High |
| *Columba palumbus* | Common Wood Pigeon | Open-cup | Ground | High |
| *Cuculus canorus* | Common Cuckoo | Open-cup | Above ground | High |
| *Cyanistes caeruleus* | Eurasian Blue Tit | Cavity | Above ground | Low |
| *Dendrocopos major* | Great Spotted Woodpecker | Cavity | Above ground | High |
| *Dendrocopos medius* | Middle Spotted Woodpecker | Cavity | Above ground | - |
| *Dryocopus martius* | Black Woodpecker | Cavity | Above ground | High |
| *Emberiza citrinella* | Yellowhammer | Ground | Ground | Low |
| *Erithacus rubecula* | European Robin | Ground | Ground | Low |
| *Ficedula hypoleuca* | European Pied Flycatcher | Cavity | Above ground | Low |
| *Fringilla coelebs* | Common Chaffinch | Open-cup | Above ground | High |
| *Garrulus glandarius* | Eurasian Jay | Open-cup | Above ground | High |
| *Lophophanes cristatus* | European Crested Tit | Cavity | Above ground | Low |
| *Muscicapa striata* | Spotted Flycatcher | Open-cup | Above ground | Low |
| *Oriolus oriolus* | Eurasian Golden Oriole | Open-cup | Above ground | High |
| *Parus major* | Great Tit | Cavity | Above ground | Low |
| *Periparus ater* | Coal Tit | Cavity | Above ground | Low |
| *Phylloscopus bonelli* | Western Bonelli's Warbler | Ground | Above ground | Low |
| *Phylloscopus collybita* | Common Chiffchaff | Ground | Above ground | Low |
| *Phylloscopus sibilatrix* | Wood Warbler | Ground | Above ground | - |
| *Phylloscopus trochilus* | Willow Warbler | Ground | Above ground | Low |
| *Picus canus* | Grey-headed Woodpecker | Cavity | Ground | High |
| *Picus viridis* | European Green Woodpecker | Cavity | Ground | High |
| *Poecile montanus* | Willow Tit | Cavity | Above ground | Low |
| *Poecile palustris* | Marsh Tit | Cavity | Above ground | Low |
| *Prunella modularis* | Dunnock | Open-cup | Ground | Low |
| *Pyrrhula pyrrhula* | Eurasian Bullfinch | Open-cup | Above ground | Low |
| *Regulus regulus* | Goldcrest | Open-cup | Above ground | Low |
| *Rgulus ignicapilla* | Common Firecrest | Open-cup | Above ground | Low |
| *Sitta europaea* | Eurasian Nuthatch | Cavity | Above ground | High |
| *Streptopelia turtur* | European Turtle Dove | Open-cup | Ground | High |

|  |  |  |  |  |
|---|---|---|---|---|
| *Strix aluco* | Tawny Owl | Cavity | Above ground | - |
| *Sturnus vulgaris* | Common Starling | Cavity | Ground | High |
| *Sylvia atricapilla* | Eurasian Blackcap | Open-cup | Above ground | High |
| *Troglodytes troglodytes* | Eurasian Wren | Open-cup | Ground | Low |
| *Turdus merula* | Common Blackbird | Open-cup | Ground | High |
| *Turdus philomelos* | Song Trush | Open-cup | Ground | High |
| *Turdus pilaris* | Fieldfare | Open-cup | Ground | High |
| *Turdus viscivorus* | Mistle Trush | Open-cup | Ground | High |

[1]: Perrins & Cramp 1998, [2]: Diaz et al. 2013, Møller 2008 ; - no data available

**Table S2** Model estimates (± 95% CrI) of the determinants of number of territories and species in the nesting-guild-specific GLMMs. The corresponding factor categories are given in parenthesis. The missing categories are used as reference in the models

| Dependent variable | Number of territories | | Species richness | |
|---|---|---|---|---|
| Intercept | 1.029 | (0.548; 1.492) | 0.767 | (0.455; 1.090) |
| Distance (far) | 0.055 | (-0.113; 0.224) | 0.088 | (-0.115; 0.293) |
| Disturbance (high) | -0.316 | (-0.507;-0.132) | -0.210 | (-0.435; 0.009) |
| Juliandate | 0.100 | (0.041; 0.160) | 0.018 | (-0.047; 0.084) |
| Juliandate$^2$ | -0.045 | (-0.086; -0.004) | -0.042 | (-0.087; 0.004) |
| Δ Sunrise | 0.018 | (-0.040; 0.074) | 0.005 | (-0.060; 0.072) |
| Ground cover | 0.009 | (-0.033; 0.051) | 0.007 | (-0.041; 0.057) |
| Shrub cover | 0.019 | (-0.015; 0.054) | 0.024 | (-0.015; 0.066) |
| Canopy cover | -0.004 | (-0.050; 0.041) | -0.005 | (-0.060; 0.048) |
| Beeches | -0.050 | (-0.092; -0.008) | -0.048 | (-0.097; 0.003) |
| Oaks | 0.041 | (0.003; 0.080) | 0.047 | (0.003; 0.090) |
| Conifers | -0.026 | (-0.070; 0.019) | -0.023 | (-0.076; 0.029) |
| Deadwood | -0.015 | (-0.053; 0.025) | -0.003 | (-0.047;0.043) |
| Nesting-guild (ground) | -0.712 | (-0.918; -0.505) | -0.647 | (-0.894; -0.400) |
| Nesting-guild (open-cup) | 0.296 | (0.138; 0.454) | 0.368 | (0.185; 0.554) |
| Δ Sunrise × Disturbance (high) | 0.014 | (-0.059; 0.086) | 0.016 | (-0.065; 0.100) |
| Disturbance (high) × Distance (far) | 0.246 | (0.013; 0.471) | 0.137 | (-0.132; 0.405) |
| Distance (far) × Nesting-guild (ground) | -0.285 | (-0.590; 0.010) | -0.300 | (-0.666; 0.059) |
| Distance (far) × Nesting-guild (open-cup) | -0.047 | (-0.267; 0.169) | -0.087 | (-0.349; 0.171) |
| Disturbance (high) × Nesting-guild (ground) | -0.348 | (-0.657; -0.034) | -0.455 | (-0.811; -0.095) |
| Disturbance (high) × Nesting-guild (open-cup) | 0.495 | (0.285; 0.706) | 0.288 | (0.039; 0.534) |
| Distance (far) × Disturbance (high) × Nesting-guild (ground) | 0.036 | (-0.402; 0.479) | 0.183 | (-0.328; 0.689) |
| Distance (far) × Disturbance (high) × Nesting-guild (open-cup) | -0.185 | (-0.473; 0.106) | -0.063 | (-0.402; 0.280) |

*Distribution = Poisson; link function = natural logarithm; random factors = year, round, and point_ID/pair_ID/Site*

**Table S3** Model estimates (± 95% CrI) of the determinants of number of territories and species in the foraging-guild-specific GLMMs with corresponding factor categories given in parenthesis. The missing factor levels are the ones used as reference in the models

| Dependent variable | Number of territories | | Species richness | |
|---|---|---|---|---|
| Intercept | 0.848 | (0.380; 1.323) | 0.724 | (0.104; 1.039) |
| Distance (far) | 0.003 | (-0.188; 0.188) | 0.002 | (-0.205; 0.212) |
| Disturbance (high) | 0.121 | (-0.068; 0.310) | 0.075 | (-0.142; 0.290) |
| Juliandate | 0.099 | (0.043; 0.159) | 0.019 | (-0.048; 0.083) |
| Juliandate$^2$ | -0.045 | (-0.086; -0.005) | -0.042 | (-0.087; 0.003) |
| Δ Sunrise | 0.018 | (-0.039; 0.075) | 0.005 | (-0.061; 0.071) |
| Ground cover | 0.009 | (-0.031; 0.051) | 0.007 | (-0.041; 0.055) |
| Shrub cover | 0.020 | (-0.015; 0.054) | 0.025 | (-0.015; 0.066) |
| Canopy cover | -0.005 | (-0.050; 0.041) | -0.006 | (-0.060; 0.048) |
| Beeches | -0.050 | (-0.091; -0.009) | -0.048 | (-0.096; 0.001) |
| Oaks | 0.042 | (0.004; 0.080) | 0.047 | (0.005; 0.090) |
| Conifers | -0.026 | (-0.071; 0.020) | -0.023 | (-0.074; 0.028) |
| Deadwood | -0.014 | (-0.052; 0.026) | -0.002 | (-0.047; 0.043) |
| Foraging-guild (above ground) | 0.869 | (0.712; 1.023) | 0.750 | (0.576; 0.929) |
| Δ Sunrise × Disturbance (high) | 0.013 | (-0.060; 0.086) | 0.017 | (-0.067; 0.098) |
| Disturbance (high) × Distance (far) | 0.105 | (-0.134; 0.337) | 0.110 | (-0.150; 0.371) |
| Distance (far) × Foraging-guild (above ground) | -0.019 | (-0.242; 0.207) | -0.003 | (-0.259; 0.247) |
| Disturbance (high) × Foraging-guild (above ground) | -0.314 | (-0.519; -0.113) | -0.297 | (-0.530; -0.073) |
| Distance (far) × Disturbance (high) × Foraging-guild (above ground) | 0.068 | (-0.212; 0.354) | 0.027 | (-0.296; 0.351) |

*Distribution = Poisson; link function = natural logarithm; random factors = year, round, and point_ID/pair_ID/Site*

**Table S4** Model estimates (± 95% CrI) of the determinants of number of territories and species in the sensitivity-specific GLMMs. The corresponding factor levels are given in parenthesis next to the variable name whereas the missing levels are the ones used as reference in the models

| Dependent variable | Number of territories | | Species richness | |
|---|---|---|---|---|
| Intercept | 1.431 | (0.964; 1.890) | 1.198 | (0.899; 1.483) |
| Distance (far) | -0.098 | (-0.242; 0.047) | -0.066 | (-0.234; 0.102) |
| Disturbance (high) | -0.265 | (-0.420; -0.109) | -0.196 | (-0.382; -0.009) |
| Juliandate | 0.093 | (0.034; 0.152) | 0.009 | (-0.058; 0.076) |
| Juliandate$^2$ | -0.044 | (-0.084; -0.003) | -0.042 | (-0.087; 0.004) |
| Δ Sunrise | 0.024 | (-0.031; 0.081) | 0.010 | (-0.055; 0.075) |
| Ground cover | 0.009 | (-0.032; 0.051) | 0.008 | (-0.040; 0.056) |
| Shrub cover | 0.023 | (-0.012; 0.059) | 0.027 | (-0.014; 0.067) |
| Canopy cover | -0.005 | (-0.051; 0.042) | -0.008 | (-0.062; 0.047) |
| Beeches | -0.044 | (-0.085; -0.003) | -0.041 | (-0.090; 0.008) |
| Oaks | 0.047 | (0.010; 0.085) | 0.051 | (0.008; 0.093) |
| Conifers | -0.021 | (-0.066; 0.023) | -0.018 | (-0.069; 0.035) |
| Deadwood | -0.017 | (-0.056; 0.022) | -0.004 | (-0.050; 0.041) |
| Sensitivity (high) | -0.174 | (-0.317; -0.032) | -0.113 | (-0.282; 0.053) |
| Δ Sunrise × Disturbance (high) | 0.006 | (-0.064; 0.078) | 0.011 | (-0.072; 0.093) |
| Disturbance (high) × Distance (far) | 0.242 | (0.048; 0.437) | 0.184 | (-0.037; 0.405) |
| Distance (far) × Sensitivity (high) | 0.191 | (-0.015; 0.393) | 0.137 | (-0.099; 0.375) |
| Disturbance (high) × Sensitivity (high) | 0.393 | (0.202; 0.585) | 0.205 | (-0.017; 0.423) |
| Distance (far) × Disturbance (high) × Sensitivity (high) | -0.208 | (-0.471; 0.065) | -0.122 | (-0.433; 0.188) |

*Distribution = Poisson; link function = natural logarithm; random factors = year, round, and point_ID/pair_ID/Site*

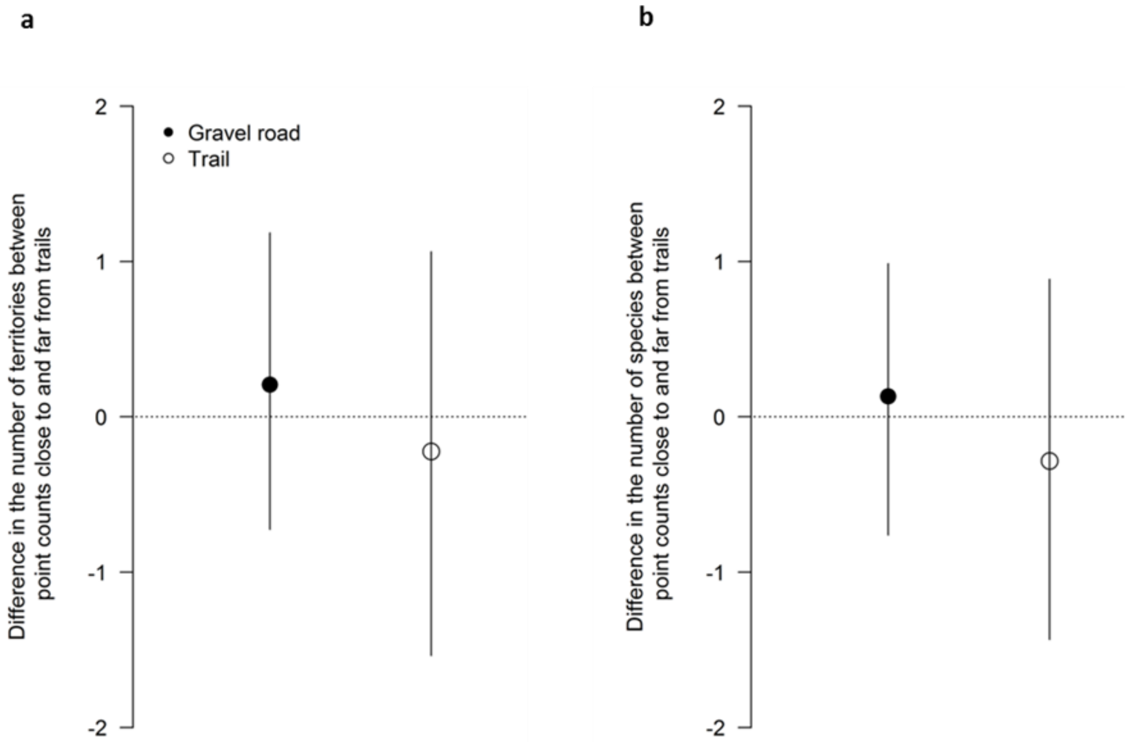

**Fig. S1** Mean differences (± 95% CrI) in number of territories (a) or species (b) between close and far points within forests with a low level of recreation, when considering the path type (Trails versus gravel roads)

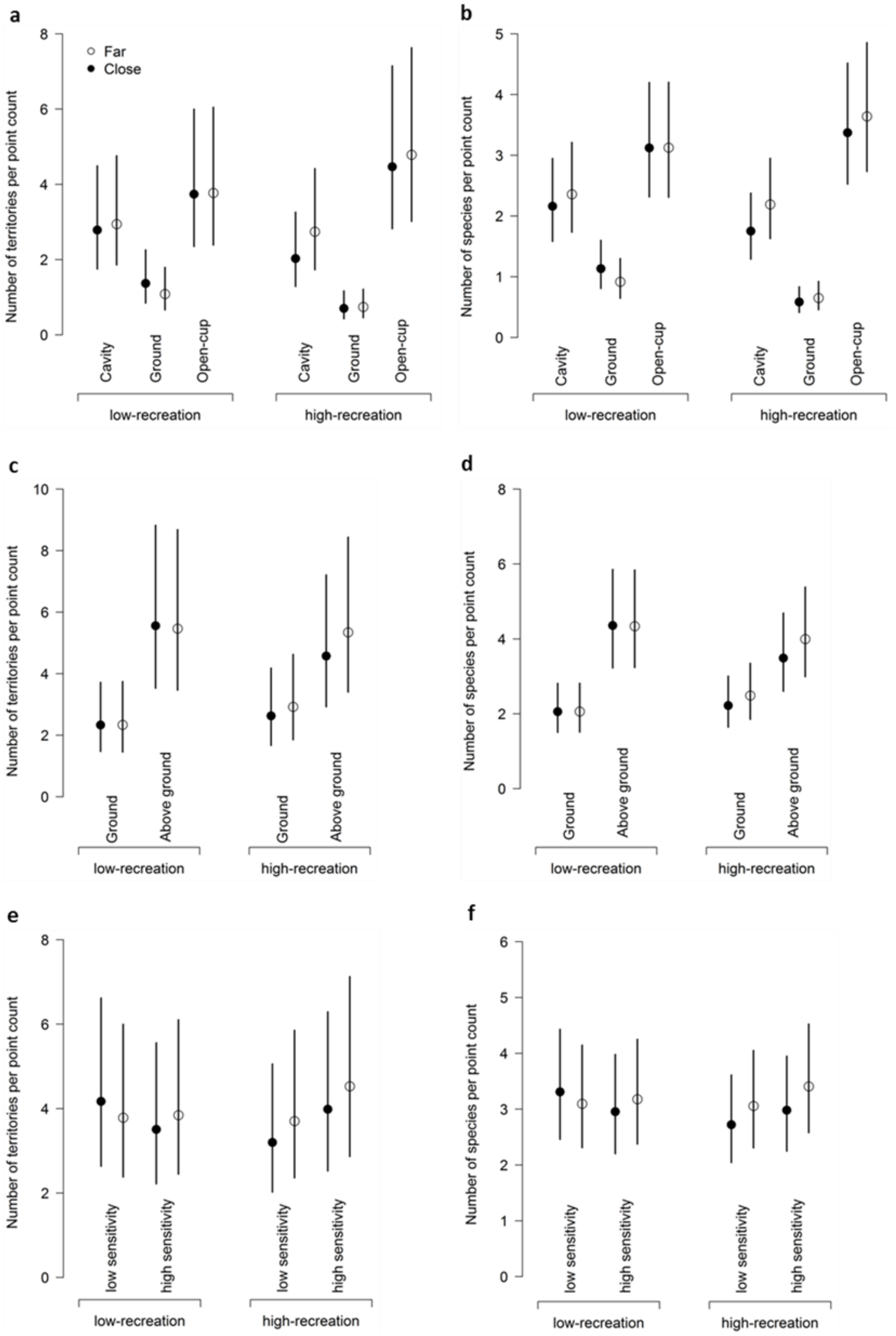

**Fig. S2** Number (mean ± 95% CrI) of territories and species, respectively, between close and far points for low- and high-recreation forests for: (a) and (b) nesting-guilds, (c) and (d) foraging-guilds, and (e) and (f) sensitivity towards humans

# CHAPTER 2

## Effect of human recreation on bird anti-predatory response

Yves Bötsch, Selina Gugelmann, Zulima Tablado and Lukas Jenni

Formatted for **Biology Letters**

Illustration credit: Yves Bötsch

# Effect of human recreation on bird anti-predatory response

Yves Bötsch[1, 2], Selina Gugelmann[3], Zulima Tablado[1] and Lukas Jenni[1]

[1]Swiss Ornithological Institute, Seerose 1, CH-6204 Sempach, Switzerland

[2]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, CH-8057 Zurich, Switzerland

[3]ETH Zurich, Rämistrasse 101, 8092 Zurich, Switzerland

## Abstract

Wildlife perceives humans as predators, and therefore normally flushes. Flight initiation distance (FID), is the distance a human can approach an animal on steady pace until it flushes. Recently several studies showed differences in within-species FID between urban and rural habitats, with urban birds showing reduced FID. However, urban and rural habitats also differ in structure which might affect FID. Therefore, we investigated whether differences in FID are also present in natural habitats (forests) differing only in the intensity of human use for recreation. We found distinctly shorter FIDs in forests used intensely by humans than in a forest hardly frequented by humans. Whether this finding is driven by non-random settlement of different personalities or phenotypic plasticity (habituation-potential) cannot be assessed with our data. Studies relying on FIDs should also incorporate human recreation intensity, as this affects the measurements strongly.

**Key words:** Flush distance, escape distance, human disturbance, habituation

## INTRODUCTION

Human disturbance through recreational activities has recently been found to negatively affect wildlife (Thiel *et al.* 2007; Kangas *et al.* 2010; Coppes *et al.* 2017; Bötsch, Tablado & Jenni 2017). To protect wild animals from the negative effects of recreation, zones with restricted access or buffer zones around breeding areas are a widely recommended mitigation measure (Rodgers & Smith 1995; Fernández-Juricic, Jimenez & Lucas 2001; Blumstein *et al.* 2003; Ikuta & Blumstein 2003). To define buffer zones an appropriate set-back distance, matching the focal species needs, has to be chosen. Unfortunately conservation measures often have to be defined quickly and ad hoc, without time for area-specific in-depth studies. Often the so called flight initiation distance (FID) has been used to define a minimal set-back distance. FID is the distance at which humans can approach a species before triggering its anti-predatory/escape behaviour. FIDs have been used widely for decades and still are considered a good surrogate for set-back distances (Samia *et al.* 2017). Many modulating factors have been found to affect these FIDs (Gutzwiller & Marcum 1997; Eason *et al.* 2006; Thiel *et al.* 2007; Carrete & Tella 2010; Legagneux & Ducatez 2013; Cavalli *et al.* 2016; Wilson-Aggarwal *et al.* 2016; Lethlean *et al.* 2017). There are intrinsic differences between species and individuals (Blumstein *et al.* 2003; Carrete & Tella 2010), but also many habitat- and context-specific effects have been reported, such as shorter FIDs in denser habitats (Tablado & Jenni 2017). Recently, studies have shown differences in bird tolerance to human approach across an urban-rural gradient, with urban populations showing reduced FIDs compared to rural conspecifics (McGiffin *et al.* 2013; Møller *et al.* 2013; Cavalli *et al.* 2016). These reduced FIDs have been attributed to habituation to humans and/or the selection of human-tolerant individuals (personalities) in urban environments (McGiffin *et al.* 2013; Cavalli *et al.* 2016; Vincze *et al.* 2016; Samia *et al.* 2017; Sprau & Dingemanse 2017). These studies demonstrate an effect of highly anthropogenic environments on bird escape reactions. However, urban and rural habitats also differ in habitat structure which might affect FID (Whittingham *et al.* 2004; Thiel *et al.* 2007), and rural habitats may also be frequented strongly by humans. Therefore it remains unclear whether the differences in FIDs between urban and rural environments are due to differences between habitats or the frequency of humans. Moreover, little is known about the effect of lower levels of human presence, such as that occurring during recreation in natural areas, on bird anti-predatory behaviour.

Therefore, the aim of this study was to investigate whether FIDs of birds in forests near large urban settlements, and thus often frequented by humans, differ from bird FIDs in rarely visited forests of similar structure.

## MATERIALS AND METHODS

### Study sites

We measured FIDs in three different forests, two of which were close to cities (the “Allschwilerwald” near Basel (193,000 inhabitants), Switzerland, 47°32’N 7°32’E and the “Sihlwald” near Zurich (415,000 inhabitants), Switzerland, 47°16’N8°33’E) and therefore heavily frequented by humans, and one forest where human recreation occurred at a very low level (“Forêt de Chaux” >9km from Dole (23,000 inhabitants), Département du Franche-Comté , France, 47°5’N 5°41’E). These forests were all deciduous and fully free to access for people. The Allschwilerwald and the Forêt de Chaux are both dominated by pedunculate oak (*Quercus robur*) whereas the Sihlwald mainly consists of European beech (*Fagus sylvatica*). In 2015 we measured FIDs in the “Forêt de Chaux”, whereas in 2016 we measured FIDs in all three forests.

### FID-measures

As the vegetation density affects visibility (detection of humans by birds), and therefore also FID, we took FID measures only in early spring, from the beginning of March until the end of April, to avoid the foliated season. By measuring FIDs only in these two months we were also reducing the noise caused by variations in antipredatory-responses across life-history stages. To be able to approach birds on a straight line at steady pace, we selected rather open forest areas, with a poor shrub layer but a closed canopy (for forest details see also Bötsch et al. in prep). To obtain a sufficient sample size we focused on a few common species: common blackbird (*Turdus merula*), common chaffinch (*Fringilla coelebs*), Eurasian nuthatch (*Sitta europaea*), European robin (*Erithacus rubecula*), great tit (*Parus major*), marsh tit (*Poecile palustris*), short-toed treecreeper (*Certhia brachydactyla*), song thrush (*Turdus philomelos*) and winter wren (*Troglodytes troglodytes*).

FID was measured by a single person approaching a located bird, that did not yet react visibly to our presence (e.g. by alert posture or alarm calling), at steady pace. Only single birds, either singing, feeding or resting were measured, as birds on a nest or birds in groups have been shown to flush differently (Fernández-Juricic, Jimenez & Lucas 2002). FID was measured with range finding binoculars (ZEISS Victory 10x45 T* RF) as the horizontal line between the observer and the tree, bush or ground where the bird was before flushing. We also measured the height above ground where the bird was sitting as well as the distance at which the measuring person discovered the individual (starting distance) (Blumstein 2003).

### Data analysis

We applied a generalized linear mixed model using the lme4-package in R v. 3.3.0 (Bates *et al.* 2015; R Core Team 2016).

We included as explanatory variables: starting distance, height above ground, time of day (daytime), Julian date, species, recreation level (low or highly frequented forest), and the interaction between species and recreation. All continuous variables were standardised to facilitate model convergence (mean=0, sd=1). We included year and observer as random factors to account for variability among years and the five observers. To account for phylogenetic relatedness between the species, we included the family of each species as random factor into the model. We visually checked for the goodness of fit by plotting residuals.

For making inference we used a Bayesian approach (after Korner -Nievergelt *et al.* (Korner-Nievergelt *et al.* 2015)). We simulated 10,000 random samples from the posterior distribution by using the sim-function from the R-package arm (Gelman & Su 2015). From these random samples we used the 2.5 % and 97.5 % quantiles as the limits of the 95 % credible interval (CrI). To be able to investigate species-specific differences between the forests, we computed posterior probabilities (PP). PPs describe the probability that the difference in FID (for a given species) between two forests is different from zero: PPs can take values between 0.5 (no difference) and 1 (different).

## RESULTS

For each species we had the following FID sample sizes: 73 for common blackbird, 121 for common chaffinch, 62 for Eurasian nuthatch, 94 for European robin, 132 for great tit, 39 for marsh tit, 23 for short-toed treecreeper, 26 for song thrush and 74 for winter wren.

For many species, we found differences in FID between heavily frequented and the less frequented forest (figure 1 and tables 1, 2). Overall, birds in the less frequented forest showed larger FIDs compared to heavily frequented forests although the strength of this difference was species dependent (see figure 1, table 2). Within species FIDs between the two heavily frequented forests never differed substantially between each other (see table 2).

The higher above ground a bird was located, the shorter was its FID (table 1), whereas the starting distance was positively correlated with the FID (table 1).

## DISCUSSION

We found that birds had shorter FIDs in the frequently visited forests than in the less frequented forest. This indicates that the shorter FID is due to human presence, because the habitat was very similar. It also indicates that the shorter FIDs found in urban than rural environments (Cavalli *et al.* 2016) may be mainly due to human presence rather than habitat differences. People may be perceived by naive wildlife as predators (Frid & Dill 2002; Beale & Monaghan 2004a). This may explain why we find large FIDs in forests where birds did not have that much experience with humans ("non-habituated"). However, in forests with higher human frequentation birds could have "habituated" to non-threatening recreationists and reduce their behavioural anti-predatory response. An alternative possible explanation for our finding could be a redistribution of personalities, as recently shown by Sprau & Dingemanse (Sprau & Dingemanse 2017). That is, they showed that personality types are non-randomly distributed along an urban gradient with bolder animals being more frequent in urban areas and shyer individuals in more sub-urban areas. This might also partially explain why we found for most species shorter FIDs in the heavily frequented forests, compared to the less frequented one, but whether non-random settlement or phenotypic plasticity is the driving factor cannot be disentangled with our data.

In conclusion, FID can be affected by human frequentation. Thus, when FID is to be used for defining set-back distances, local FIDs should be measured to avoid mismatching between bird tolerances in areas where the FID was measured and the ones in the local area where it will be applied. If human disturbance already occurred at a given site, the most vulnerable species or individuals might already have left the site, therefore FIDs always have to be used as minimal set-back distances (although mostly average FID plus one or two standard deviations are used). Our finding implies that future studies, measuring FIDs, should also incorporate site-specific human recreation intensity as a modulating factor for FIDs.

## ACKNOWLEDGMENTS

We thank M. Romanski and R. Schmidt who permitted us to measure FIDs in the Forêt de Chaux and the Sihlwald. The following people measured FIDs and we thank them for their effort: B. Garde, H.F. Lemke, and J. Vasseur.

## TABLES

**Table 1:** Model output of the FID-model with the mean FID estimate and the corresponding 95 % credible interval (CrI). The reference category is the Common blackbird from the Allschwilerwald.

| Variable | Mean FID estimate | 95% CrI |
|---|---|---|
| Intercept | 12.43 | (6.53; 18.36) |
| Starting distance | 6.94 | (6.38; 7.50) |
| Height | -2.51 | (-3.06; -1.97) |
| Time | -0.23 | (-0.72; 0.26) |
| Julian date | -0.09 | (-0.58; 0.40) |
| Forêt de Chaux (FdC) | 13.69 | (8.62; 18.60) |
| Sihlwald (Sw) | -2.99 | (-6.72; 0.77) |
| Common chaffinch (CC) | -3.10 | (-10.13; 4.12) |
| Short-toed treecreeper (StT) | -8.17 | (-16.56; 0.24) |
| Eurasian nuthatch (EN) | -4.48 | (-11.65; 2.81) |
| Great tit (GT) | -2.42 | (-9.44; 4.68) |
| European robin (ER) | -4.14 | (-11.32; 3.10) |
| Song thrush (ST) | -7.15 | (-13.66; -0.60) |
| Marsh tit (MT) | -2.58 | (-10.17; 5.22) |
| Winter wren (WW) | -4.03 | (-11.32; 3.05) |
| Forest (FdC) × Species (CC) | -7.00 | (-12.44; -1.41) |
| Forest (FdC) × Species (StT) | -7.49 | (-15.22; 0.18) |
| Forest (FdC) × Species (EN) | -10.37 | (-16.10; -4.50) |
| Forest (FdC) × Species (GT) | -12.37 | (-17.66; -7.00) |
| Forest (FdC) × Species (ER) | -7.74 | (-13.34; -2.16) |
| Forest (FdC) × Species (ST) | -7.36 | (-15.68; 1.15) |
| Forest (FdC) × Species (MT) | -13.01 | (-19.61; -6.48) |
| Forest (FdC) × Species (WW) | -11.02 | (-16.81; -5.13) |
| Forest (Sw) × Species (CC) | 3.27 | (-1.38; 7.95) |
| Forest (Sw) × Species (StT) | 4.89 | (-3.10; 12.67) |
| Forest (Sw) × Species (EN) | 3.57 | (-2.47; 9.53) |
| Forest (Sw) × Species (GT) | 2.34 | (-2.79; 7.50) |
| Forest (Sw) × Species (ER) | 2.88 | (-2.01; 7.71) |
| Forest (Sw) × Species (ST) | 7.76 | (0.14; 15.40) |
| Forest (Sw) × Species (MT) | 4.48 | (-2.16; 10.98) |
| Forest (Sw) × Species (WW) | 3.46 | (-1.58; 8.38) |

**Table 2:** Within species posterior probabilities between forests. Posterior probabilities can take values between 0.5 (no difference) and 1 (fully different) and are a measure to represent the strength of a difference between two measures (levels). The “Forêt de Chaux” (FdC) was seldom used for recreation whereas the other two forests (Allschwilerwald: Aw and Sihlwald: Sw) were heavily frequented by recreationists.

| **Species** | **Aw vs FdC** | **Sw vs FdC** | **Aw vs Sw** |
|---|---|---|---|
| Common blackbird | >0.99 | >0.99 | 0.94 |
| Common chaffinch | >0.99 | >0.99 | 0.59 |
| Short-toed treecreeper | 0.98 | 0.91 | 0.70 |
| Eurasian nuthatch | 0.98 | 0.88 | 0.59 |
| Great tit | 0.87 | 0.87 | 0.64 |
| European robin | >0.99 | >0.99 | 0.52 |
| Song thrush | 0.97 | 0.72 | 0.92 |
| Marsh tit | 0.62 | 0.63 | 0.71 |
| Winter wren | 0.95 | 0.90 | 0.61 |

## FIGURES

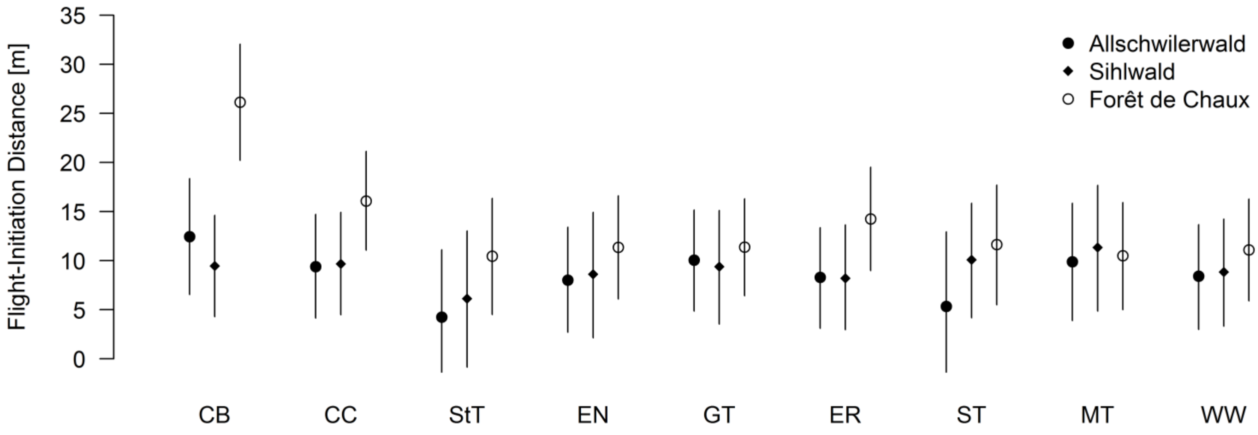

**Figure 1:** Model estimates (± 95 CrI) of species-specific flight-initiation distances for the three different study sites. The “Forêt de Chaux” is rarely frequented by humans (open symbol) whereas the two other forests (closed symbols) are highly frequented by humans. Explanation of the acronyms: CB: Common blackbird (*Turdus merula*), CC: Common chaffinch (*Fringilla coelebs),* StT: Short-toed treecreeper (*Certhia brachydactyla*), EN: Eurasian nuthatch (*Sitta europaea*), GT: Great tit (*Parus major*), ER: European robin (*Erithacus rubecula*), ST: Song thrush (*Turdus philomelos*), MT: Marsh tit (*Poecile palustris*), WW: Winter wren (*Troglodytes troglodytes*).

# CHAPTER 3

## Experimental evidence of human recreational disturbance effects on bird-territory establishment

Yves Bötsch, Zulima Tablado and Lukas Jenni

Published in **Proceedings of the Royal Society B: 284: 20170846**

Illustration credit: Fanny le Bagousse (Former trainee)

# Experimental evidence of human recreational disturbance effects on bird-territory establishment

Yves Bötsch[1, 2, *], Zulima Tablado[1] and Lukas Jenni[1]

[1]Swiss Ornithological Institute, Seerose 1, CH-6204 Sempach, Switzerland

[2]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, CH-8057 Zurich, Switzerland

## ABSTRACT

The worldwide increase in human outdoor activities raises concerns for wildlife. Human disturbances, even at low levels, are likely to impact species during sensitive periods of the annual cycle. However, experimental studies during the putative sensitive period of territory establishment of birds which not only investigate low disturbance levels, but which also exclude the effect of habitat modification (e.g. walking trails) are lacking. Here, we experimentally disturbed birds in forest plots by walking through twice a day during territory establishment. Later we compared the breeding bird community of experimentally disturbed plots with that of undisturbed control plots. We discovered that the number of territories (-15.0%) and species richness (-15.2%) in disturbed plots were substantially reduced compared to control plots. Species most affected included those sensitive to human presence (assessed by flight-initiation distances), open-cup nesters and above-ground foragers. Long-distance migrants, however, were unaffected due to their arrival after experimental disturbance took place. These findings highlight how territory establishment is a sensitive period for birds, when even low levels of human recreation may be perceived as threatening, and alter settlement decisions. This can have important implications for the conservation of species, which might go unnoticed when focussing only on already established birds.

**Key words:** Forest birds, nesting guild, foraging guild, flight-initiation distance, nature-based activities, outdoor recreation.

## INTRODUCTION

Outdoor recreational activities have increased substantially in the past decades (Boyle & Samson 1985; Balmford *et al.* 2009), which has led to repeated encounters between people and wildlife. These encounters may provoke wildlife responses, such as increased vigilance, heightened stress-hormone levels, anti-predator escape responses and, in some cases, a decrease in survival and/or reproduction or even abandonment of an area (Ikuta & Blumstein 2003; Thiel *et al.* 2008; Mathot *et al.* 2012; Arlettaz *et al.* 2015; Tarjuelo *et al.* 2015; Tablado & Jenni 2017). Wildlife responses to human recreation will not only depend on the characteristics of the animals involved (e.g. species, sex) and on the type of human disturbance (e.g. noise level, number of people), but also on the environmental conditions (e.g. habitat) and on the specific period in an animal's life history in which the encounter with humans occurs (Tablado & Jenni 2017).

The timing of disturbance events also warrants more attention from researchers (Buckley 2013). Although a number of studies have been conducted during sensitive periods, such as reproduction or other periods of energetic constraints (Arroyo & Razin 2006; Strasser & Heath 2013; Arlettaz *et al.* 2015; Martín *et al.* 2015), territory establishment remains understudied (Götmark 1992; Tablado & Jenni 2017). During this phase, even low-intensity and short-lasting disturbance events could prompt animals to perceive habitats as risky and influence their decision on where to breed, thus altering the density and species richness of the breeding community. An increase from no disturbance to low-level disturbance is likely to have a proportionally stronger ecological impact than a change from low to medium-level disturbance, or from medium to high-level disturbance (Hill *et al.* 1997; Steidl & Powell 2006; Steven, Pickering & Castley 2011; Monz, Pickering & Hadwen 2013). This may apply particularly to the sensitive phase of territory establishment.

In the field of avian biology, human outdoor recreation has been linked to lower abundance and reduced species richness (Van der Zande *et al.* 1984; Patthey *et al.* 2008;

Kangas *et al.* 2010). However, these studies did not focus on the underlying processes being altered by disturbance (e.g. prevention from settling vs. later breeding failure), and often cannot separate direct effects of human presence from indirect effects (e.g. habitat alterations normally associated with recreation). That is, human recreational activities are mostly bound to roads or trails and, thus always occur with habitat alterations (Forman & Alexander 1998), which are known to impact species distribution and abundance (Fernández-Juricic 2000; Butler *et al.* 2012). Therefore, experimental studies are needed to determine the direct effects of human presence on birds and the processes involved (Hill *et al.* 1997; Gill 2007).

The aim of this study was to experimentally investigate whether human recreational activities at relatively low levels altered bird-settlement decisions during territory establishment, and thus, the resulting breeding-bird community. We expected that experimental disturbance during territory establishment would lead to lower densities of breeding birds. Depending on species-specific tolerances towards disturbance, we also predicted changes in species richness and composition. Notably, we expected a reduction in the abundance and number of bird species sensitive to human disturbance, such as ground-nesting, ground-foraging (Langston *et al.* 2007; Mallord *et al.* 2007; Kangas *et al.* 2010; Thompson 2015), and disturbance-sensitive species (Blumstein *et al.* 2003; Weston *et al.* 2012; Livezey, Fernández-Juricic & Blumstein 2016).

## MATERIALS AND METHODS

### Study site

This study was done in the “Forêt domaniale de Chaux”, a large (200 km$^2$) oak-hornbeam forest in eastern France (47°05’N, 05°40’E) fulfilling all legal and animal welfare regulations (permit number 2014157-0012 of the “Direction Régionale de l’Environnement, de l’Aménagement et du Logement de Franche-Comté”). This forest is subdivided into approximately rectangular 10 ha plots, where harvest is managed by the “Office Nationale des Forêts”. The plots were separated from each other by small treeless tracks but otherwise natural vegetation, generated by harvest-machines. One side was bordered by a gravel road. The forest was only accessible to the public on foot or by bike, with the exception of two paved roads crossing the forest. Recreational activities were concentrated mainly near the town of Dole (23,000 inhabitants) located at the western border of the forest (figure 1) and near Besançon (117,000 inhabitants) which is 15 km to the east of the forest. In most of the forest, the frequency of human recreational activities was extremely low, and occurred primarily in autumn (i.e. mushroom collection and hunting). During our fieldwork (continuous from March to June of 2014 and 2015, 50 h / week) we rarely saw people off-trail within the plots (less than one person per month) and approximately one person per week on the gravel roads near the study plots.

### Experimental design

We used plots (mean size: 9.2 ha, range: 7.5 - 13 ha) in the centre of the forest (> 9 km from Dole and Besançon, figure 1) where no timber harvesting occurred during the study period (2014-2015; as agreed with the “Office National des Forêts”). The composition and structure of the vegetation was homogeneous within plots and similar among plots. The plots were dominated by pedunculate oaks *Quercus robur*, many older than 100 years (M. Romanski pers. comm.), with admixed European beech *Fagus* *sylvatica* and European hornbeam *Carpinus betulus*, as well as Norway spruce *Picea abies* or Douglas fir *Pseudotsuga menziesii* in small numbers. The plots were at least 600 m apart from each other to prevent confounding neighbouring effects. We divided all plots in two halves (split-plots, mean 4.7 ha); one half was experimentally disturbed while the other half served as a control. The split-plots receiving the disturbance treatment were chosen randomly with the only constraint that half of them were bordered by the gravel road and the other half not.

Since our objective was to examine the effect of human recreation during bird-territory establishment, we only disturbed birds during the pre-breeding season, from early March until mid-April (7 March - 22 April) (von Blotzheim, Bauer & Bezzel 1993). Disturbance events consisted of a group of two or three people, carrying a loudspeaker (Hama, smartphone speaker, power: 3 W with a Samsung digital audio player F3) and walking through a pre-established mower-pattern transect with back and forth lines separated by 20 m (figure 1). The loudspeakers were continuously playing human conversations (obtained from several sources and languages; from TV shows to audio books) at an average human-conversation volume level (approximately 60 dB at 1 m distance  (Byrne *et al.* 1994; Hacki 1996)). The orientation of the path was turned 90 degrees from one disturbance event to the next to reduce predictability of the disturbance. These disturbance events lasted around 45 minutes depending on the split-plot area (mean = 42 min, sd = 13 min) and occurred one to three times per day during daytime. The order in which the split-plots were disturbed changed daily to avoid biases in the time of disturbance.

Due to logistic reasons and man-power limitations, the experimental disturbance in 2014 was restricted to six treatment plots which were disturbed on average 1.6 times per day (each plot at least once each day). In 2015, we were able to extend the experiment to 12 plots which were disturbed 2.3 times per day (each plot at least once per day). In the case of the six plots that were common for both years, we switched the disturbed and control split-plots from one year to the next to exclude possible split-plot-specific effects. In 2014, we therefore disturbed each of the six split-plots 73 times during 45 days, and in 2015, each of the 12 split-plots 105 times during 46 days. The low number of disturbance events allowed us to examine the effects of recreation at intensities much lower than most previous studies in recreation ecology (see for example (Van der Zande *et al.* 1984; Beale & Monaghan 2004a)), thus enabling us to test whether even low levels of disturbance could have an impact when applied during sensitive periods.

## Bird territory mapping

The breeding bird territories were censused in all plots three times per season in both years of the study (first census round 20 April – 6 May, second 6 May – 22 May, third 28 May – 17 June) to include the breeding season of all forest-bird species, from residents to late-arriving long-distance migrants. We did not census earlier, to be sure that birds were already settled and that we did not disturb the control split-plots during the territory establishment period. Censuses started at sunrise and lasted 30 to 66 minutes (mean = 42 min) depending on plot size. Censuses followed the Swiss standard breeding-bird survey protocol (Bibby *et al.* 2000; Schmid & Spiess 2008) and consisted of recording all birds seen or heard showing territorial behaviour on a map, while following a mower-pattern transect (lines 60 m apart) covering the entire plot (including both disturbed and control split-plots; figure 1). The censuses were performed by the same two observers in both years, each of which always surveyed the same plots. For each round, we determined the number of contacts per species, but counted pairs and families as one to approach the *number of territories* detected. Long-distance migrants were not considered as breeders, but as transients, if seen or heard before usual arrival dates (according to Schmid *et al.* (Schmid *et al.* 1998); see electronic supplementary material table S1).

## Vegetation surveys

In June 2015, we characterised the vegetation of all twelve plots by using a stratified random sampling, i.e. distributing one survey point per 0.5 ha grid cell, which resulted in 7 to13 points per split-plot (210 survey points in total, figure 1). At each point the following variables were measured: canopy cover (visual estimation of percentage of cover in the observer's visual field when looking straight up; always measured by the same person), ground vegetation cover (in 2x2 m quadrats), shrub cover (in 3x3 m quadrats), and number of trees per species and standing dead trunks with diameter at breast height (dbh) larger than 5 cm in 8x8 m quadrats. Before analyses, we averaged vegetation measures to create mean values per split-plot. There were no significant within-plot differences in any of the vegetation variables between the disturbed and the control split-plots (pairwise t-tests or Wilcoxon tests, depending on data distributions, $p > 0.05$).

## Data analysis

We tested for the effect of human disturbance during territory establishment on the number of territories and on species richness, both following a Poisson distribution, with two separate generalized linear mixed models (GLMM) (table 1). The factor *disturbance* treatment (disturbed vs. control split-plot) was included as explanatory variable. To differentiate between birds whose territory-establishment period overlapped with the experimental treatment (residents and short-distance migrants) and long-distance migrants arriving afterwards and not being exposed to the disturbance, both number of territories and species richness were calculated separately for these two groups and a two-level factor *migration type* ("long-distance migrants" vs. "others"; see electronic supplementary material table S1) was added to the models. To describe the structure and composition of the vegetation we included the following explanatory variables: *ground vegetation* cover, *shrub* cover, *canopy* cover, amount of *deadwood,* and *tree diversity*

(Shannon-diversity index (Spellerberg & Fedor 2003) of the main tree species: pedunculate oak *Quercus robur*, European beech *Fagus sylvatica*, European hornbeam *Carpinus betulus* and two species of conifers; *Picea abies, Pseudotsuga menziesii*). Additionally, we incorporated the presence/absence of a gravel *road* along the split-plot to control for further possible habitat differences between split-plots, the linear and quadratic effect of *Julian date* to account for bird-breeding phenology, and the *year* (2014 vs. 2015) to control for inter-annual differences in the intensity of disturbance and in climatic conditions. We also added the two and three-way interactions between *year*, *disturbance* and *migration type*. We included the *split-plot area* (in ha) into the models to account for unequal plot sizes (Connor & McCoy 1979; Korner-Nievergelt *et al.* 2015). For the model on the number of territories we had to include the logarithm of the split-plot area as an offset term to model territory densities (after Korner-Nievergelt *et al.* (Korner-Nievergelt *et al.* 2015)), while for the model on species richness, we included the quadratic effect of area (*Split-plot area*$^2$).

Additionally, in order to investigate the effects of experimental disturbance on the density and richness of specific types of birds, we classified all bird species according to their *nesting guild (*ground, open-cup, and cavity nesters (Perrins & Cramp 1998)), their tolerance to human approach (*sensitivity;* high vs. low), and their *foraging guild* (ground vs. above ground (Perrins & Cramp 1998)) (see electronic supplementary material table S1). For each of the three classifications, we then applied two models (i.e. for number of territories and species) similar to the ones above, but replacing the factor *migration type* by the factor corresponding to each classification (i.e. *nesting guild*, *sensitivity*, or *foraging guild*). These six models were performed without long-distance migrants (i.e. with only those species whose territory-establishment period overlapped with experimental disturbance). Bird *sensitivity* classes were approximated by using the mean flight initiation distance (FID) of the given species during the breeding period in non-urban areas, as obtained from Díaz *et al.* (Díaz *et al.* 2013). Low sensitivity species had an average FID lower or equal to the overall median value of FID for all species observed breeding in our plots (median FID = 13.13m), whereas high sensitivity species had FID larger than the overall median FID. We acknowledge that FID might not always truly represent species sensitivity, as modulating factors (e.g. vegetation) may influence birds antipredator behaviour (Tablado & Jenni 2017); however, FID is an acceptable and widely available measure for approximating sensitivity towards human disturbance (Blumstein *et al.* 2003).

In all models, to account for observer effect we included *observer* (two-level factor) as a random factor. To account for variations among rounds and plots, census *round* (first, second, third) and *split-plot-ID* were nested within *plot-ID*. All analyses were performed in R 3.3.0 (R Core Team 2016) with the function glmer from package lme4 (Bates *et al.* 2015). All numeric explanatory variables were standardized (mean = 0 and sd = 1) to facilitate model convergence. We used a Bayesian framework to calculate the 95% credible intervals (CrI) of the parameter estimates and model predictions. To do so we simulated random samples (N = 10,000) from the joint posterior distribution of the model parameters using the function *sim* from the R-package *arm* (Gelman & Su 2015) (electronic supplementary material figure S3 and S4), from which we used the 2.5% and 97.5% quantiles as the lower and upper limit of the 95% CrI. To assess how split-plot type (disturbed and control) interacted with year and bird characteristics, we calculated the posterior probability (between 0.5 and 1; using Monte Carlo simulation) of the hypothesis that the mean number of territories or of species at disturbed sites was lower than at control sites (see figure 2 and 3). Using this approach, higher probabilities represent a stronger difference between treatments. Goodness-of-fit was assessed through visual examination of plotted residuals, and we confirmed that there was no overdispersion (Values of the R-function *dispersion_glmer* always below 1, after Korner-Nievergelt et al., 2015). Note that the numbers of territories and species obtained are not absolute numbers, since we did not account for imperfect detection. Accounting for imperfect detection would have added a layer of complexity to our models which would have been incompatible with sample size (over-parameterisation) and caused problems of convergence.

## RESULTS

Both the number of territories and species richness were substantially lower in disturbed split-plots than in the control ones (table 1, figure 2). Moreover, this effect was only observed for resident and short-distance migrant species which experienced the experimental disturbance (figure 2a,c). It was not observed for species arriving later in the season (long-distance migrants; figure 2b,d). We found a reduction of about 15% in the number of territories for residents and short-distance migrants per mean disturbed split-plot compared to the control split-plot over both years (19.8% in 2014 and 10.2% in 2015). Species richness of resident and short-distance migrants also dropped by 15% in the disturbed split-plots compared to control split-plots (19.4% in 2014 and 10.9% in 2015). Independent of the disturbance treatment, the number of territories detected decreased with Julian date.

The response to experimental disturbance varied depending on the characteristics of the species (electronic supplementary material figure S1 and figure S2). The effect of disturbance appeared to be largest on open-cup nesters compared to cavity or ground nesters (figure 3a; electronic supplementary material table S2). High-sensitivity species showed a stronger negative response to disturbance than low-sensitivity species (figure 3b; electronic supplementary material table S3). Finally, above-ground foragers appeared more affected by disturbance than ground foragers (figure 3c; electronic supplementary material table S4). Overall, there seemed to be a stronger effect of disturbance on the number of territories and species richness in the first year (2014) compared to the second year (2015).

## DISCUSSION

Our findings confirm our hypothesis that even low levels of disturbance during territory-establishment, with no concomitant habitat alteration, can have a negative effect on both density of breeding birds and species richness. Such an effect was not apparent in long-distance migrants, as they arrived after the end of the experimental disturbance, and thus, were not exposed to it. These findings are in agreement with Steven *et al.* (Steven, Pickering & Castley 2011) and Monz *et al.* (Monz, Pickering & Hadwen 2013) which state, that even low levels of disturbance (as ours) can have significant importance. Contrary to other experimental studies, which also show a negative link between human disturbance and bird density and/or diversity (Riffell, Gutzwiller & Anderson 1996; Gutzwiller & Anderson 1999; Baines & Richardson 2007; Holm & Laursen 2009), we restricted disturbance to the territory-establishment period. Thus, our results suggest that territory establishment may be a sensitive period, in which human disturbances could greatly affect the density and diversity of breeding birds.

During the territory-establishment period birds select breeding sites, and the presence of humans might “invisibly” lower the quality of the habitat (Reed & Merenlender 2008). A possible explanation for the observed effects could be that birds perceive recreationists as predators (Beale & Monaghan 2004a). Indeed, the presence of predators has been shown to strongly affect breeding-site selection (Norrdahl & Korpimäki 1998; Fontaine & Martin 2006). Birds are therefore anticipated to select against habitats with more recreational activity, resulting in altered breeding-bird communities as shown in this study. These results emphasize the important role played by human disturbance on species abundance and diversity.

As predicted, we found that the effect of experimental disturbance varied according to species characteristics. Open-cup nesters were more affected than cavity nesters. This finding is in accordance with Kangas *et al.* (Kangas *et al.* 2010) and Martin & Li (Martin &

Li 1992) suggesting that cavities confer extra protection, which lowers the effect of disturbance and predation. Surprisingly, we did not observe an effect of experimental recreation on ground-nesting birds, as has been previously suggested by Kangas *et al.* (Kangas *et al.* 2010). Similarly, there was no effect of experimental disturbance on ground-foragers. This was probably due to the low number of ground-nesting and ground-foraging species in our study sites (see electronic supplementary material table S1), making an effect of disturbance hard to detect. As expected, we demonstrated a stronger impact of experimental disturbance on the more sensitive species (i.e. with larger flight initiation distance (FID)) than on the less sensitive species. Species with larger FID are generally larger-bodied species (Blumstein *et al.* 2005) and therefore human disturbance is expected to affect these species the most.

The negative response of birds to the experimental disturbance in the first study year was stronger than in the second year, despite increased disturbance intensity in the second year. This finding could be a consequence of the greater total number of territories found in the second year, which could have forced birds to also accept non-preferred (i.e. disturbed) habitats (Komdeur *et al.* 1995; Reijnen *et al.* 1995; Ferrer & Donazar 1996; Rodenhouse *et al.* 2003), diminishing the differences between treatments in the second study year. Habituation effects, on the other hand, can be ruled out due to the treatment switching from the first to the second study year. Carry-over effects from the first to the second year in interaction with treatment switching, could also partially explain this inter-annual difference in impact. That is, if birds experiencing the disturbance split-plot in the first year tried to avoid it in the second year, this could lead to lower starting numbers in this split-plot which became the control split-plot in the second year. This uneven starting number could have partially obscured the effect of disturbance the second year. However, the overall increased numbers of territories in both split-plots in the second year suggest that these carry-over effects, if at all present, would play only a marginal role. Another partial explanation to this decreased effect in the second year could be differences in weather conditions or food availability was better in the second year, thus increasing the perceived quality of disturbed split-plots. Unfortunately, we did not measure food resources.

Our findings highlight how the impacts of disturbance can go unnoticed when examined later in the season. Indeed, individuals and species establish breeding territories early in the season. A pre-selection in favour of bolder personalities and species might have already occurred during the pre-breeding phase of territory establishment (by tourists or researchers visiting and area). We should therefore be careful when planning and interpreting the results of studies occurring during the breeding season *sensu stricto*. Future studies should investigate the consequences of these recreation-driven reductions in number of territories and species for subsequent breeding parameters, survival, and overall population dynamics.

In conclusion, this study emphasizes that negative effects of human recreational disturbance can already occur after low-intensity disturbance events, even when occurring over a short time period. This is especially relevant during territory establishment in early spring, when improving weather conditions entail an increase in outdoor recreation (at least in temperate regions; R. Schmidt unpublished data). Given the potential conservation implications of these results, we suggest that conservationists and park managers should not only manage disturbance during the main breeding season, but also during territory establishment. Disturbance management could include limiting human access to certain areas that are likely to be used by vulnerable species to establish breeding territories. Additionally, the network of trails open to the public could be reduced temporarily to increase the size of the undisturbed patches. Furthermore, appropriate information should be provided to visitors about the importance of staying on trails to minimize their impacts on wildlife. These measures could help protect sensitive birds (species or individuals of certain personalities) that would settle in an area if there were no human activities during the pre-breeding season.

## ACKNOWLEDGMENTS

We greatly thank all field assistants and trainees who helped during the disturbance phase, which laid the basis to the entire experiment; in alphabetical order: C. Arnace, R. Baffoin, M. Crespo Ballester, S. Bühler, B. Garde, L. Gillespie, M. Hitt, F. Le Bagousse, H. Lemke, F. Leugger, N. Mortier, J. Nouri, M. Quetstroey, A. Rouméas, J. Vasseur. We thank H. Lemke, for doing half of the bird censuses, M. Romanski and J.L. Dessolin from the Office National des Forêts (ONF) as well as B. Dorbani from the DREAL (Direction Régionale de l'Environnement, de l'Aménagement et du Logement de Franche-Comté) for allowing us to do this study in the Forêt domaniale de Chaux. We thank R. Scheifler from the University Franche-Comté, Besançon, who advised us on local affairs and permits during the preparation of this study. We thank three anonymous reviewers for their helpful comments, K. L. Dhanjal-Adams for improving the English and B. Almasi, M. Kéry and F. Korner-Nievergelt for support with the statistics.

## TABLES

**Table 1:** Results of the GLMMs testing the effect of experimental disturbance (human recreation) on the number of bird territories and species richness. Represented are the estimates of the effect of each variable with the corresponding 95% credible intervals (CrI).

| | Number of Territories | | Species richness | |
|---|---|---|---|---|
| Terms | Estimate | CrI | Estimate | CrI |
| Intercept | 0.8810 | 0.5780; 1.1814 | 1.9444 | 1.6828; 2.2046 |
| Disturbance | | | | |
| disturbed | -0.2232 | -0.4308; -0.0092 | -0.2151 | -0.4790; 0.0584 |
| control | / | / | / | / |
| Type | | | | |
| others | / | / | / | / |
| long-distance migrant | -3.9117 | -4.8799; -2.9224 | -3.4014 | -4.3907; -2.3873 |
| Ground vegetation cover | 0.0253 | -0.0723; 0.1203 | -0.0261 | -0.1163; 0.0664 |
| Shrub cover | 0.1084 | -0.0125; 0.2260 | 0.1057 | -0.0151; 0.2272 |
| Canopy cover | 0.0294 | -0.0855; 0.1478 | -0.0343 | -0.1736; 0.1071 |
| Tree diversity | -0.0235 | -0.1224; 0.0738 | -0.0728 | -0.1704; 0.0261 |
| Deadwood | 0.0259 | -0.0806; 0.1336 | 0.0479 | -0.0782; 0.1735 |
| Road | | | | |
| presence | 0.0190 | -0.1559; 0.1941 | -0.0226 | -0.2317; 0.1800 |
| absence | / | / | / | / |
| Juliandate | -0.1231 | -0.2153; -0.0328 | -0.0155 | -0.1327; 0.1072 |
| Juliandate$^2$ | -0.0524 | -0.1555; 0.0529 | -0.0111 | -0.1405; 0.1184 |
| Year | | | | |
| 2014 | / | / | / | / |
| 2015 | 0.1018 | -0.0801; 0.2828 | 0.0519 | -0.1757; 0.2807 |
| Surface | -0.0502 | -0.1469; 0.0461 | 0.2374 | -0.7693; 1.2876 |
| Surface$^2$ | - | - | 0.9647 | -0.1803; 2.0994 |
| Disturbance × Type | | | | |
| disturbed: long-distance migrant | -0.0873 | -1.5989; 1.3863 | -0.1135 | -1.6684; 1.3940 |
| Disturbance × Year | | | | |
| disturbed: 2015 | 0.1131 | -0.1484; 0.3746 | 0.0966 | -0.2403; 0.4227 |
| Type × Year | | | | |
| long-distance migrant: 2015 | 0.3329 | -0.8118; 1.4819 | 0.3098 | -0.8357; 1.4698 |
| Disturbance × Type × Year | | | | |
| disturbed: long-distance migrant: 2015 | 0.2277 | -1.4639; 1.9970 | 0.2847 | -1.4482; 1.9820 |

/ = reference categories

- = Parameter not tested in the given model

*Distribution = Poisson; link function = natural logarithm; random factors = observer, round and split-plot ID nested within plot ID.*

## FIGURES

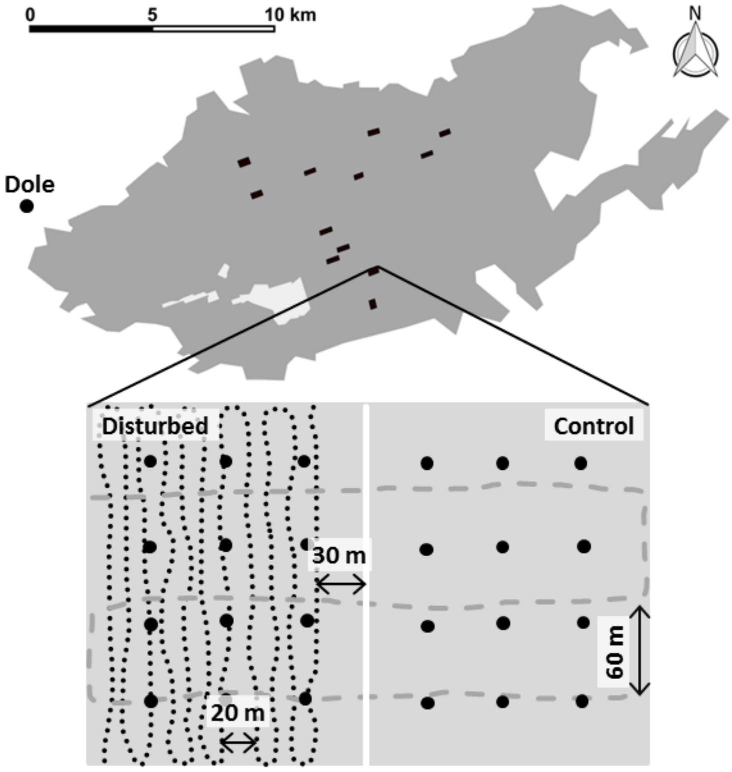

**Figure 1.** Study site “Forêt domaniale de Chaux” (dark grey area) with the twelve different plots (black rectangles) and “Dole” as the next town. Shown in detail is a schematic representation of a study plot with the two split-plots (one disturbed, one control). The black-dotted line represents an example of a disturbance walk (the orientation of this transect was turned 90° between disturbance events). A 30 m buffer was left between the disturbance path and the line separating the split-plots (white-continuous line), to lower a potential confounding effect into the control split-plot. This distance was selected considering the information available in the literature about flight initiation distances (FID) of bird species found in this forest (FID for more than 80% of the species is below 30 m). The grey-dashed line represents the breeding-bird census transect and the individual black dots are vegetation-survey points (for simplicity depicted systematically, although stratified random sampling was used).

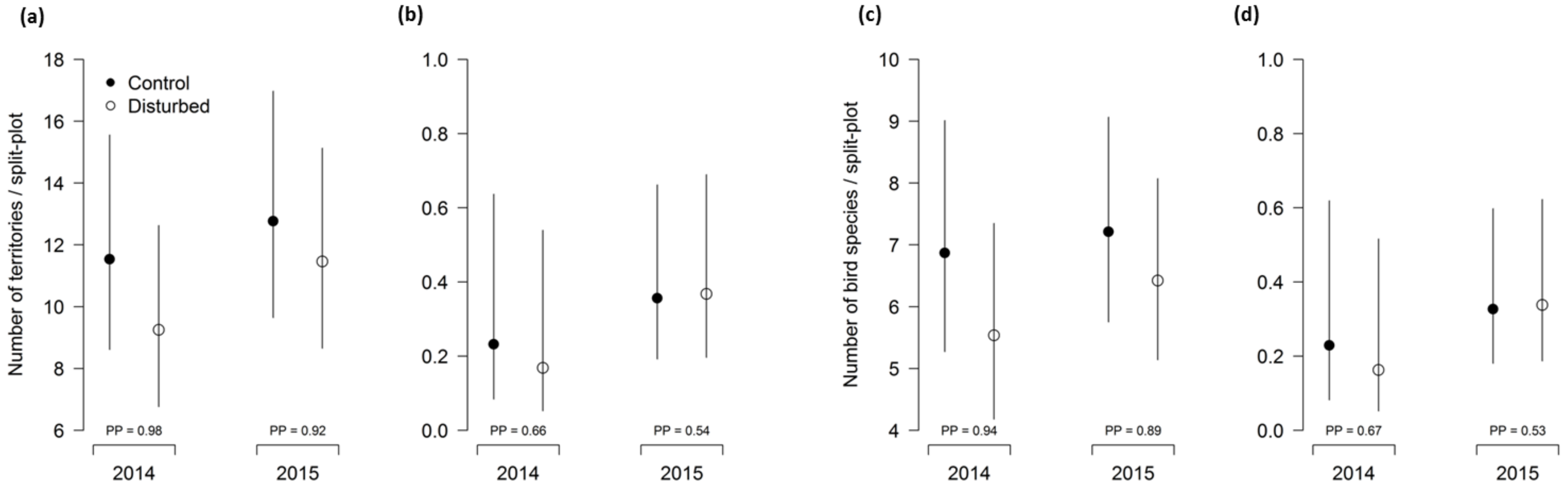

**Figure 2.** Effects of experimental human disturbance on the number of territories (*a*, *b*) and species richness (*c*, *d*) per split-plot (4.7 ha) according to *year* and *migration type*: the graphs (*a*) and (*c*) include only the resident and short-distance migrant species, while the graphs (*b*) and (*d*) only the long-distance migrants. Note the different y-axes. Represented are mean fitted values with 95% credible intervals (table 1) and the posterior probability (PP, from 0.5 to 1) that the difference between disturbed and control split-plots is different from zero. The larger the PP the more likely it is that disturbed and control split-plots are different.

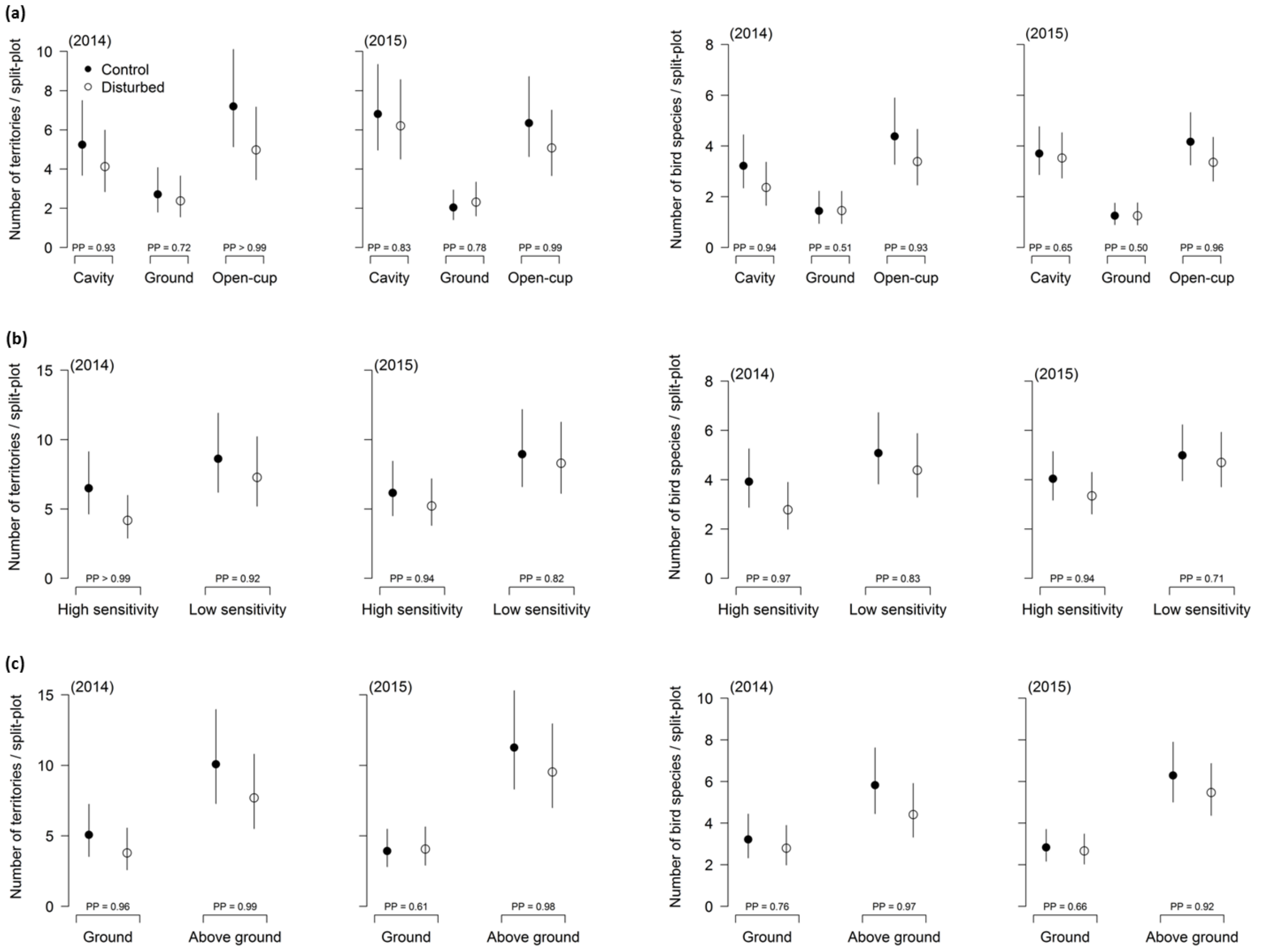

**Figure 3.** Effect of experimental human disturbance on the number of territories and species richness per split-plot (4.7 ha) according to (*a*) nesting-guild (cavity, ground and open-cup nesters), (*b*) sensitivity of the species (high = FID > median FID, low = FID ≤ median FID), and (*c*) foraging guild (ground and above ground) in 2014 and 2015, respectively (only for residents and short distance migrants). Represented are mean fitted values with 95% credible intervals and the corresponding posterior probabilities (PP) that the differences between disturbed and control split-plots are different from zero.

## SUPPORTING INFORMATION

**Table S1.** Bird species recorded during the breeding bird censuses in 2014 and 2015 (n = 34), with their scientific and English names, as well as the abbreviations used for the figures (Electronic supplementary material figure S1 and S2). We also added the threshold dates after which a species was considered as a breeding bird and not a migrant passing through (according to [37]), and the classification into *migration type* (long-distance migrants versus others (residents and short-distance migrants)), *nesting guild* (cavity, ground and open-cup nesters), *foraging guild* (ground, above ground) and *sensitivity* according to flight initiation distance (FID); FID > median FID = high sensitivity, FID ≤ median FID = low sensitivity.

| **Scientific name** | **Abreviation** | **English name** | **Threshold date** | **Typ[1]** | **Nesting guild[1]** | **Foraging guild[1]** | **Sensitivity[2]** |
|---|---|---|---|---|---|---|---|
| *Aegithalos caudatus* | AEGCAU | Long-tailed Tit | 15 April | Others | Open-cup | Above ground | Low |
| *Anthus trivialis* | ANTTRI | Tree Pipit | 25 April | Long-distance migrant | - | - | - |
| *Buteo buteo* | BUTBUT | Common Buzzard | 15 April | Others | Open-cup | Above ground | High |
| *Certhia brachydactyla* | CERBRA | Short-toed Treecreeper | 15 April | Others | Open-cup | Above ground | Low |
| *Coccothraustes coccotraustes* | COCCOC | Hawfinch | 15 April | Others | Open-cup | Above ground | High |
| *Columba palumbus* | COLPAL | Common Wood Pigeon | 15 April | Others | Open-cup | Ground | High |
| *Cuculus canorus* | CUCCAN | Common Cuckoo | 15 April | Others | Open-cup | Above ground | High |
| *Cyanistes caeruleus* | CYACAE | Eurasian Blue Tit | 15 April | Others | Cavity | Above ground | Low |
| *Dendrocopos major* | DENMAJ | Great Spotted Woodpecker | 15 April | Others | Cavity | Above ground | High |
| *Dendrocopos medius* | DENMED | Middle Spotted Woodpecker | 15 April | Others | Cavity | Above ground | na |
| *Dendrocopos minor* | DENMIN | Lesser Spotted Woodpecker | 15 April | Others | Cavity | Above ground | na |
| *Erithacus rubecula* | ERIRUB | European Robin | 15 April | Others | Ground | Ground | Low |
| *Fringilla coelebs* | FRICOE | Common Chaffinch | 15 April | Others | Open-cup | Ground | High |
| *Garrulus glandarius* | GARGLA | Eurasian Jay | 15 April | Others | Open-cup | Above ground | High |
| *Lophophanes cristatus* | LOPCRI | European Crested Tit | 15 April | Others | Cavity | Above ground | Low |
| *Oriolus oriolus* | ORIORI | Eurasian Golden Oriole | 10 May | Long-distance migrant | - | - | - |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Parus major* | PARMAJ | Great Tit | 15 April | Others | Cavity | Above ground | Low |
| *Periparus ater* | PERATE | Coal Tit | 15 April | Others | Cavity | Above ground | Low |
| *Phylloscopus collybita* | PHYCOL | Common Chiffchaff | 15 April | Others | Ground | Above ground | Low |
| *Phylloscopus sibilatrix* | PHYSIB | Wood Warbler | 1 May | Long-distance migrant | - | - | - |
| *Phylloscopus trochilus* | PHYTRO | Willow Warbler | 25 April | Long-distance migrant | - | - | - |
| *Picus canus* | PICCAN | Grey-headed Woodpecker | 15 April | Others | Cavity | Ground | High |
| *Poecile palustris* | POEPAL | Marsh Tit | 15 April | Others | Cavity | Above ground | Low |
| *Regulus ignicapilla* | REGIGN | Common Firecrest | 15 April | Others | Open-cup | Above ground | Low |
| *Regulus regulus* | REGREG | Goldcrest | 15 April | Others | Open-cup | Above ground | Low |
| *Sitta europaea* | SITEUR | Eurasian Nuthatch | 15 April | Others | Cavity | Above ground | High |
| *Streptopelia turtur* | STRTUR | European Turtle Dove | 15 May | Long-distance migrant | - | - | - |
| *Sturnus vulgaris* | STUVUL | Common Starling | 15 April | Others | Cavity | Ground | High |
| *Sylvia atricapilla* | SYLATR | Eurasian Blackcap | 15 April | Others | Open-cup | Above ground | Low |
| *Sylvia borin* | SYLBOR | Garden Warbler | 10 May | Long-distance migrant | - | - | - |
| *Troglodytes troglodytes* | TROTRO | Eurasian Wren | 15 April | Others | Open-cup | Ground | Low |
| *Turdus merula* | TURMER | Common Blackbird | 15 April | Others | Open-cup | Ground | High |
| *Turdus philomelos* | TURPHI | Song Trush | 15 April | Others | Open-cup | Ground | High |
| *Turdus viscivorus* | TURVIS | Mistle Trush | 15 April | Others | Open-cup | Ground | High |

[1]: Bibby et al. 2000; [2]: Díaz et al. 2013; na: no data available, -: not included in this analysis

**Table S2.** Results of the GLMMs testing the effect of experimental disturbance on the number of territories and species richness according to their nesting guild (Long-distance migrants were not included in these analyses, see electronic supplementary material table S1). Represented are the estimates of the effect of each variable with its corresponding 95% credible intervals (CrI).

| | | Number of territories | | Species richness | |
|---|---|---|---|---|---|
| Terms | | Estimate | CrI | Estimate | CrI |
| Intercept | | 0.0483 | -0.3087; 0.3986 | 1.1631 | 0.8530; 1.4874 |
| Disturbance | | | | | |
| | disturbed | -0.2346 | -0.5455; 0.0807 | -0.3098 | -0.7076; 0.0796 |
| | control | / | / | / | / |
| Guild | | | | | |
| | cavity | / | / | / | / |
| | ground | -0.6571 | -1.0120; -0.3006 | -0.8042 | -1.2656; -0.3459 |
| | open-cup | 0.3208 | 0.0554; 0.5891 | 0.3053 | -0.0292; 0.6480 |
| Ground vegetation | | 0.0053 | -0.0793; 0.0899 | -0.0471 | -0.1299; 0.0360 |
| Shrub | | 0.0779 | -0.0266; 0.1821 | 0.0573 | -0.0555; 0.1652 |
| Canopy | | 0.0288 | -0.0787; 0.1341 | -0.0451 | -0.1716; 0.1652 |
| Tree diversity | | -0.0213 | -0.1071; 0.0660 | -0.0732 | -0.1602; 0.0135 |
| Deadwood | | -0.0031 | -0.0978; 0.0932 | 0.0057 | -0.1096; 0.1213 |
| Road | | | | | |
| | presence | 0.0556 | -0.1013; 0.2101 | -0.0081 | -0.2001; 0.1772 |
| | absence | / | / | / | / |
| Julian date | | -0.1178 | -0.2009; -0.0369 | -0.0326 | -0.1363; 0.0759 |
| Julian date$^2$ | | 0.0118 | -0.0826; 0.1046 | 0.0229 | -0.0944; 0.1363 |
| Year | | | | | |
| | 2014 | / | / | / | / |
| | 2015 | 0.2638 | 0.0094; 0.5105 | 0.1381 | -0.1785; 0.4572 |
| Split-plot area | | -0.0043 | -0.0853; 0.0783 | 0.9629 | 0.0471; 1.8548 |
| Split-plot area$^2$ | | - | - | 1.0298 | 0.0228; 2.0199 |
| Disturbance × Year | | | | | |
| | disturbed: 2015 | 0.1387 | -0.2203; 0.4998 | 0.2598 | -0.2037; 0.7344 |
| Guild × Year | | | | | |
| | ground: 2015 | -0.5492 | -0.9891; -0.1033 | -0.2793 | -0.8464; 0.2898 |
| | open-cup: 2015 | -0.3911 | -0.7079; -0.0620 | -0.1872 | -0.5968; 0.2193 |
| Disturbance × Guild | | | | | |
| | disturbed: ground | 0.1008 | -0.4181; 0.6215 | 0.3193 | -0.3427; 0.9934 |
| | disturbed: open-cup | -0.1343 | -0.5497; 0.2759 | 0.0554 | -0.4552; 0.5694 |
| Disturbance × Guild × Year | | | | | |
| | disturbed: ground: 2015 | 0.1248 | -0.5289; 0.7614 | -0.2708 | -1.0868; 0.5439 |
| | disturbed: open-cup: 2015 | 0.0080 | -0.4928; 0.5046 | -0.2207 | -0.8364; 0.3924 |

*/ = Reference categories*

*- = Parameter not tested in this model*

*Distribution = Poisson; link function = natural logarithm; random factors = observer, round and split-plot ID nested within plot ID*

**Table S3.** Results of the GLMMs testing the effect of the experimental disturbance on the number of territories and species richness according to their sensitivity towards humans according to flight initiation distances (only resident and short-distance migrants were included in these analyses, see electronic supplementary material table S1). Represented are the estimates of the effect of each variable with its corresponding 95% credible intervals (CrI).

| | | Number of territories | | Species richness | |
|---|---|---|---|---|---|
| Terms | | Estimate | CrI | Estimate | CrI |
| Intercept | | 0.2675 | -0.0746; 0.6043 | 1.3662 | 1.0782; 1.6631 |
| Disturbance | | | | | |
| | disturbed | -0.4433 | -0.7342; -0.1508 | -0.3408 | -0.7058; 0.0209 |
| | control | / | / | / | / |
| Sensitivity | | | | | |
| | high | / | / | / | / |
| | low | 0.2790 | 0.0353; 0.5234 | 0.2582 | -0.0578; 0.5698 |
| Ground vegetation | | 0.0046 | -0.0799; 0.0872 | -0.0459 | -0.1264; 0.0364 |
| Shrub | | 0.0751 | -0.0311; 0.1820 | 0.0539 | -0.0547; 0.1647 |
| Canopy | | 0.0268 | -0.0801; 0.1385 | -0.0460 | -0.1701; 0.0810 |
| Tree diversity | | -0.0223 | -0.1106; 0.0623 | -0.0762 | -0.1627; 0.0087 |
| Deadwood | | -0.0065 | -0.1021; 0.0897 | 0.0014 | -0.1115; 0.1168 |
| Road | | | | | |
| | presence | 0.0533 | -0.1003; 0.2092 | -0.0150 | -0.1983; 0.1699 |
| | absence | / | / | / | / |
| Julian date | | -0.1218 | -0.2048; -0.0403 | -0.0369 | -0.1414; 0.0713 |
| Julian date$^2$ | | 0.0148 | -0.0808; 0.1104 | 0.0281 | -0.0911; 0.1440 |
| Year | | | | | |
| | 2014 | / | / | / | / |
| | 2015 | -0.0535 | -0.2850; 0.1811 | 0.0338 | -0.2541; 0.3176 |
| Split-plot area | | -0.0060 | -0.0893; 0.0742 | 0.8990 | 0.0159; 1.8099 |
| Split-plot area$^2$ | | - | - | 1.0680 | 0.0500; 2.0681 |
| Disturbance × Year | | | | | |
| | disturbed: 2015 | 0.2777 | -0.0700; 0.6299 | 0.1470 | -0.2918; 0.5915 |
| Sensitivity × Year | | | | | |
| | low: 2015 | 0.0930 | -0.2130; 0.3868 | -0.0484 | -0.4248; 0.3225 |
| Disturbance × Sensitivity | | | | | |
| | disturbed: low | 0.2752 | -0.1038; 0.6549 | 0.1987 | -0.2661; 0.6651 |
| Disturbance × Sensitivity × Year | | | | | |
| | disturbed: low: 2015 | -0.1892 | -0.6374; 0.2749 | -0.0634 | -0.6258; 0.4978 |

*/ = Reference category*

*- = Parameter not tested in this model*

*Distribution = Poisson; link function = natural logarithm; random factors = observer, round and split-plot ID nested within plot ID*

**Table S4.** Results of the GLMMs testing the effect of experimental disturbance on the number of territories and species richness according to their foraging guild (only resident and short-distance migrants were included in these analyses, see electronic supplementary material table S1). Represented are the estimates of the effect of each variable with its corresponding 95% credible intervals (CrI).

| | Number of territories | | Species richness | |
|---|---|---|---|---|
| Terms | Estimate | CrI | Estimate | CrI |
| Intercept | 0.0164 | -0.3425; 0.3790 | 1.1662 | 0.8441; 1.4838 |
| Disturbance | | | | |
| disturbed | -0.2922 | -0.6133; 0.0225 | -0.1403 | -0.5187; 0.2421 |
| control | / | / | / | / |
| Foraging guild | | | | |
| ground | / | / | / | / |
| above ground | 0.6905 | 0.4285; 0.9422 | 0.5933 | 0.2723; 0.9105 |
| Ground vegetation | 0.0051 | -0.0785; 0.0883 | -0.0467 | -0.1286; 0.0360 |
| Shrub | 0.0772 | -0.0290; 0.1829 | 0.0575 | -0.0504; 0.1644 |
| Canopy | 0.0288 | -0.0823; 0.1347 | -0.0452 | -0.1707; 0.0816 |
| Tree diversity | -0.0205 | -0.1054; 0.0660 | -0.0726 | -0.1598; 0.0133 |
| Deadwood | -0.0027 | -0.0997; 0.0927 | 0.0056 | -0.1100; 0.1207 |
| Road | | | | |
| presence | 0.0552 | -0.1005; 0.2127 | -0.0093 | -0.1977; 0.1792 |
| absence | / | / | / | / |
| Julian date | -0.1178 | -0.1995; -0.0333 | -0.0313 | -0.1372; 0.0762 |
| Julian date$^2$ | 0.0101 | -0.0860; 0.1057 | 0.0220 | -0.0929; 0.1379 |
| Year | | | | |
| 2014 | / | / | / | / |
| 2015 | -0.2529 | -0.5274; 0.0191 | -0.1262 | -0.4515; 0.1987 |
| Split-plot area | -0.0051 | -0.0878; 0.0776 | 0.9686 | 0.0647; 1.8545 |
| Split-plot area$^2$ | - | - | 1.0306 | 0.0348; 2.0477 |
| Disturbance × Year | | | | |
| disturbed: 2015 | 0.3240 | -0.0733; 0.7331 | 0.0770 | -0.3888; 0.5528 |
| Foraging guild × Year | | | | |
| above ground: 2015 | 0.3637 | 0.0398; 0.6917 | 0.2076 | -0.1901; 0.5991 |
| Disturbance × Foraging guild | | | | |
| disturbed: above ground | 0.0234 | -0.3597; 0.4042 | -0.1368 | -0.6103; 0.3280 |
| Disturbance × Foraging guild × Year | | | | |
| disturbed: above ground: 2015 | -0.2227 | -0.7073; 0.2558 | 0.0577 | -0.5175; 0.6353 |

*/ = Reference category*

*- = Parameter not tested in this model*

*Distribution = Poisson; link function = natural logarithm; random factors = observer, round and split-plot ID nested within plot ID*

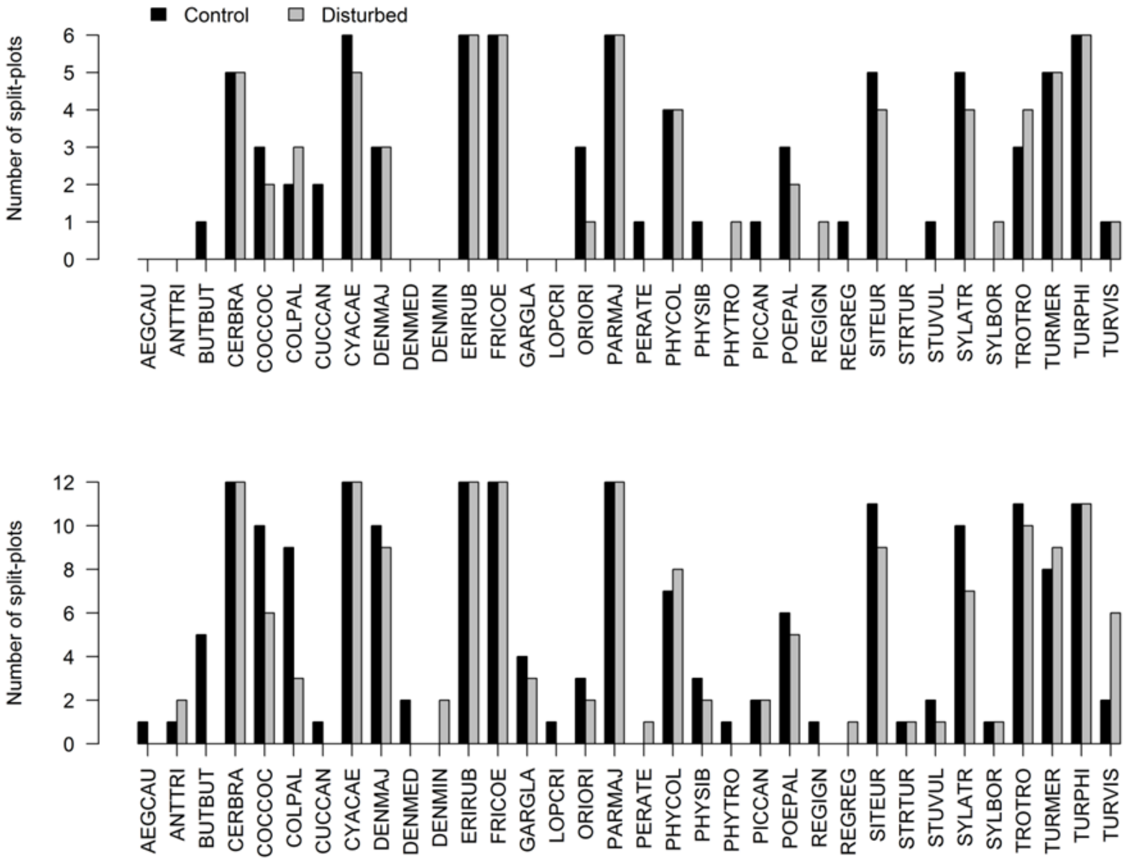

**Figure S1.** Number of split-plots in which each species was detected at least once during the three breeding-bird censuses, separately for disturbed and control split-plots. In 2014 (a) a species could be seen in a maximum of 6 split-plots while in 2015 (b) the maximum was 12. For species abbreviations see electronic supplementary material table S1.

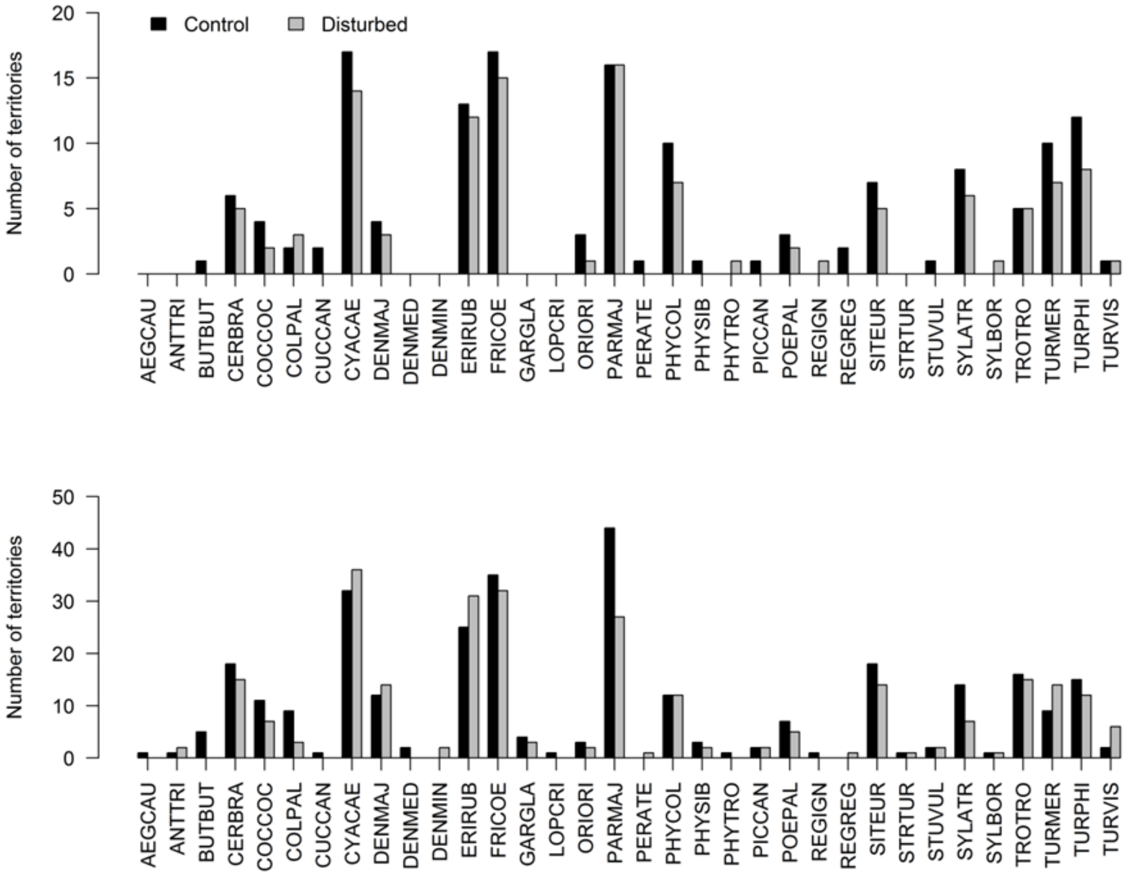

**Figure S2.** Number of territories per species for disturbed and control split-plots in the six plots of 2014 (a) and in the 12 plots of 2015 (b). For each year, the maximum number of territories per species detected in each split-plot out of the three censuses was taken and summed over all split-plots. For species abbreviations see electronic supplementary material table S1.

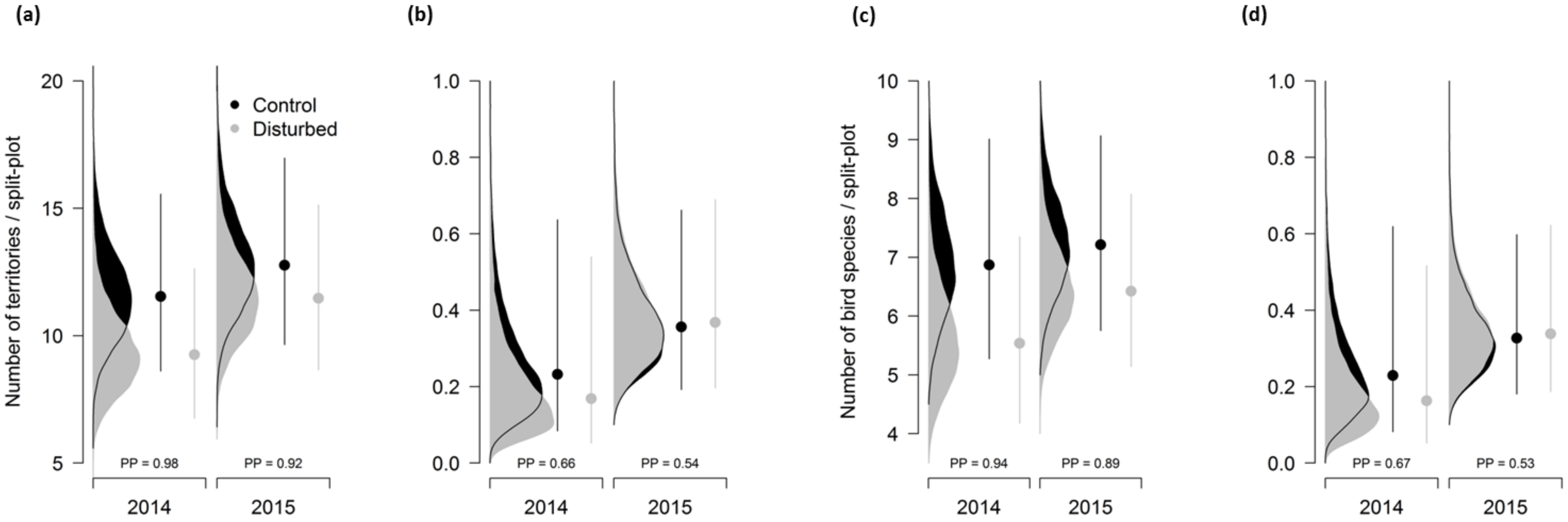

**Figure S3.** Effect of experimental human disturbance on the number of territories (a,b) and species richness (c,d) per split-plot (4.7 ha) according to *year* and *migration type*: the graphs (a) and (c) include only the resident and short-distance migrant species, while the graphs (b) and (d) only the long-distance migrants. Note the different y-axes. Represented are mean fitted values with 95% credible intervals (table 1) as well as the corresponding posterior distributions. The posterior probability (PP) shows the strength of the difference between disturbed and control split-plots.

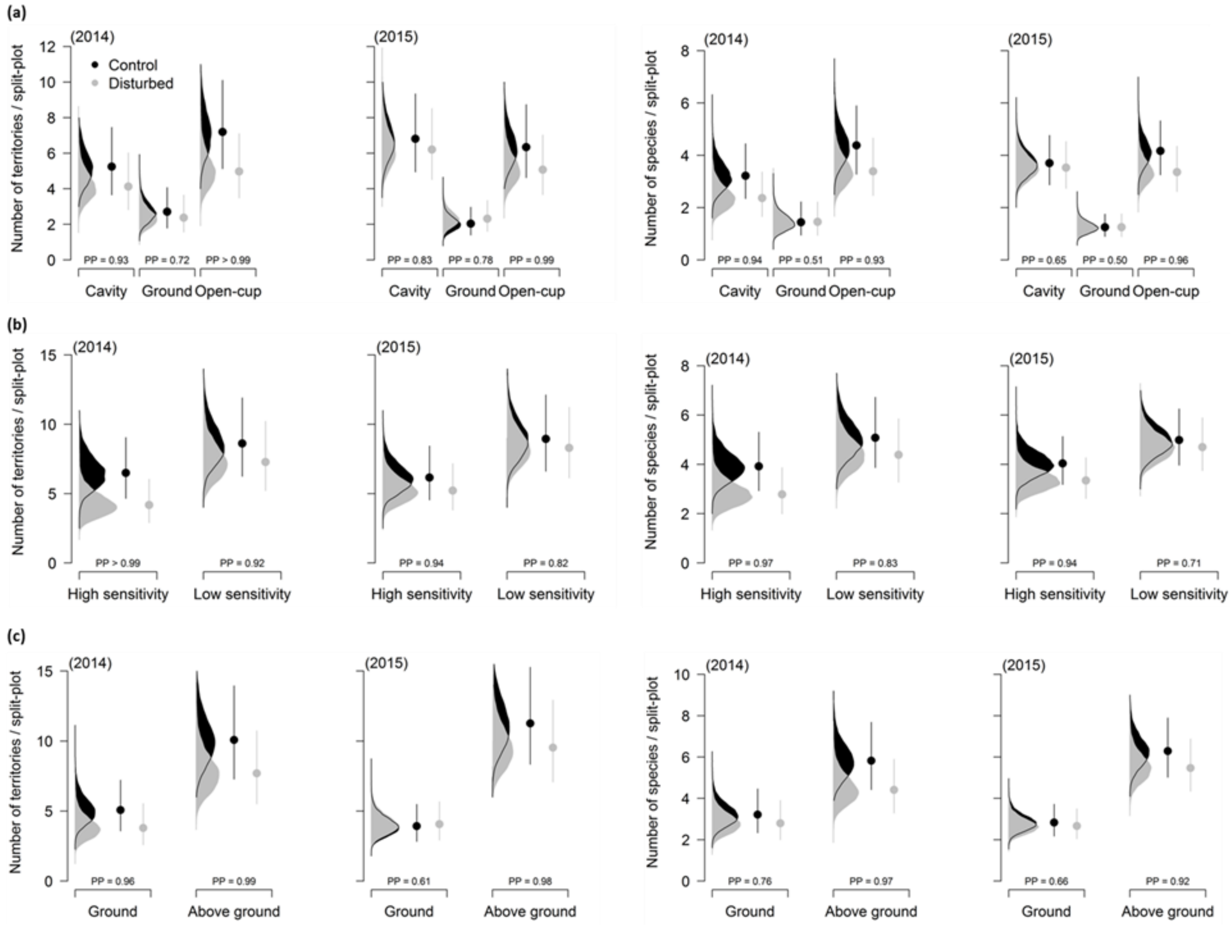

**Figure S4.** Effect of experimental human disturbance on the number of territories and species richness per split-plot (4.7 ha) according to (a) nesting-guild (cavity, ground and open-cup nesters), (b) sensitivity (based on flight initiation distance (FID); high = FID > median FID, low = FID ≤ median FID), and (c) foraging guild (ground and above ground) in 2014 and 2015, respectively (only for resident and short distance migrants). Represented are mean fitted values with 95% credible intervals (Electronic supplementary material table S2-S4) as well as the corresponding posterior distributions and the posterior probability (PP) that the differences between disturbed and control split-plots are different from zero.

# CHAPTER 4

## Human recreation decreases maternal antibodies in bird chicks: an overlooked effect of disturbance

Yves Bötsch, Zulima Tablado and Lukas Jenni

Formatted for the **Journal of Experimental Biology**

Illustration credit: Yves Bötsch

# Human recreation decreases maternal antibodies in bird chicks: an overlooked effect of disturbance

Yves Bötsch[1, 2], Zulima Tablado[1] and Lukas Jenni[1]

[1]Swiss Ornithological Institute, Seerose 1, CH-6204 Sempach, Switzerland

[2]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, CH-8057 Zurich, Switzerland

## ABSTRACT

Outdoor recreational activities are booming nowadays and animals perceive humans as predators, which trigger behavioural and/or physiological reactions (e.g. heart rate increase, activation of the Hypothalamic-Pituitary-Adrenal axis (HPA)). Hormones have been shown to affect the immune system of a given animal and therefore also the amount of maternal antibodies a female transmits to her offspring. A few studies showed that predator presence affected the amount of maternal antibodies deposited into eggs. We wanted to experimentally test, whether human recreation induces the same predator-like effects in breeding birds, and whether these changes in maternal antibody deposition have an effect on the offspring. Great tit chicks of disturbed mothers had lower maternal antibody titres compared to control chicks. The disturbance impact was depending on the vegetation density, as an interaction between disturbance and shrub cover showed, with denser vegetation reducing the negativ impact of disturbance. The hatching success of great tits was positively correlated with the amount of maternal antibodies deposited. All of the aforementioned findings do not hold for blue tits, but they are apparently mainly affected by the presence of great tits. Chicks which received more maternal antibodies were heavier at an early stage of life, but this positive effect dilutes towards fledging.

Through this dilution of the positive effect of maternal antibodies during chick growth, body mass gain was negatively correlated with maternal antibody titres, but this does not imply a cost of maternal antibodies. We suggest that our findings can be explained through an activation of the HPA-axis, mainly an increase in corticosterone, which is known to have an immunosuppressive action. Therefore human disturbance can negatively affect the survival of chicks at an early life stage, when they are mainly relying on maternal antibodies, and finally this could reduce breeding success and therefore the parents' fitness.

**Key words:** Outdoor activities, human disturbance, immunology, trans-generational effects, *Parus major*, *Cyanistes caeruleus*

## INTRODUCTION

Human sport activities and recreation often occur in nature and may negatively impact wildlife (Larson *et al.* 2016; Bötsch, Tablado & Jenni 2017). Humans are often perceived as predators by wildlife (Frid & Dill 2002), which usually react with behavioural (e.g. flight response; Blumstein, 2010) and/or physiological responses, such as the activation of the hypothalamic-pituitary-adrenal-axis (HPA-axis; Almasi et al., 2015; Fowler, 1999; Thiel et al., 2008). If these behavioural and physiological responses occur frequently they may lead to long term increases in stress levels, which might compromise health and fitness (Tablado & Jenni 2017). For instance, stressed individuals tend to have increased levels of circulating glucocorticoid hormones (Saino *et al.* 2003, 2005; Hayward & Wingfield 2004), which in turn have been shown to have an immunosuppressive function (Råberg *et al.* 1998) and lead to a reduced amount of circulating immunoglobulins (Bourgeon & Raclot 2006; Hargitai *et al.* 2009; Gao, Sanchez & Deviche 2016). These altered levels of glucocorticoids and antibodies can then have trans-generational effects if they are transmitted to the offspring (Rubolini *et al.* 2005; Saino *et al.* 2005). In the case of birds, stressful events occurring during the egg-laying phase may therefore have important impacts on chicks, through stressed mothers depositing higher levels of the main glucocorticoid hormone (i.e. corticosterone in birds) and altered levels of antibodies in the eggs (Saino *et al.* 2005; Hargitai, Prechl & Török 2006; Hargitai *et al.* 2009; Morosinotto *et al.* 2013).

Maternal Antibodies (matAbs) represent the mother's entire repertoire of antibodies against antigens she was exposed to in her life (Lemke, Hansen & Lange 2003; Lemke, Coutinho & Lange 2004) and freshly hatched chicks depend almost entirely on these matAbs for their immune responses up to the first weeks of their life (Grindstaff, Brodie & Ketterson 2003; Pihlaja, Siitari & Alatalo 2006; Gasparini *et al.* 2009). Therefore, the amount of matAbs deposited into the eggs, positively correlates with chick survival and growth (Pihlaja, Siitari & Alatalo 2006; Grindstaff 2008).

The aim of this study was then to experimentally test, whether human recreational activities during the early breeding season, would trigger anti-predator physiological reactions in breeding females which in turn would result in lower matAb deposition into eggs (measured later in newly hatched chicks). Moreover, we wanted to examine whether this altered deposition of matAbs in eggs was correlated with lower hatching success and chick growth. We predicted that chicks hatched in areas with higher human frequentation would have a lower amount of matAbs compared to broods in control areas with no human frequentation. We also expected that the reduced amount of matAbs would be correlated with reduced hatching success and lower growth rate compared to control chicks.

## MATERIALS AND METHODS

### Study area and experimental design

The study was carried out in the early breeding season of 2014 and 2015 in the “Forêt domaniale de Chaux” in France (47°05’N, 05°40’E), which is a forest consisting primarily of pedunculate oaks (*Quercus robur*) and European hornbeam (*Carpinus betulus*) and whose harvest is managed by the “Office National des Forêts” (ONF). We worked in 12 plots (mean size 9.2 ha, range: 7.5-13 ha), which fulfilled the following criteria: (1) homogeneous vegetation structure, (2) well separated from each other (> 600 m), to avoid spill-over effects, (3) no timber harvesting in the study plots during the entire study period, and (4) location far away from urban settlements (> 9 km) to reduce other sources of disturbance. In early February 2014 we installed 210 nest boxes (Schwegler, Type B1, with 32 mm entrance diameter) for small cavity nesters (mainly tit species) at a density of about two nest-boxes per ha (i.e. not exceeding the natural breeding density of tits; Krebs, 1971). After the first breeding season, in autumn 2014, we cleaned and removed the nest boxes and installed them again in February 2015, to have twice the same experimental setup for the two study years.

Each plot was divided into two and each split-plot either received an experimental-disturbance treatment (during early spring; 7 March – 22 April in 2014 and 2015, see also Fig. 1) or served as control. The treatment consisted in mimicking a common human recreational activity (i.e. people hiking in the forest), by having groups of 2 to 3 people walking back and forth through the split-plots on a regular mower-pattern transect (distance between walking lines 20 m, for details see Bötsch et al., 2017). This treatment was applied one to three times every day and people were carrying a loudspeaker (Hama, smartphone speaker, power 3W, with a Samsung digital audio player F3) broadcasting human conversation (e.g. TV shows or audio books) at an average volume level of 60 dB at 1 m distance (Byrne *et al.* 1994; Hacki 1996) to reproduce normal hiking conversation.

We varied the direction of the mower-pattern transects by 90° between visits, as well as the time of the day of the visit, to maintain unpredictability. Due to man power limitations in 2014 we could only apply the treatment to 6 plots, while in 2015 the treatment was applied to all 12 plots. The six split-plots which were "disturbed" in 2014 became control split-plots the next year and vice versa. This experiment was approved by the local authorities and the French ringing scheme C.R.B.P.O. "Centre de Recherches sur la Biologie des Populations d'Oiseaux" (permit number 2014157-0012 of the "Direction Régionale de l'Environnement, de l'Aménagement et du Logement de Franche-Comté" and permit number 15006 for blue- and great tits (*Cyanistes caeruleus* and *Parus major*, respectively) for 2014-2016 from the C.R.B.P.O., for details see also Bötsch et al., 2017).

### Blood sampling

From 20 April all 210 nest boxes were checked every second week. Nest boxes with full clutches were checked daily around the estimated hatching date to determine the exact hatching date. Blue- and great tit chicks were blood sampled at the age of six days (mean=6.2 days, sd=0.6), when they were large enough to bear blood-sampling but still have underdeveloped immune systems, thus still maintaining the matAb titres (Grindstaff 2008; Hasselquist & Nilsson 2009; King, Owen & Schwabl 2010). All chicks of a brood were weighed to the nearest 0.1g with a digital balance and a subsample of 1 - 5 chicks per brood were blood sampled through vein puncturing with a 0.3 mm syringe at the metatarsus and collecting the effluent blood with a heparinized capillary. Up to 40 µl were sampled and directly centrifuged in the field for 5 minutes at 8000 rpm (Hettich, EBA 3S) to separate the plasma from the cells. Both blood cells and plasma were then stored in liquid nitrogen or deep freezers (-20°C) until analysis.

When chicks were 15 days old, they were weighed again and ringed with an aluminium ring from the C.R.B.P.O. The number of ringed chicks per nest box served as surrogate for the number of fledglings, since chick mortality at this stage is assumed to be low (Lindén, Gustafsson & Pärt 1992; Oddie 2000). In 2015 we additionally marked blood-sampled chicks with small-coloured elastic bands and therefore could identify them individually when ringing. Therefore the analysis of growth and weight gain is only based on the second study year (2015).

### Maternal antibody measurement

MatAbs were measured in the lab using an Enzyme-linked Immunosorbent Assay (ELISA). Plates with ninety-six-wells were coated with an anti-chicken IgG (Sigma C-6409) diluted 1:180 in a 0.05M carbonate buffer (pH 9.6) and incubated overnight at 4°C. Afterwards the plates were washed three times with PBS (Phosphate-buffered saline)/Tween20 (3x 250 µl) and blocked (for at least one hour at room temperature) with 250 µl 1% BSA (Bovine serum albumin) diluted in 0.01M PBS/Tween20 (from now on referred as BSA-PBS/Tween20). After being washed again, the test plasma was added to the wells. The plasma samples (3 µl) of blue tits were diluted 1:100 and those of great tits 1:500. For each sample 100 µl were added (in duplicates) to the wells (Diluent: BSA-PBS/Tween20), two wells were filled with the BSA-PBS/Tween20 buffer, as blanks and two wells were filled with an 1:160,000 diluted chicken plasma as internal control (Diluent: BSA-PBS/Tween20). On the same plate we added in duplicates a standard dilution series of a chicken plasma-pool: pure buffer as negative control and seven dilutions from 1:10,000 up to 1:640,000 (Diluent: BSA-PBS/Tween20). All plasma-sample measures were then expressed relative to this standard in units per µl. The plates were incubated for three hours at room temperature and afterwards washed again three times with 250 µl PBS/Tween20. Then 100 µl of 1:3000 diluted (BSA-PBS/Tween20) peroxidase-conjugated rabbit anti-chicken-IgG (Sigma A9046) was added to each well, except the blanks where 100 µl BSA-PBS/Tween20-buffer was added instead. The plates were incubated over night at 4°C and again washed three times with 250 µl PBS/Tween20. Then 100 µl of the substrate solution was added. This substrate solution consisted of 20 ml citrate buffer (pH 4), 80 µl of 1:40 diluted 30% hydrogen peroxide (diluted in distilled water) and 200 µl ABTS (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulphonic acid)). The plate was then put for 15 min on a plate shaker and the absorbance measured with an ELISA plate reader at 405 nm (BIO-RAD, Benchmark Microplate Reader). For all the consecutive analyses the mean of the duplicate measures were computed.

### Vegetation mapping

In June 2015 we conducted a vegetation survey. With a stratified random sampling we distributed one survey point per 0.5 ha (n=210) and measured the following habitat variables: ground cover (%) on a 2x2m area, shrub cover (%) on a 3x3m area, number of trees (diameter at breast height > 5 cm) per species and standing deadwood on a 8x8m area and canopy cover (%, by looking straight up to the canopy and estimating the amount of covered sky by the canopy in the observer’s visual field). The vegetation measures were averaged within each split-plot, and from these means we computed a Principal Component Analysis (PCA). Since the first axis of the PCA explained 59% percent of the variation by itself, we used only the first axis score for further analyses.

### Statistical analyses

Only first broods whit at least one egg laid during the experimental disturbance period were used (see Fig. 1). Predated broods were excluded from all analyses since they do not reflect the effect of human disturbance. All analyses were done using the lme4-package in R 3.3.0 (Bates *et al.* 2015; R Core Team 2016). To investigate the potential effect of the experimental disturbance on matAbs in great- and blue tit chicks, we used two linear mixed models (Table 1). MatAb measures were log (natural logarithm) transformed to fulfil model assumptions. As explanatory variables we included the two-level factor *disturbance* (disturbed vs. control split-plots), the vegetation, as the first principal component of the vegetation PCA (*First principal component (vegetation)*) and the interaction between disturbance and vegetation. Furthermore we tested for the linear and quadratic effect of laying date of the first egg (*Julian date first egg, Julian date first egg*$^2$), the distance to the nearest gravel road (*Distance to road [m]*), the *chick age* and the difference in body mass between the measured chick and its heaviest sibling (*Difference in body mass to heaviest sibling [g]*), as a surrogate for hatching order. To account for the stressful effects of competition, we included the number of occupied nest boxes (independent of the species) within a 100m radius (*total number of occupied neighbouring nest boxes*), as a nest-box specific measure of breeding density. Given than among tits, great tits appear to have the most dominant behaviour we also tested for the proportion of nest boxes per split-plot that were occupied by great tits (i.e. number of nest boxes occupied by great tits divided by all occupied nest boxes occupied in a split-plot; *relative GT occupancy*).

For the analyses investigating the relationship between matAbs and hatching success in both great and blue tits, we used two generalized linear mixed models with a binomial error distribution (Table 2), in which hatching success was introduced as number of hatchlings divided by the number of eggs (clutch size). Since not all broods were sampled for matAbs at the same exact age, the effect of matAbs was included in this model as the residuals of the linear model regressing average matAb titres per brood against average chick age per brood (with th); *Residuals of mean Ab titre*). We also controlled for the effect of *Relative GT occupancy*, *total number of occupied neighbouring nest boxes*, *Julian date first egg, Julian date first egg*$^2$*, Distance to road [m]* and *First principal component (vegetation)*.

In the four aforementioned models we accounted for the non-independence of the different years and nest boxes by including the random factors year and a random factor nest-box-ID, nested within split-plot-ID, nested within plot-ID. To account for the non-independence of matAb measures between plates and runs (several plates per lab run), we included in the first two models a random factor plate-ID, nested within batch-ID. For the two models on hatching success, we accounted for this non-independence of plates with the same random factors already in the linear model where we computed the residuals (*Residuals of mean Ab titre*).

In order to examine the relationship between matAbs and chick growth we performed two different types of models (Table 3). First, we modelled the variations in chick growth with matAbs by including an interaction between the natural logarithm of chick age and the matAb titre (*MatAb titre [units µl-1] × log (Chick age)*). We also accounted for the effect of *Relative GT occupancy, Total number of occupied neighbouring nest boxes, Julian date first egg*, *Julian date first egg*$^{2}$, *Distance to road[m]* and vegetation (*First principal component (vegetation)*). Moreover, we also tested for the effect of brood size on growth by including the number of fledged chicks (*Number of fledglings*), and the effect of time of the day on chick mass (*Minutes since sunrise*) both alone and in interaction with the natural logarithm of chick age (*Minutes since sunrise × log (Chick age)*). To account for the non-independence of multiple chick measures, we included as random factors chick-ID nested within nest-box-ID, nested within split-plot-ID, nested within plot-ID. Since these data were available only in 2015, it was not necessary to introduce the year effect. Secondly, we did a similar model with the same explanatory variables, but with body mass gain per day as response variable. This variable was calculated as the difference in body mass between the two measures divided by the difference in chick age (days) and followed a normal distribution. Since in this case chick age was already offset in the response variable, the two interactions from the precedent model ceased. Consequently the matAb titre (*MatAb titre [units µl-1]*) was now included as additive factor, whereas daytime (*Minutes since sunrise*) was not included anymore as we computed the change in body mass over several days and the random factor chick-ID was not necessary anymore.

For allowing proper interpretation of the models, especially when including an interaction, we computed 95% credible intervals (CrI) and posterior-probabilities using a Bayesian framework. Therefore we simulated 10,000 random samples from the joint posterior distribution of the model parameters using the sim-function from the arm-package (Gelman & Su 2015) and computed the 95% CrI (lower and upper limit, 2.5% and 97.5% quantiles, respectively). For the posterior probabilities we computed the mean of the 10,000 differences between “disturbed” and “control” estimates, which were different from zero (either larger or smaller than zero). The resulting probability lies between 0.5 and 1 and is a measure for the strength of the difference, with larger values representing a stronger difference.

## RESULTS

The experimental disturbance resulted in a reduction of matAbs in young nestlings, compared to control broods, in great tits, but not in blue tits (Fig. 2, Table 1). The interaction between disturbance and the first principal component (vegetation) for great tits showed that vegetation density (the *First principal component (vegetation)* is highly correlated with shrub-cover) modulated the impact of disturbance on matAb transmission (Fig. 3, Table 1). In the case of the blue tit, we did not find an effect of the experimental disturbance, but there seemed to be a negative effect of the relative density of breeding great tits on matAbs (Fig. 4, Table 1). For both species Julian date of the first egg had a positive effect on matAb titres while the difference to the heaviest sibling had a negative effect (Table 1). We also found a positive effect of chick age on the matAb titre for great tits (Table 1).

We found a positive correlation between matAb titres and hatching success for great tits, but not for blue tits (Fig. 5 and Table 2). For great tits, we also found that the proportion of nest boxes occupied by conspecifics and the total number of occupied nest boxes in the near surroundings both had a negative effect on hatching success (Table 2).

For both species we found that matAbs were positively correlated with chick body mass (Fig. 6 A,B and Table 3). At day six larger chicks had higher matAb titres, but these positive relationships disappeared towards fledging (Fig. 6 A,B) due to a lower variability in fledgling body mass. This translated in an overall lower body mass gain in chicks with higher matAb titres as shown in the negative correlation between body mass gain per day and matAb titres at day six (Fig. 6 C,D and Table 3). We also found a quadratic effect of Julian date of the first egg on body mass gain for both tit species, which implies that the earliest and latest broods show a higher weight gain per day as the broods in the middle of the season (Table 3).

## DISCUSSION

In this study we showed that experimental human disturbance during egg-laying reduced antibody titres in great tit chicks. We hypothesize that human disturbance increased circulating corticosterone in laying females, reduced their antibody titres through the immunosuppressive action of corticosterone, and in turn reduced the amount of antibodies transferred to eggs. We could not confirm the exact mechanism since, to prevent nest abandonment and reduce additional sources of stress (i.e. beyond the experimental disturbance), we could not capture laying females to measure their corticosterone levels. However, corticosterone is known to be released in stressful situations, including disturbance by humans (Müllner, Linsenmair & Wikelski 2004; Almasi *et al.* 2015). The immunosuppressive effect of corticosterone has been shown by several authors (see for example Rubolini et al., 2005; Saino et al., 2003; Stier et al., 2009). Thus, we think that this physiological cascade is a likely mechanism through which our experimental disturbance resulted in lower matAb titres in chicks. In line with others, we also found an effect of laying order on matAb titres, with later hatched chicks (assuming representing the laying order) having lower matAb titres (Hayward & Wingfield 2004; Love *et al.* 2008).

Moreover, we found that the effect of human disturbance was not homogeneous throughout space, but that it depended on the type of vegetation. We found that higher amounts of shrub vegetation lowered the negative impact of the disturbance on matAb titres. Vegetation may have acted as protective shield, buffering the stress caused by human presence (Tablado & Jenni 2017). Interestingly, we did not find the same pattern in blue tits. In this case we did not find an effect of the disturbance treatment or interaction with vegetation on matAbs in nestlings, but we found an effect of the relative abundance of great tits in the split-plot. A plausible explanation for this would be that great tits are an important biological stressor for blue tits, and thus, the presence of great tits is overriding or obscuring the negative effects of human presence. Great tits are dominant over blue tits. Our nest boxes had an entrance diameter which permitted both species to enter the nest box and great tits have been shown to supress the settlement of blue tits (Löhrl 1977).

We also found a positive correlation between matAb titres and the hatching success for great tits. This could be due to several reasons. MatAbs might protect from infections, which would otherwise cause the death either of the embryo or the freshly hatched young. Note that we counted the number of hatchlings at day six, and therefore we do not know whether failed eggs or dead young chicks caused the difference between clutch size and number of “hatchlings”. Additionally matAbs could be correlated with other non-measured variables. That is, chicks with lower matAb titres could be linked to more stressed mothers which are likely to have laid lower quality eggs and/or transmitted more corticosterone into eggs, thus resulting in lower hatching success (Hayward & Wingfield 2004).

Similarly, we found a positive correlation of matAbs and body mass at day six, which was lost at later ages, which translated into reduced body mass gain with time in larger freshly hatched chicks. This coincides with the findings of Ismail et al., (2015). They suggested a cost of maternal antibodies on body mass gain. However, in our case it seems to be due to chicks with larger amounts of matAbs being also the largest chicks and thus to gain less mass to reach fledging body mass than smaller chicks (see Fig 6. C,D).

Whether human recreation trans-generationally negatively affects birds, through changes in matAb deposition clearly also depends on several modulators. These include the disturbance intensity, the type of human recreation activity, the mother’s stress tolerance, e.g. habituation towards humans and, as we could show, the vegetation density, as denser vegetation lowers the disturbance impact. There are also other factors than disturbance, driving matAb titres, like body condition of the mother (e.g. food availability), clutch size or the health status of the mother in general (Klasing & Leshchinsky 1998; Grindstaff, Brodie & Ketterson 2003; Boulinier & Staszewski 2008; Hasselquist & Nilsson 2009).

Up to now effects of human disturbance on reproduction mainly occurred through prevention of feeding, interruption of incubation or indirectly via noise (Safina & Burger 1983; Zanette *et al.* 2011; Schroeder *et al.* 2012). In this study, we could show that human disturbance affects matAb titres and that these affect hatching rate, body mass gain and therefore probably also survival (see Pihlaja et al., 2006). If the disturbance would continue through the entire breeding season, potentially the catch up in body mass, as we found, would not be possible. Therefore we propose that this cascade of stress, via corticosterone, and reduced matAb titres, depicts a new way of how human disturbance affects reproduction.

## ACKNOWLEDGMENTS

We thank all the field assistants who helped walking through the plots and collected blood samples from the chicks, in alphabetical order: C. Arnace, R. Baffoin, M. Crespo Ballester, S. Bühler, B. Garde, L. Gillespie, M. Hitt, F. Le Bagousse, H.F. Lemke, F. Leugger, N. Mortier, J. Nouri, M. Quetstroey, A. Rouméas, J. Vasseur. We thank M. Romanski and J.L. Dessolin from the Office National des Forêts (ONF) as well as B. Dorbani from the DREAL (Direction Régionale de l'Environnement, de l'Aménagement et du Logement de Franche-Comté) for permitting us to do this study in the Forêt domaniale de Chaux. We thank R. Scheifler from the University Franche-Comté, Besançon, who advised us on local affairs and permits during the preparation of this study and O. Dehorter from the C.R.B.P.O. for giving us the permit to work on the two tit species. We thank B. Almasi, S. Jenni-Eiermann and J. Olano-Marin for their support and guidance in the lab.

## TABLES

**Table 1: Model estimates with their corresponding 95% credible intervals (CrI) of the matAb model examining the effect of experimental disturbance.**

The reference categories are nests from control split-plots. The factor level of each categorical variable is given in parenthesis. GT: Great tit, BT: Blue tit.

| Variable | GT estimate | GT 95% CrI | BT estimate | BT 95% CrI |
|---|---|---|---|---|
| Intercept | 5.402 | 5.120; 5.674 | 4.030 | 3.659; 4.413 |
| First principal component (vegetation) | -0.007 | -0.139; 0.121 | -0.076 | -0.300; 0.143 |
| Disturbance (disturbed) | -0.127 | -0.279; 0.025 | 0.053 | -0.201; 0.308 |
| Julian date first egg | 0.212 | 0.099; 0.328 | 0.178 | 0.006; 0.346 |
| Julian date first egg $^2$ | -0.054 | -0.123; 0.015 | -0.042 | -0.182; 0.102 |
| Distance to road [m] | -0.010 | -0.099; 0.078 | 0.052 | -0.080; 0.184 |
| Difference in weight to heaviest sibling [g] | -0.223 | -0.265; -0.179 | -0.106 | -0.175; -0.035 |
| Chick age | 0.130 | 0.020; 0.244 | 0.118 | -0.087; 0.320 |
| Relative GT occupancy | -0.045 | -0.157; 0.072 | -0.224 | -0.478; 0.022 |
| Total number of occupied neighbouring nest boxes | -0.003 | -0.087; 0.080 | 0.058 | -0.080; 0.189 |
| First principal component (vegetation) × Disturbance (disturbed) | 0.243 | 0.068; 0.421 | 0.089 | -0.149; 0.328 |

*Distribution: normal; random factors: year and nest box ID nested within split-plot ID nested within plot ID and plate ID nested within batch ID.*

**Table 2: Model estimates with their corresponding 95% credible intervals (CrI) for the analysis of hatching success depending on matAbs.** GT: Great tit, BT: Blue tit.

| Variable | GT estimate | GT 95% CrI | BT estimate | BT 95% CrI |
|---|---:|---:|---:|---:|
| Intercept | 2.651 | 2.302; 2.998 | 2.050 | 1.636; 2.471 |
| First principal component (vegetation) | -0.049 | -0.327; 0.234 | -0.054 | -0.375; 0.267 |
| Residuals of mean Ab titre | 0.223 | -0.018; 0.462 | -0.172 | -0.507; 0.170 |
| Relative GT occupancy | -0.348 | -0.665; -0.033 | -0.172 | -0.589; 0.243 |
| Total number of neighbouring occupied nest boxes | -0.243 | -0.471; -0.005 | 0.158 | -0.204; 0.521 |
| Julian date first egg | -0.045 | -0.345; 0.262 | 0.063 | -0.278; 0.412 |
| Julian date first egg $^2$ | -0.018 | -0.225; 0.189 | -0.088 | -0.375; 0.193 |
| Distance to road [m] | 0.177 | -0.074; 0.427 | 0.050 | -0.289; 0.379 |

*Distribution: binomial, link function logit; random factors: year and nest box ID nested within split-plot ID nested within plot ID.*

**Table 3: Estimates of the body mass development and body mass gain models depending on matAb titres with their corresponding 95% credible intervals (CrI) for great tits (GT) and blue tits (BT).**

| Variable | GT estimate | GT 95% CrI | BT estimate | BT 95% CrI |
|---|---|---|---|---|
| **Effect on body mass development** [a] | | | | |
| Intercept | -12.429 | -13.505; -11.322 | -6.275 | -8.219; -4.365 |
| First principal component (vegetation) | -0.078 | -0.239; 0.080 | 0.011 | -0.331; 0.352 |
| MatAb titre [units $\mu l^{-1}$] | 0.020 | 0.016; 0.024 | 0.053 | 0.027; 0.079 |
| Log (Chick age) | 11.603 | 11.127; 12.070 | 7.013 | 6.212; 7.838 |
| Minutes since sunrise | -0.104 | -0.643; 0.426 | 0.178 | -0.625; 0.966 |
| Relative GT occupancy | 0.095 | -0.057; 0.246 | 0.115 | -0.214; 0.448 |
| Total number of occupied neighbouring nest boxes | 0.067 | -0.089; 0.222 | -0.087 | -0.401; 0.227 |
| Julian date first egg | 0.150 | -0.008; 0.302 | -0.026 | -0.324; 0.265 |
| Julian date first egg $^2$ | -0.036 | -0.167; 0.097 | -0.386 | -0.698; -0.082 |
| Number of fledglings | 0.017 | -0.135; 0.170 | -0.089 | -0.384; 0.211 |
| Distance to road [m] | -0.049 | -0.200; 0.105 | -0.058 | -0.375; 0.254 |
| MatAb titre [units $\mu l^{-1}$] × log (Chick age) | -0.007 | -0.009; -0.006 | -0.021 | -0.032; -0.010 |
| Minutes since sunrise × log (Chick age) | 0.153 | -0.076; 0.387 | -0.147 | -0.483; 0.199 |
| **Effect on body mass gain per day** [b] | | | | |
| Intercept | 1.213 | 1.148; 1.277 | 0.733 | 0.616; 0.854 |
| First principal component (vegetation) | -0.010 | -0.043; 0.022 | -0.020 | -0.074; 0.033 |
| MatAb titre [units $\mu l^{-1}$] | -0.001 | -0.001; -0.001 | -0.003 | -0.005; -0.002 |
| Relative GT occupancy | -0.001 | -0.031; 0.028 | -0.011 | -0.063; 0.043 |
| Total number of occupied neighbouring nest boxes | -0.022 | -0.051; 0.007 | -0.005 | -0.066; 0.056 |
| Julian date first egg | -0.009 | -0.038; 0.021 | 0.042 | -0.017; 0.099 |
| Julian date first egg $^2$ | 0.026 | 0.002; 0.050 | 0.079 | 0.020; 0.139 |
| Number of fledglings | -0.012 | -0.040; 0.017 | 0.028 | -0.032; 0.088 |
| Distance to road [m] | 0.013 | -0.017; 0.041 | 0.034 | -0.023; 0.092 |

[a] *Distribution: normal; random factors: chick ID nested within nest box ID nested within split-plot ID nested within plot ID.*

[b] *Distribution: normal; random factors: nest box ID nested within split-plot ID nested within plot ID.*

## FIGURES

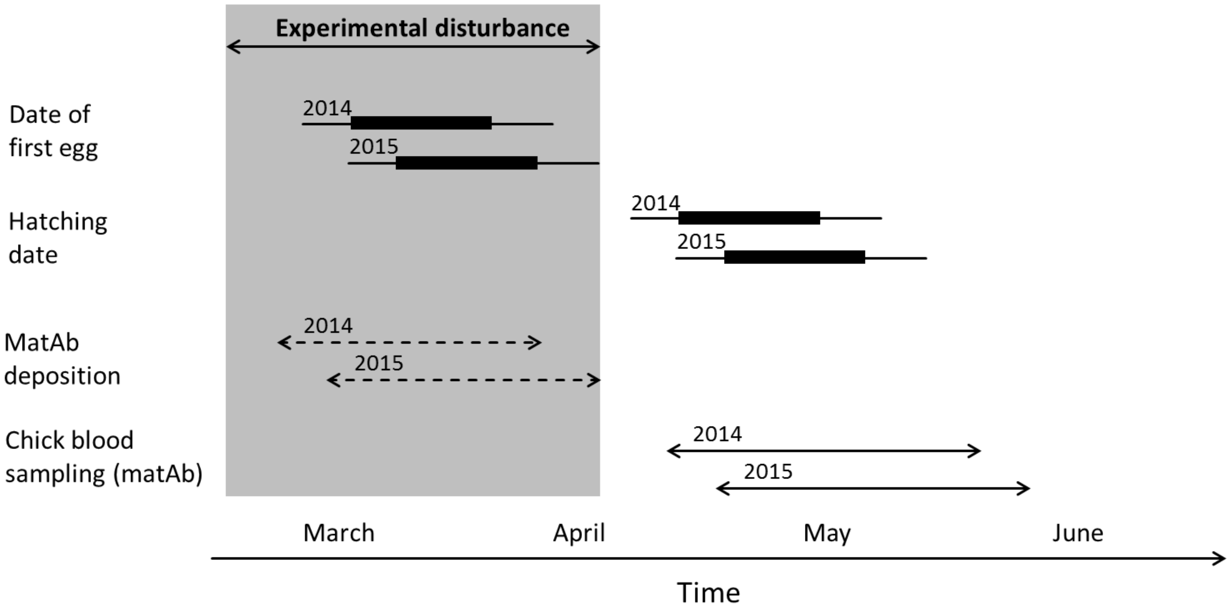

**Fig. 1. Diagram of the temporal overlap of experimental disturbance (grey square) and breeding stages (egg-laying and hatching).** Note that the deposition of the maternal antibodies (matAb) in eggs overlaps with the disturbance phase, whereas hatching and the following feeding period do not. Breeding in the second study year (2015) was about 1 week later than in the first study year (2014).

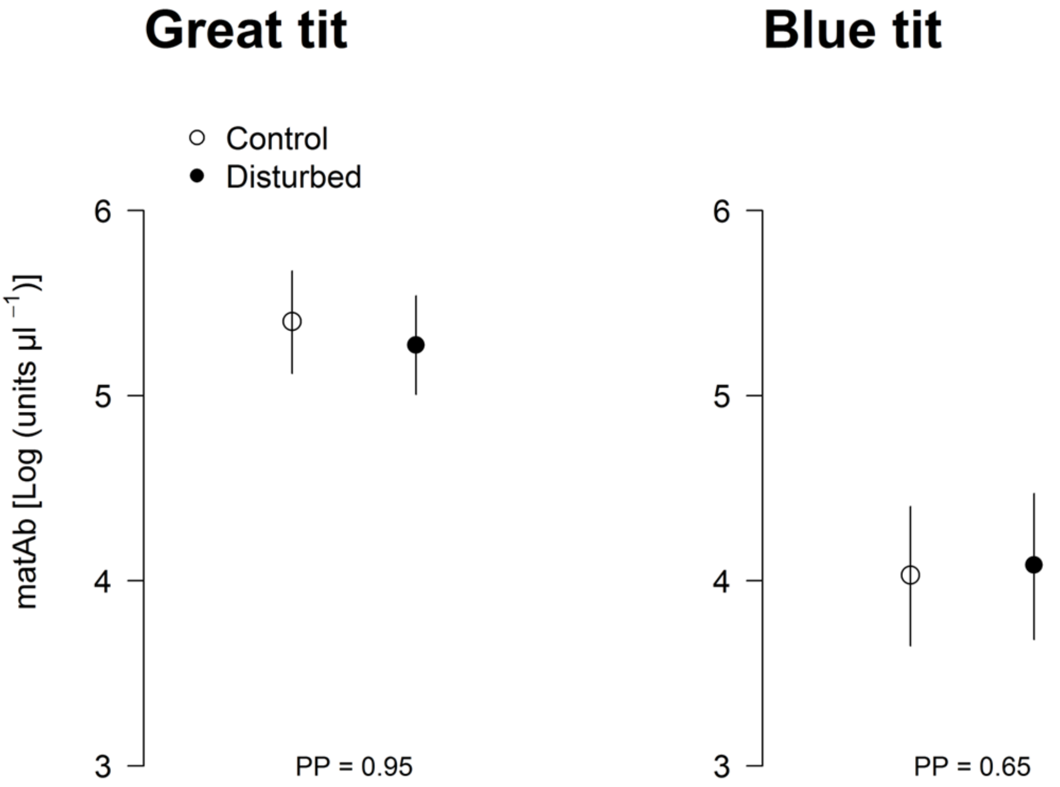

**Fig. 2. Effect of experimental disturbance on matAb titres in tit chicks.** Model estimates ± 95% CrI of the species-specific matAb titres between disturbed and control split-plots with their corresponding posterior probability (PP). PPs can take values from 0.5 to 1 and the higher the probability, the stronger is the difference between treatments.

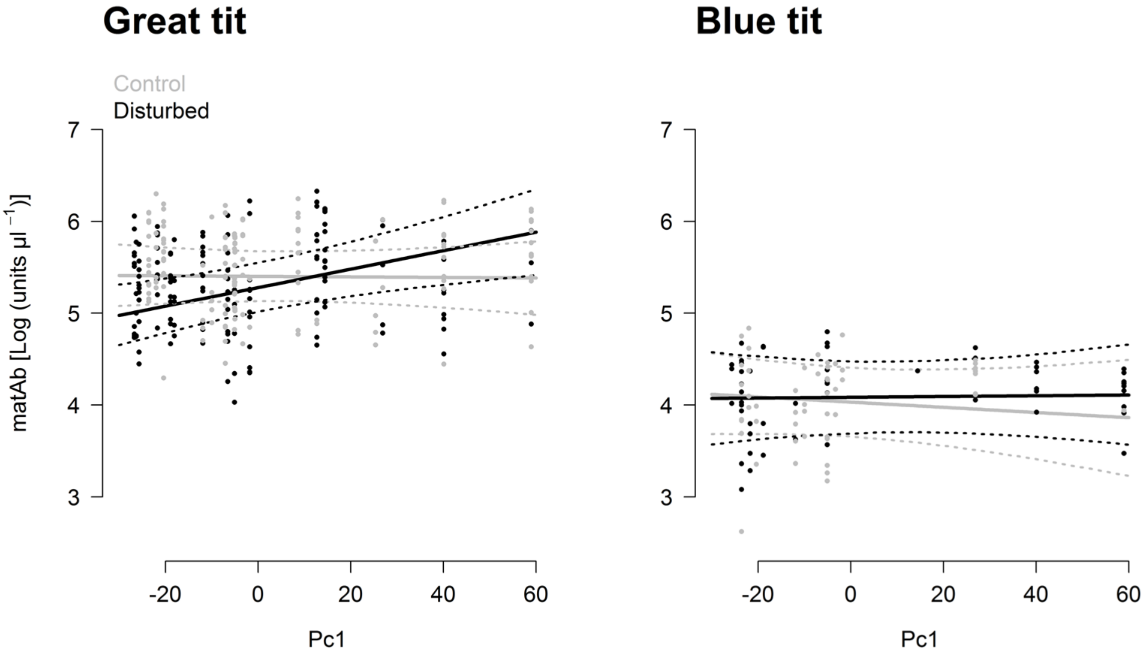

**Fig. 3. Effect of experimental disturbance on matAb titres in tit chicks in relation to vegetation (Pc1).** Model estimates (solid lines) ± 95% CrI (dotted lines) of the species-specific matAb titres depending on Pc1 between disturbed and control split-plots. Pc1 is positively correlated with shrub cover and negatively with ground cover and canopy cover, therefore representing a measure for visibility. The dots represent the data points (grey: control split-plots, black: disturbed split-plots).

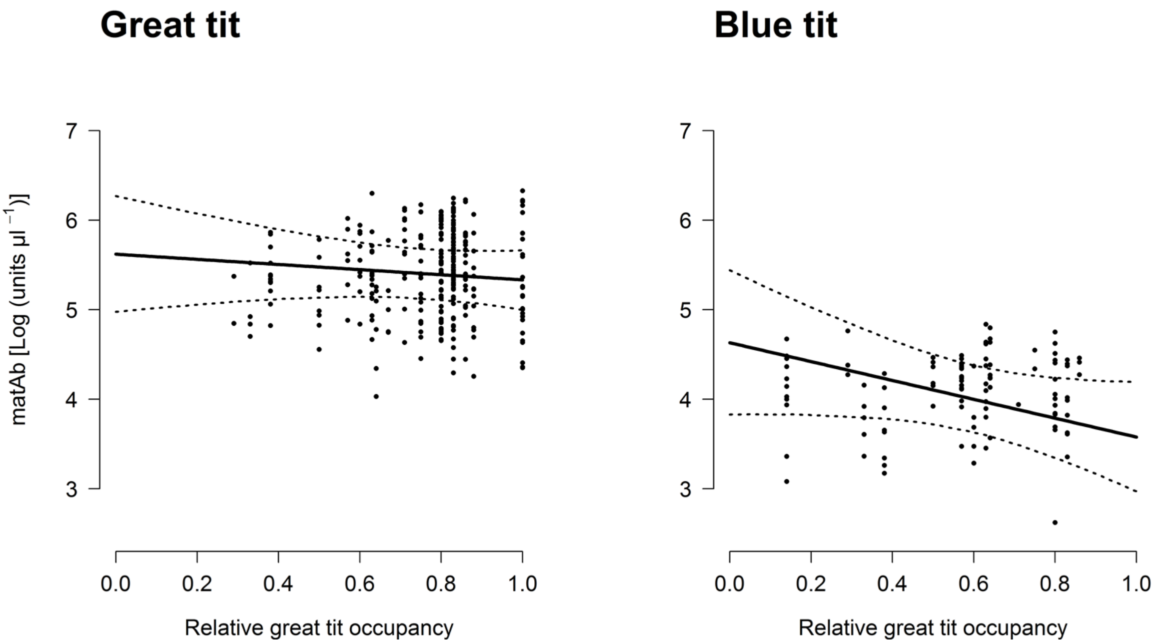

**Fig. 4. Effect of the split-plot specific relative great tit nest box occupancy on species-specific matAb titres in chicks.** Represented are model estimates (solid lines) ± 95% CrI (dotted lines). The dots represent the data points.

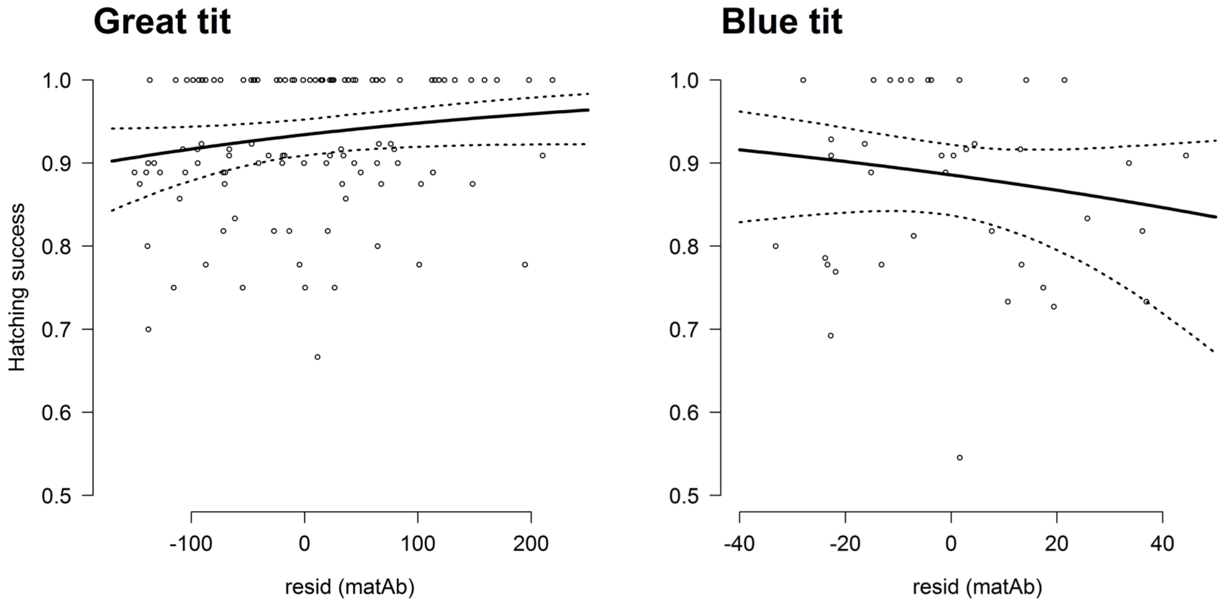

**Fig. 5. Effect of matAb titres on hatching success.** Model estimates for hatching success (with corresponding 95% CrIs; dotted lines) depending on mean matAb titres per brood (solid lines). Plotted are the matAb residuals (resid (matAb)) corrected for chick age. Open circles depict the data points. Note the different x-axes ranges.

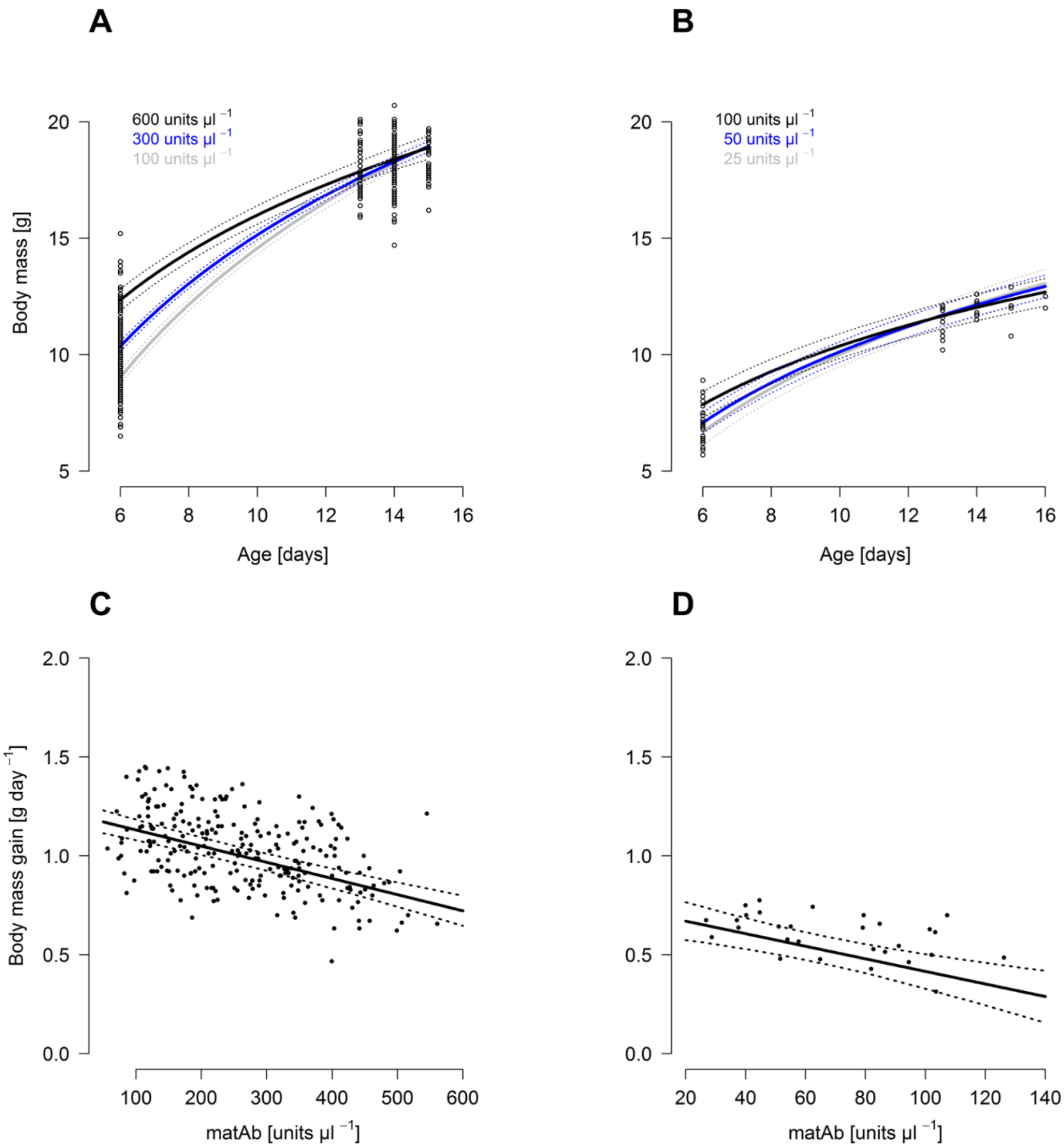

**Fig. 6. Body mass development and daily body mass gain until fledging, dependent on matAb titres.** A and B: Model estimates ± 95% CrI of chick body mass development from day six until fledging, depending on matAb titres (three selected species-specific titres shown). C and D: Model estimates ± 95% CrI of chick body mass gain per day depending on matAb titres. A and C: Great tits (*Parus major*), B and D: Blue tits (*Cyanistes caeruleus*), open/closed circles represent the data points. Note the different x-axis ranges for figures C and D.

# GENERAL DISCUSSION

Diverse outdoor recreational activities are widely practiced, have many followers and affect most habitats during many (sometimes all) periods of a year. Wildlife is therefore confronted with humans almost continuously and, even when not suffering from consumption (e.g. hunting, fishing), face direct effects through human encounters or get indirectly affected through changes in their habitat (Wilkes 1977; Boyle & Samson 1985; Reed & Merenlender 2008). However, these effects are not always obvious or well-known. Although a lot of research has been done to investigate these effects, studies so far, have neglected two aspects: 1) disentangling the effects of direct human presence from those of habitat modifications linked to recreation and 2) considering the effects of low levels of disturbance, as most studies focus on areas with an already considerable amount of disturbance. In this thesis we tackled these problems by using a combination of well-thought comparative studies and experiments in the field.

## Disentangling direct from indirect disturbance effects

We define an indirect human impact as an impact of humans on a resource (e.g. habitat (vegetation), food, nesting sites, or flows of communication) of a given species which, via changing these resources, affects the individual. One of the most common indirect impacts of human recreation is the construction of trails. Firstly, trails entail a habitat change by clearing the vegetation or just by repeated trampling by humans (Monz, Pickering & Hadwen 2013). Secondly, previously connected habitat gets split into fragments, which may reduce animal movements and therefore population connectivity, which results in reduced gene flow (Saunders, Hobbs & Margules 1991; Reed, Johnson-Barnard & Baker 1996; Forman & Alexander 1998; Bregman, Sekercioglu & Tobias 2014). The severity of trail impacts clearly depends on their extent (e.g. width, coating) and also on the species characteristics (small versus large and highly mobile versus less mobile).

Thirdly, depending on the habitat, clearing of the natural vegetation results in changes in abiotic factors, such as light conditions, water balance or temperature (Trombulak & Frissell 2000). These changes in conditions promote a change in vegetation along trails, with potentially negative or positive effects on birds.

By comparing areas with similar types of trails but differences in human frequentation, we were able to separate the effect of the trail *per se* from the effect of the presence of people. Our study comparing bird compositions between forests with different intensities of human use showed that most birds avoided sites close to trails when they were heavily used by humans, but not when human passages were very infrequent. This finding implies that in these forests, although used for recreation since many years, humans still scare off many birds and that they apparently did not entirely habituate to these activities.

On the other hand the changes in vegetation through trails, leads to trail-proximate habitats becoming more suitable for some species (e.g. ground nesters) but less for others. Ground nesters may profit from trail edges, as the improved light conditions favour ground vegetation, compared to the dark interior of forests, which promotes better nesting sites. We found that in our study ground nesters indeed preferred areas close to trails, however only for trails with low frequentation. Still, the most apparent finding was, apart from changes in vegetation through trails, that the humans using these trails are the much stronger factor driving bird communities. The important effect of the degree of human frequentation on trails could also explain why different studies looking at trail impacts found opposing results (Miller, Knight & Miller 1998; Deluca & King 2014). Although trails might have substantial effects through changes in vegetation, and through promoting access into forests for both humans and certain predators, they also guide recreationists through space and since most of them stay on the trails, they reduce the negative effects of human off-trail activities (Coppes & Braunisch 2013). This also facilitates wildlife habituation as the human movements on trails become predictable (Taylor & Knight 2003).

### Effects of human recreation in previously undisturbed areas

By comparing the antipredator response of birds in areas with and without recreation, we were able to confirm that the impact of human disturbance might be obscured in areas where recreation has been already established for a long time. Our study showed that in areas with a high human frequentation, species tolerated a closer human approach before fleeing than in areas largely unfrequented by humans. This could be explained by two different processes. First, behavioural habituation towards human presence can occur, where birds learn that humans are not dangerous and reduce their reactions. This has been shown to strongly depend on the species as well as on individual personality (Walker, Dee Boersma & Wingfield 2006; Rodríguez-Prieto, Martín & Fernández-Juricic 2011; Samia *et al.* 2015; Vincze *et al.* 2016). Secondly, it may occur through selection of certain individuals that are more human tolerant (Carrete & Tella 2013; Miranda *et al.* 2013; Sprau & Dingemanse 2017). This entails directional selection towards human tolerant individuals in human frequented habitats, which would drive evolution and therefore reduce the diversity of personalities (like Allendorf and Hard, 2009 showed for harvested animals). These variations of reactions in birds depending on human frequentation would partially explain why some studies found effects on birds at certain levels of human recreation while other did not.

Therefore, in order to study the real magnitude of the effect of human disturbance, we chose the forest that had very low numbers of visitors to experimentally test the effect of low levels of disturbance. With our experimental study we showed that human recreational activities (hiking in our study), negatively affected forest bird territory establishment. Consequently reduced breeding bird densities and species richness were the outcomes. The season during which a disturbance event happens and its intensity clearly have an important influence on the strength of its impact (Tablado & Jenni 2017). Apparently the pre-breeding period is very important for birds, as they then decide where to breed and this finally can affect their fitness. These findings can only be the result of a direct human disturbance effect, as there was no change in habitat resulting from our hikes.

Our disturbance intensity was quite low (two to three passages per day) and not representative for recreational hotspot areas. Still, we found that even low disturbance intensities can have severe impacts on bird territory establishment. In theory different relationships between disturbance intensity and impact severity have been proposed (Figure 1, adapted after: Monz et al., 2013; Steidl and Powell, 2006; Steven et al., 2011).

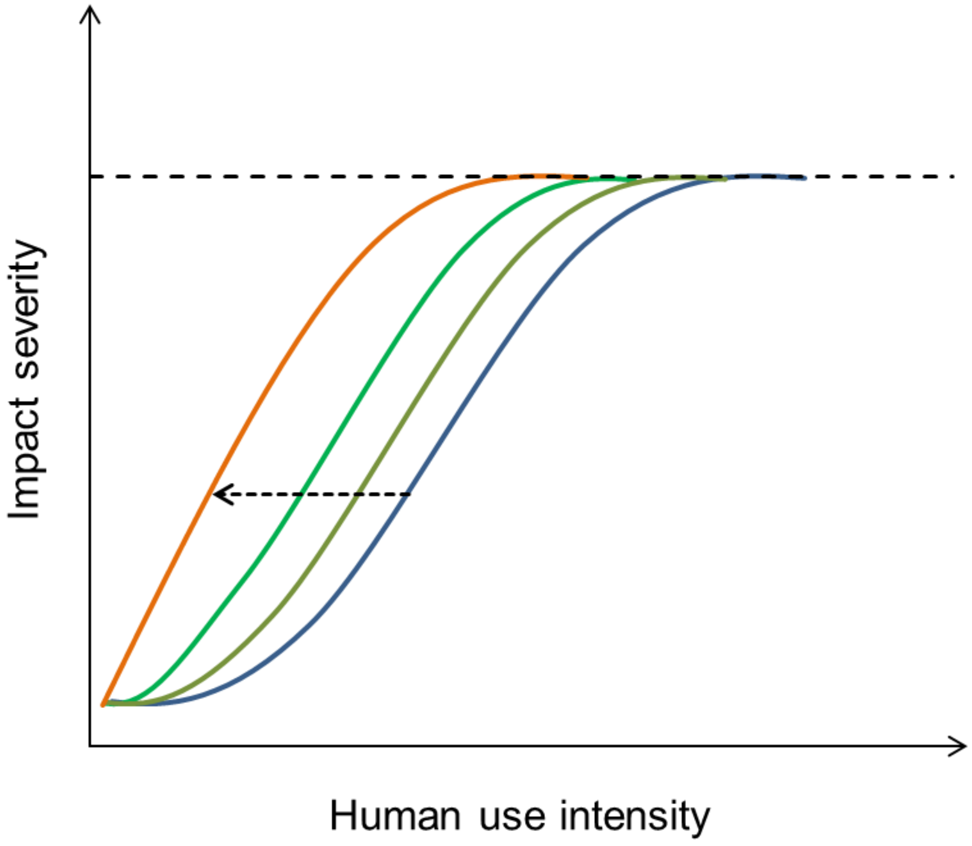

**Figure 1:** Generalizations of the impact of human disturbance on the severity of its impact. The dotted arrow indicates the direction from more to less experience with humans. The dotted line depicts a theoretical impact maximum.

The impact severity at low disturbance levels therefore depends on the shape of the curve (Figure 1) which likely depends on the species, the season (pre-breeding in our case), and also on the individuals former experience with human recreation. What actually drives the shape of this curve is an open question, which needs further investigation, especially concerning wildlife.

With our experiments we also could show that even low levels of disturbance can lead to trans-generational effects through variations in maternal antibody deposition into eggs by disturbed females. Mechanistically this could be driven via corticosterone, the main glucocorticoid in birds, which has an immunosuppressive function. That is, human presence would stress birds, leading to an increase in the release of corticosterone (Thiel *et al.* 2008; French *et al.* 2010; Almasi *et al.* 2015; Arlettaz *et al.* 2015). This increased corticosterone level in turn, would work as an immuno-suppressive agent reducing the antibodies available to be deposited into eggs (maternal antibodies; French et al., 2010; Pihlaja et al., 2006; Saino et al., 2003). The species or site specific short-term reactions (physiological and/or behavioural) can be unimportant for an individual's survival, but not for its offspring where even short changes in parent behaviour can have drastic impacts (Zanette *et al.* 2011).

## Conclusions and implications for conservation

Human outdoor recreation often has a negative impact on birds and it is likely to continue increasing in the future. In order to mitigate human recreation impact on wildlife, conservation measures have to be implemented specifically adapted to the season, the recreational activity type and the target species. In general, visitor guidance along or through rare habitats is highly recommended to keep the negative impacts through human recreation as low as possible. Human disturbances can already have severe impacts at low intensities and short duration; therefore also research(er) related impacts have to be taken into account (Götmark 1992; Giese 1996).

Restricted access or at least stay-on-trail directives are valuable and often necessary conservation measures. Therefore also trail networks should not be too dense and if new trails have to be constructed the surrounding habitats and the local species' requirements should be taken into account (Rodríguez-Prieto *et al.* 2014). Also timber harvesting roads should be re-built/renaturalized to firstly limit the direct impact on the habitat and secondly to not promote human and predator access into before undisturbed areas. Trail effects should also be taken into account for bird monitoring schemes which are often conducted from trails or roads, where local abundance and species richness can be affected too (Hanowski & Niemi 1995; Šálek, Svobodová & Zasadil 2010).

Human presence can have short time effects like physiological or behavioural reactions, which might not severely affect the individual directly, but which might affect the offspring (trans generational effect, as we could show with maternal antibodies) or the individuals fitness via reduced breeding success (Pihlaja, Siitari & Alatalo 2006; French *et al.* 2010; Almasi *et al.* 2015). Such impacts are much harder to detect and to investigate and might only gradually impact populations (Blickley *et al.* 2012). Permanent, high intensity recreational activities, on the other hand, can trigger physiological reactions which lower apparent survival, force wildlife to adapt their behaviour (spatially and temporarily) or even cause animals to leave a given area (local extinction).

From time to time new outdoor activities pop up and sometimes get large numbers of followers like for example the recent trend for stand-up paddling (SUP). Such new activities might affect other habitat types or access new areas and therefore need to attract a conservationist's attention, which then should assess its impact. Conservation biologists should then propose conservation measures and support their implementation to "bridge the gap" between researchers and practitioners (Arlettaz *et al.* 2010).

# REFERENCES

Allendorf, F.W. & Hard, J.J. (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences*, **106**, 9987–9994.

Almasi, B., Béziers, P., Roulin, A. & Jenni, L. (2015) Agricultural land use and human presence around breeding sites increase stress-hormone levels and decrease body mass in barn owl nestlings. *Oecologia*, **179**, 89–101.

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355–366.

Arlettaz, R., Nusslé, S., Baltic, M., Vogel, P., Palme, R., Jenni-Eiermann, S., Patthey, P., Genoud, M., Nussle, S., Baltic, M., Vogel, P., Palme, R., Jenni-Eiermann, S., Patthey, P. & Genoud, M. (2015) Disturbance of wildlife by outdoor winter recreation: allostatic stress response and altered activity-energy budgets. *Ecological Applications*, **25**, 1197–1212.

Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T.S., Sierro, A., Watson, J.E.M. & Braunisch, V. (2010) From publications to public actions: when conservation biologists bridge the gap between research and implementation. *BioScience*, **60**, 835–842.

Arroyo, B., Mougeot, F. & Bretagnolle, V. (2017) Individual variation in behavioural responsiveness to humans leads to differences in breeding success and long-term population phenotypic changes. *Ecology Letters*, **20**, 317–325.

Arroyo, B. & Razin, M. (2006) Effect of human activities on bearded vulture behaviour and breeding success in the French Pyrenees. *Biological Conservation*, **128**, 276–284.

Baines, D. & Richardson, M. (2007) An experimental assessment of the potential effects of human disturbance on Black Grouse *Tetrao tetrix* in the North Pennines, England. *Ibis*, **149**, 56–64.

Balmford, A., Beresford, J., Green, J., Naidoo, R., Walpole, M. & Manica, A. (2009) A global perspective on trends in nature-based tourism. *PLoS Biology*, **7**, 1–6.

Batáry, P., Fronczek, S., Normann, C., Scherber, C. & Tscharntke, T. (2014) How do edge effect and tree species diversity change bird diversity and avian nest survival in Germany's largest deciduous forest? *Forest Ecology and Management*, **319**, 44–50.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.

Baudains, T.P. & Lloyd, P. (2007) Habituation and habitat changes can moderate the impacts of human disturbance on shorebird breeding performance. *Animal Conservation*, **10**, 400–407.

Beale, C.M. & Monaghan, P. (2004a) Human disturbance: people as predation-free predators? *Journal of Applied Ecology*, **41**, 335–343.

Beale, C.M. & Monaghan, P. (2004b) Behavioural responses to human disturbance: a matter of choice? *Animal Behaviour*, **68**, 1065–1069.

Bejder, L., Samuels, A., Whitehead, H., Finn, H. & Allen, S. (2009) Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*, **395**, 177–185.

Benninger-Truax, M., Vankat, J.L. & Schaefer, R.L. (1992) Trail corridors as habitat and conduits for movement of plant species in Rocky Mountain National Park, Colorado, USA. *Landscape Ecology*, **6**, 269–278.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H. (2000) *Bird Census Techniques*, 2nd edn. Academic Press, London.

Blickley, J.L., Word, K.R., Krakauer, A.H., Phillips, J.L., Sells, S.N., Taff, C.C., Wingfield, J.C. & Patricelli, G.L. (2012) Experimental chronic noise is related to elevated fecal corticosteroid metabolites in lekking male Greater Sage-Grouse (*Centrocercus urophasianus*). *PLoS ONE*, **7**, e50462.

von Blotzheim, U.N.G., Bauer, K. & Bezzel, E. (1993) *Handbuch der Vögel Mitteleuropas*. Akademische Verlagsgesellschaft, Frankfurt aM.

Blumstein, D.T. (2003) Flight-initiation distance in birds is dependent on intruder starting distance. *The Journal of Wildlife Management*, **67**, 852–857.

Blumstein, D.T. (2010) Flush early and avoid the rush: A general rule of antipredator behavior? *Behavioral Ecology*, **21**, 440–442.

Blumstein, D.T., Anthony, L.L., Harcourt, R. & Ross, G. (2003) Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation*, **110**, 97–100.

Blumstein, D.T., Fernández-Juricic, E., Zollner, P.A. & Garity, S.C. (2005) Inter-specific variation in avian responses to human disturbance. *Journal of Applied Ecology*, **42**, 943–953.

Bonier, F., Martin, P.R. & Wingfield, J.C. (2007) Urban birds have broader environmental tolerance. *Biology Letters*, **3**, 670–673.

Bötsch, Y., Arlettaz, R. & Schaub, M. (2012) Breeding dispersal of Eurasian Hoopoes (*Upupa epops*) within and between years in relation to reproductive success, sex, and age. *The Auk*, **129**, 283–295.

Bötsch, Y., Tablado, Z. & Jenni, L. (2017) Experimental evidence of human recreational disturbance effects on bird-territory establishment. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20170846.

Boulinier, T. & Staszewski, V. (2008) Maternal transfer of antibodies: raising immuno-ecology issues. *Trends in Ecology & Evolution*, **23**, 282–288.

Bourgeon, S. & Raclot, T. (2006) Corticosterone selectively decreases humoral immunity in female eiders during incubation. *Journal of Experimental Biology*, **209**, 4957–4965.

Boyle, S.A. & Samson, F.B. (1985) Effects of nonconsumptive recreation on wildlife: a review. *Wildlife Society Bulletin*, **13**, 110–116.

Bregman, T.P., Sekercioglu, C.H. & Tobias, J.A. (2014) Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biological Conservation*, **169**, 372–383.

Buckley, R. (2013) Next steps in recreation ecology. *Frontiers in Ecology and the Environment*, **11**, 399.

Burger, J. (1981) The effect of human activity on birds at a coastal bay. *Biological Conservation*, **21**, 231–241.

Butler, L.K., Ries, L., Bisson, I.-A., Hayden, T.J., Wikelski, M.M. & Romero, L.M. (2012) Opposite but analogous effects of road density on songbirds with contrasting habitat preferences. *Animal Conservation*, **16**, 77–85.

Byrne, D., Dillon, H., Tran, K., Arlinger, S., Wilbraham, K., Cox, R., Hagerman, B., Hetu, R., Kei, J., C. Lui, J.K., Kotby, M.N., Nasser, N.H.A., Kholy, W.A.H. El, Nakanishi, Y., Oyer, H., Powel, R., Stephens, D., Meredith, R., Sirimanna, T., Tavartkiladze, G., Frolenkov, G.I., Westerman, S. & Ludvigsen, C. (1994) An international comparison of long-term average speech spectra. *The Journal of the Acoustical Society of America*, **96**, 2108–2120.

Caprio, E., Ellena, I. & Rolando, A. (2009) Assessing habitat/landscape predictors of bird diversity in managed deciduous forests: a seasonal and guild-based approach. *Biodiversity and Conservation*, **18**, 1287–1303.

Carrete, M. & Tella, J.L. (2010) Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection . *Biology letters* , **6**, 167–170.

Carrete, M. & Tella, J.L. (2013) High individual consistency in fear of humans throughout the adult lifespan of rural and urban burrowing owls. *Scientific Reports*, **3**.

Cavalli, M., Baladrón, A. V., Isacch, J.P., Biondi, L.M. & Bó, M.S. (2016) Differential risk perception of rural and urban Burrowing Owls exposed to humans and dogs. *Behavioural Processes*, **124**, 60–65.

Ciucci, P., Boitani, L., Francisci, F. & Andreoli, G. (1997) Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology*, **243**, 803–819.

Clevenger, A.P., Chruszcz, B. & Gunson, K.E. (2003) Spatial patterns and factors influencing small vetebrate fauna road-kill agregations. *Biodiversity Conservation*, **109**, 15–26.

Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species-area relationship. *The American Naturalist*, **113**, 791–833.

Coppes, J. & Braunisch, V. (2013) Managing visitors in nature areas: where do they leave the trails? A spatial model. *Wildlife Biology*, **19**, 1–11.

Coppes, J., Burghardt, F., Hagen, R., Suchant, R. & Braunisch, V. (2017) Human recreation affects spatio-temporal habitat use patterns in red deer (*Cervus elaphus*). *PLoS One*, **12**, e0175134.

Deluca, W. V & King, D.I. (2014) Influence of hiking trails on montane birds. *Journal of Wildlife Management*, **78**, 494–502.

Díaz, M., Møller, A.P., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., Markó, G. & Tryjanowski, P. (2013) The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS One*, **8**, e64634.

Eason, P.K., Sherman, P.T., Rankin, O. & Coleman, B. (2006) Factors affecting flight initiation distance in American robins. *Journal of Wildlife Management*, **70**, 1796–1800.

Evans, J., Boudreau, K. & Hyman, J. (2010) Behavioural syndromes in urban and rural populations of song sparrows . *Ethology* , **116**, 588–595.

Fernández-Juricic, E. (2000) Local and regional effects of pedestrians on forest birds in a fragmented landscape. *The Condor*, **102**, 247–255.

Fernández-Juricic, E., Jimenez, M.D. & Lucas, E. (2001) Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environmental Conservation*, **28**, 263–269.

Fernández-Juricic, E., Jimenez, M.D. & Lucas, E. (2002) Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology*, **80**, 1212–1220.

Fernández-Juricic, E., Venier, M.P., Renison, D. & Blumstein, D.T. (2005) Sensitivity of wildlife to spatial patterns of recreationist behavior: a critical assessment of minimum approaching distances and buffer areas for grassland birds. *Biological Conservation*, **125**, 225–235.

Ferrer, M. & Donazar, J.A. (1996) Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology*, **77**, 69–74.

Fontaine, J.J. & Martin, T.E. (2006) Habitat selection responses of parents to offspring predation risk: an experimental test. *The American naturalist*, **168**, 811–818.

Forman, R.T.T. & Alexander, L.E. (1998) Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, **29**, 207–231.

Fowler, G.S. (1999) Behavioral and hormonal responses of Magellanic penguins (*Spheniscus magellanicus*) to tourism and nest site visitation. *Biological Conservation*, **90**, 143–149.

French, S.S., Denardo, D.F., Greives, T.J., Strand, C.R. & Demas, G.E. (2010) Human disturbance alters endocrine and immune responses in the Galapagos marine iguana (*Amblyrhynchus cristatus*). *Hormones and Behavior*, **58**, 792–799.

Frid, A. & Dill, L. (2002) Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, **6**, 11.

Gao, S., Sanchez, C. & Deviche, P.J. (2016) Corticosterone rapidly suppresses innate immune activity in the House Sparrow (*Passer domesticus*). *The Journal of Experimental Biology*, **220**, 322–327.

Garber, S.D.. & Burger, J. (1995) A 20-Yr study documenting the relationship between turtle decline and human recreation. *Ecological Applications*, **5**, 1151–1162.

Gasparini, J., Bize, P., Piault, R., Wakamatsu, K., Blount, J.D., Ducrest, A.-L. & Roulin, A. (2009) Strength and cost of an induced immune response are associated with a heritable melanin-based colour trait in female tawny owls. *Journal of Animal Ecology*, **78**, 608–616.

Geist, C., Liao, J., Libby, S. & Blumstein, D.T. (2005) Does intruder group size and orientation affect flight initiation distance in birds? *Animal biodiversity and conservation*, **28**, 69–73.

Gelman, A. & Su, Y.-S. (2015) arm: Data analysis using regression and multilevel/hierarchical models. R package version 1.8-6. https://CRAN.R-project.org/package=arm.

George, S.L. & Crooks, K.R. (2006) Recreation and large mammal activity in an urban nature reserve. *Biological Conservation*, **133**, 107–117.

Gerland, P., Raftery, A.E., Ševčíková, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B.K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G.K. & Wilmoth, J. (2014) World population stabilization unlikely this century. *Science*, **346**, 234–237.

Giese, M. (1996) Effects of human activity on adelie penguin *Pygoscelis adeliae* breeding success. *Biological Conservation*, **75**, 157–164.

Gill, J.A. (2007) Approaches to measuring the effects of human disturbance on birds. *Ibis*, **149**, 9–14.

Glądalski, M., Bańbura, M., Kaliński, A., Markowski, M., Skwarska, J., Wawrzyniak, J., Zieliński, P., Cyżewska, I., Mańkowska, D. & Bańbura, J. (2016) Effects of human-related disturbance on breeding success of urban and non-urban blue tits (*Cyanistes caeruleus*). *Urban Ecosystems*, **19**, 1325–1334.

Goodwin, H. (1996) In pursuit of ecotourism. *Biodiversity and Conservation*, **5**, 277–291.

Götmark, F. (1992) The effects of investigator disturbance on nesting birds. *Current Ornithology* (ed D.M. Power), pp. 63–104. Springer US, Boston, MA.

Grindstaff, J.L. (2008) Maternal antibodies reduce costs of an immune response during development. *The Journal of experimental biology*, **211**, 654–660.

Grindstaff, J.L., Brodie, E.D. & Ketterson, E.D. (2003) Immune function across generations: integrating mechanism and evolutionary process in maternal antibody transmission. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2309–

2319.

Gutzwiller, K.J. & Anderson, S.H. (1999) Spatial extent of human-intrusion effects on subalpine bird distributions. *Condor*, **101**, 378–389.

Gutzwiller, K.J. & Marcum, H.A. (1997) Bird reactions to observer clothing color: implications for distance-sampling techniques. *The Journal of Wildlife Management*, **61**, 935–947.

Gutzwiller, K.J., Marcum, H.A., Harvey, H.B., Roth, J.D., Anderson, S.H., Harvey, H.B., Roth, J.D. & Anderson, S.H. (1998) Bird tolerance to human intrusion in Wyoming montane forests. *The Condor*, **100**, 519–527.

Gutzwiller, K.J., Wiedenmann, R.T., Clements, K.L. & Anderson, H. (1994) Effects of human intrusion on song occurrence and singing consistency in subalpine birds. *The Auk*, **111**, 28–37.

Hacki, T. (1996) Comparative speaking, shouting and singing voice range profile measurement: physiological and pathological aspects. *Logopedics Phoniatrics Vocology*, **21**, 123–129.

Hammitt, W.E., Cole, D.N. & Monz, C.A. (2015) *Wildland Recreation: Ecology and Management*. John Wiley & Sons, Chichester, West Sussex UK.

Hanowski, J.M. & Niemi, G.J. (1995) A comparison of on- and off-road bird counts: do you need to go off road to count birds accurately? *Journal of Field Ornithology*, **66**, 469–483.

Hargitai, R., Arnold, K.E., Herényi, M., Prechl, J. & Török, J. (2009) Egg composition in relation to social environment and maternal physiological condition in the collared flycatcher. *Behavioral Ecology and Sociobiology*, **63**, 869–882.

Hargitai, R., Prechl, J. & Török, J. (2006) Maternal immunoglobulin concentration in Collared Flycatcher (*Ficedula albicollis*) eggs in relation to parental quality and laying order. *Functional Ecology*, **20**, 829–838.

Hasselquist, D. & Nilsson, J.-A. (2009) Maternal transfer of antibodies in vertebrates: trans-generational effects on offspring immunity. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **364**, 51–60.

Hayward, L.S. & Wingfield, J.C. (2004) Maternal corticosterone is transferred to avian yolk and may alter offspring growth and adult phenotype. *General and Comparative Endocrinology*, **135**, 365–371.

Hill, D., Hockin, D., Price, D., Tucker, G., Morris, R. & Treweek, J. (1997) Bird disturbance: Improving the quality and utility of disturbance research. *Journal of Applied Ecology*, **34**, 275–288.

Holm, T.E. & Laursen, K. (2009) Experimental disturbance by walkers affects behaviour and territory density of nesting Black-tailed Godwit *Limosa limosa*. *Ibis*, **151**, 77–87.

Ihaka, R. & Gentleman, R. (1996) R: a language for data analysis and graphics. *Journal of* *computational and graphical statistics*, **5**, 299–314.

Ikuta, L.A. & Blumstein, D.T. (2003) Do fences protect birds from human disturbance? *Biological Conservation*, **112**, 447–452.

Ismail, A., Jacquin, L., Haussy, C., Perret, S. & Gasparini, J. (2015) Food availability modulates the effects of maternal antibodies on growth and immunity in young feral pigeons. *Journal of Avian Biology*, **46**, 489–494.

Kangas, K., Luoto, M., Ihantola, A., Tomppo, E. & Siikamäki, P. (2010) Recreation-induced changes in boreal bird communities in protected areas. *Ecological Applications*, **20**, 1775–1786.

King, M.O., Owen, J.P. & Schwabl, H.G. (2010) Are maternal antibodies really that important? Patterns in the immunologic development of altricial passerine House Sparrows (*Passer domesticus*). *PLoS ONE*, **5**, e9639.

Klasing, K.C. & Leshchinsky, T. V. (1998) Functions, costs, and benefits of the immune system during development and growth. *Proc. 22 Int. Ornithol. Congress*, 2817–2835.

Koch, S.L. & Paton, P.W.C. (2014) Assessing anthropogenic disturbances to develop buffer zones for shorebirds using a stopover site. *Journal of Wildlife Management*, **78**, 58–67.

Komdeur, J., Huffstadt, A., Prast, W., Castle, G., Mileto, R. & Wattel, J. (1995) Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour. *Animal Behaviour*, **49**, 695–708.

Korner-Nievergelt, F., Roth, T., von Felten, S., Guélat, J., Almasi, B. & Korner-Nievergelt, P. (2015) *Bayesian Data Analysis in Ecology Using Linear Models with R, BUGS, and Stan*. Academic Press, London.

Krebs, J.R. (1971) Territory and breeding density in the Great Tit, *Parus major* L. *Ecology*, **52**, 2–22.

Langston, R.H.W., Liley, D., Murison, G., Woodfield, E. & Clarke, R.T. (2007) What effects do walkers and dogs have on the distribution and productivity of breeding European Nightjar *Caprimulgus europaeus*? *Ibis*, **149**, 27–36.

Larson, C.L., Reed, S.E., Merenlender, A.M. & Crooks, K.R. (2016) Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS ONE*, **11**.

Laurance, W.F., Goosem, M. & Laurance, S.G.W. (2009) Impacts of roads and linear clearings on tropical forests. *Trends in Ecology & Evolution*, **24**, 659–669.

Laurance, S.G.W., Stouffer, P.C. & Laurence, W.F. (2004) Effects of road clearings on movement patterns of understory rainforest birds in Central Amazonia. *Conservation Biology*, **18**, 1099–1109.

Legagneux, P. & Ducatez, S. (2013) European birds adjust their flight initiation distance to road speed limits . *Biology letters* , **9**, 20130417.

Lemke, H., Coutinho, A. & Lange, H. (2004) Lamarckian inheritance by somatically acquired maternal IgG phenotypes. *Trends in Immunology*, **25**, 180–186.

Lemke, H., Hansen, H. & Lange, H. (2003) Non-genetic inheritable potential of maternal antibodies. *Vaccine*, **21**, 3428–3431.

Lethlean, H., Van Dongen, W.F.D., Kostoglou, K., Guay, P.-J. & Weston, M.A. (2017) Joggers cause greater avian disturbance than walkers. *Landscape and Urban Planning*, **159**, 42–47.

Lindén, M., Gustafsson, L. & Pärt, T. (1992) Selection on fledging mass in the collared flycatcher and the great tit. *Ecology*, **73**, 336–343.

Livezey, K.B., Fernández-Juricic, E. & Blumstein, D.T. (2016) Database and metadata of bird flight initiation distances worldwide to assist in estimating human disturbance effects and delineating buffer areas. *Journal of Fish and Wildlife Management*, **7**, 1–11.

Löhrl, H. (1977) Nistökologische und ethologische Anpassungserscheinungen bei Höhlenbrütern. *Die Vogelwarte*, **29**, Sonderheft: 92-101.

Love, O.P., Wynne-Edwards, K.E., Bond, L. & Williams, T.D. (2008) Determinants of within- and among-clutch variation in yolk corticosterone in the European starling. *Hormones and Behavior*, **53**, 104–111.

Mallord, J.W., Dolman, P.M., Brown, A.F. & Sutherland, W.J. (2007) Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology*, **44**, 185–195.

Martín, B., Delgado, S., de la Cruz, A., Tirado, S. & Ferrer, M. (2015) Effects of human presence on the long-term trends of migrant and resident shorebirds: Evidence of local population declines. *Animal Conservation*, **18**, 73–81.

Martin, T.E. & Li, P. (1992) Life history traits of open- vs. cavity-nesting birds. *Ecology*, **73**, 579–592.

Martinez-Juarez, P., Chiabai, A., Taylor, T. & Quiroga Gómez, S. (2015) The impact of ecosystems on human health and well-being: a critical review. *Journal of Outdoor Recreation and Tourism*, **10**, 63–69.

Mathot, K.J., Wright, J., Kempenaers, B. & Dingemanse, N.J. (2012) Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*, **121**, 1009–1020.

McGiffin, A., Lill, A., Beckman, J. & Johnstone, C.P. (2013) Tolerance of human approaches by Common Mynas along an urban-rural gradient. *Emu*, **113**, 154–160.

Meyrier, E., Jenni, L., Bötsch, Y., Strebel, S., Erne, B. & Tablado, Z. (2017) Happy to breed in the city? Urban food resources limit reproductive output in western jackdaws. *Ecology and Evolution*, **7**, 1363–1374.

Miller, J.R. & Hobbs, N.T. (2000) Recreational trails, human activity, and nest predation in lowland riparian areas. *Landscape and urban planning*, **50**, 227–236.

Miller, S.G., Knight, R.L. & Miller, C.K. (1998) Influence of recreational trails on breeding bird communities. *Ecological Applications*, **8**, 162–169.

Miller, S.G., Knight, R.L. & Miller, C.K. (2001) Wildlife responses to pedestrians and dogs. *Wildlife Society Bulletin*, **29**, 124–132.

Miranda, A.C., Schielzeth, H., Sonntag, T. & Partecke, J. (2013) Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Global Change Biology*, **19**, 2634–2644.

Møller, A.P. (2008) Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*, **63**, 63–75.

Møller, A.P., Grim, T., Ibáñez-Álamo, J.D., Markó, G. & Tryjanowski, P. (2013) Change in flight initiation distance between urban and rural habitats following a cold winter. *Behavioral Ecology*, **24**, 1211–1217.

Monz, C.A., Pickering, C.M. & Hadwen, W.L. (2013) Recent advances in recreation ecology and the implications of different relationships between recreation use and ecological impacts. *Frontiers in Ecology and the Environment*, **11**, 441–446.

Morelli, F., Beim, M., Jerzak, L., Jones, D. & Tryjanowski, P. (2014) Can roads, railways and related structures have positive effects on birds? - A review. *Transportation Research Part D: Transport and Environment*, **30**, 21–31.

Morelli, F., Jerzak, L., Pruscini, F., Santolini, R., Benedetti, Y. & Tryjanowski, P. (2015) Testing bird response to roads on a rural environment: a case study from central Italy. *Acta Oecologica*, **69**, 146–152.

Morosinotto, C., Ruuskanen, S., Thomson, R.L., Siitari, H., Korpimäki, E. & Laaksonen, T. (2013) Predation risk affects the levels of maternal immune factors in avian eggs. *Journal of Avian Biology*, **44**, 427–436.

Müller, C., Jenni-Eiermann, S., Blondel, J., Perret, P., Caro, S.P., Lambrechts, M. & Jenni, L. (2006) Effect of human presence and handling on circulating corticosterone levels in breeding blue tits (*Parus caeruleus*). *General and Comparative Endocrinology*, **148**, 163–171.

Müllner, A., Linsenmair, K.E. & Wikelski, M. (2004) Exposure to ecotourism reduces survival and affects stress response in hoatzin chicks (*Opisthocomus hoazin*). *Biological Conservation*, **118**, 549–558.

Nephew, B.C., Kahn, S.A. & Romero, M.L. (2003) Heart rate and behavior are regulated independently of corticosterone following diverse acute stressors. *General and comparative endocrinology*, **133**, 173–180.

Nicolaus, M., Tinbergen, J.M., Ubels, R., Both, C. & Dingemanse, N.J. (2016) Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, **19**, 478–486.

Nisbet, I.C.T. (2000) Disturbance, habituation, and management of waterbird colonies. *Waterbirds: The International Journal of Waterbird Biology*, **23**, 312–332.

Norrdahl, K. & Korpimäki, E. (1998) Fear in farmlands: how much does predator avoidance affect bird community structure? *Journal of Avian Biology*, **29**, 79–85.

Oddie, K.R. (2000) Size matters: competition between male and female great tit offspring. *Journal of Animal Ecology*, **69**, 903–912.

Olson, T.L.., Squibb, R.C.. & Gilbert, B.K.. (1998) Brown bear diurnal activity and human use: a comparison of two salmon streams. *Ursus*, **10**, 547–555.

Patthey, P., Wirthner, S., Signorell, N. & Arlettaz, R. (2008) Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. *Journal of Applied Ecology*, **45**, 1704–1711.

Perrins, C. & Cramp, S. (1998) *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford University Press.

Pfister, C., Harrington, B.A. & Lavine, M. (1992) The impact of human disturbance on shorebirds at a migration staging area. *Biological Conservation*, **60**, 115–126.

Pihlaja, M., Siitari, H. & Alatalo, R. V. (2006) Maternal antibodies in a wild altricial bird: effects on offspring immunity, growth and survival. *Journal of Animal Ecology*, **75**, 1154–1164.

Plummer, M., Best, N., Cowles, K. & Vines, K. (2006) CODA: Convergence Diagnosis and Output Analysis for MCMC.

Putman, B.J., Drury, J.P., Blumstein, D.T. & Pauly, G.B. (2017) Fear no colors? Observer clothing color influences lizard escape behavior. , 1–13.

Råberg, L., Grahn, M., Hasselquist, D. & Svensson, E. (1998) On the adaptive significance of stress-induced immunosuppression. *Proceedings of the Royal Society B-Biological Sciences*, **265**, 1637–1641.

R Core Team. (2016) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL https://www.R-project.org/.

Rebolo-Ifrán, N., Carrete, M., Sanz-Aguilar, A., Rodríguez-Martínez, S., Cabezas, S., Marchant, T.A., Bortolotti, G.R. & Tella, J.L. (2015) Links between fear of humans, stress and survival support a non-random distribution of birds among urban and rural habitats. *Scientific Reports*, **5**, Online first, doi:10.1038/srep13723.

Reed, R.A., Johnson-Barnard, J. & Baker, W.L. (1996) Contribution of roads to forest fragmentation in the Rocky Mountains. *Conservation Biology*, **10**, 1098–1106.

Reed, S.E. & Merenlender, A.M. (2008) Quiet, nonconsumptive recreation reduces protected area effectiveness. *Conservation Letters*, **1**, 146–154.

Reijnen, R., Foppen, R., Braak, C. Ter & Thissen, J. (1995) The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. *Journal of Applied Ecology*, **32**, 187–202.

Remacha, C., Pérez-Tris, J. & Delgado, J.A. (2011) Reducing visitors’ group size increases the number of birds during educational activities: implications for management of nature-based recreation. *Journal of environmental management*, **92**, 1564–1568.

Riffell, S.K., Gutzwiller, K.J. & Anderson, S.H. (1996) Does repeated human intrusion cause cumulative declines in avian richness and abundance? *Ecological Applications*, **6**, 492–505.

Robert, H.C. & Ralph, C.J. (1975) Effects of human disturbance on the breeding success of gulls. *The Condor*, **77**, 495–499.

Rodenhouse, N.L., Sillett, T.S., Doran, P.J. & Holmes, R.T. (2003) Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2105–2110.

Rodgers, J.A. & Smith, H.T. (1995) Set-back distances to protect nesting bird colonies from human disturbance in Florida. *Conservation Biology*, **9**, 89–99.

Rodríguez-Prieto, I., Bennett, V.J., Zollner, P.A., Mycroft, M., List, M. & Fernández-Juricic, E. (2014) Simulating the responses of forest bird species to multi-use recreational trails. *Landscape and urban planning*, **127**, 164–172.

Rodríguez-Prieto, I., Fernández-Juricic, E., Martín, J. & Regis, Y. (2009) Antipredator behavior in blackbirds: habituation complements risk allocation. *Behavioral Ecology*, **20**, 371–377.

Rodríguez-Prieto, I., Martín, J. & Fernández-Juricic, E. (2011) Individual variation in behavioural plasticity: direct and indirect effects of boldness, exploration and sociability on habituation to predators in lizards. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 266–273.

Romero, L.M. (2004) Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology & Evolution*, **19**, 249–255.

Romero, L.M., Soma, K.K. & Wingfield, J.C. (1998) Hypothalamic-pituitary-adrenal axis changes allow seasonal modulation of corticosterone in a bird. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, **274**, R1338–R1344.

Rubolini, D., Romano, M., Boncoraglio, G., Ferrari, R.P., Martinelli, R., Galeotti, P., Fasola, M. & Saino, N. (2005) Effects of elevated egg corticosterone levels on behavior, growth, and immunity of yellow-legged gull (*Larus michahellis*) chicks. *Hormones and Behavior*, **47**, 592–605.

Safina, C. & Burger, J. (1983) Effects of human disturbance on reproductive success in the Black Skimmer. *The Condor*, **85**, 164–171.

Saino, N., Romano, M., Ferrari, R.P., Martinelli, R. & Møller, A.P. (2005) Stressed mothers lay eggs with high corticosterone levels which produce low-quality offspring. *Journal* *of Experimental Zoology Part A: Comparative Experimental Biology*, **303**, 998–1006.

Saino, N., Suffritti, C., Martinelli, R., Rubolini, D. & Møller, A.P. (2003) Immune response covaries with corticosterone plasma levels under experimentally stressful conditions in nestling barn swallows (*Hirundo rustica*). *Behavioral Ecology*, **14**, 318–325.

Šálek, M., Svobodová, J. & Zasadil, P. (2010) Edge effect of low-traffic forest roads on bird communities in secondary production forests in central Europe. *Landscape Ecology*, **25**, 1113–1124.

Samia, D.S.M., Blumstein, D.T., Diaz, M., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., Tätte, K., Markó, G., Tryjanowski, P. & Møller, A.P. (2017) Rural-urban differences in escape behavior of European birds across a latitudinal gradient. *Frontiers in Ecology and Evolution*, **5**.

Samia, D.S.M., Nakagawa, S., Nomura, F., Rangel, T.F. & Blumstein, D.T. (2015) Increased tolerance to humans among disturbed wildlife. *Nature Communications*, **6**.

Sapolsky, R.M., Romero, M.L. & Munck, A. (2000) How do glucocorticoids influence the stress response? *Endocrine Reviews*, **21**, 55–89.

Sauer, J.R., Link, W.A., Fallon, J.E., Pardieck, K.L. & Ziolkowski Jr., D.J. (2013) The North American breeding bird survey 1966–2011: summary analysis and species accounts. *North American Fauna*, **79**, 1–32.

Saunders, D. a, Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.

Schmid, H., Luder, R., Naef-Daener, B., Graf, R. & Zbinden, N. (1998) *Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und im Fürstentum Liechtenstein 1993-1996*. Schweizerische Vogelwarte, Sempach.

Schmid, H. & Spiess, M. (2008) *Brutvogelaufnahmen Bei BDM-Z7 und MHB: Anleitung zur Entscheidfindung bei Grenzfällen und zur Revierausscheidung. Schweizerische Vogelwarte, Sempach.*

Schroeder, J., Nakagawa, S., Cleasby, I.R. & Burke, T. (2012) Passerine birds breeding under chronic noise experience reduced fitness. *PLoS ONE*, **7**.

Sih, A., Bell, A. & Johnson, J.C. (2004) Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.

Sih, A., Mathot, K.J., Moirón, M., Montiglio, P.O., Wolf, M. & Dingemanse, N.J. (2015) Animal personality and state-behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology & Evolution*, **30**, 50–60.

Smith-Castro, J.R. & Rodewald, A.D. (2010) Behavioral responses of nesting birds to human disturbance along recreational trails. *Journal of Field Ornithology*, **81**, 130–138.

Spellerberg, I.F. & Fedor, P.J. (2003) A tribute to Claude Shannon (1916 – 2001) and a plea for more rigorous use of species richness, species diversity and the ‘ Shannon-

Wiener ’ index. *Global Ecology and Biogeography*, **12**, 177–179.

Sprau, P. & Dingemanse, N.J. (2017) An approach to distinguish between plasticity and non-random distributions of behavioral types along urban gradients in a wild passerine bird. *Frontiers in Ecology and Evolution*, **5**.

Steidl, R.J. & Powell, B.F. (2006) Assessing the effects of human activities on wildlife. *The George Wright Forum* pp. 50–58.

Steven, R. & Castley, J.G. (2013) Tourism as a threat to critically endangered and endangered birds: global patterns and trends in conservation hotspots. *Biodiversity and Conservation*, **22**, 1063–1082.

Steven, R., Pickering, C. & Castley, J.G. (2011) A review of the impacts of nature based recreation on birds. *Journal of environmental management*, **92**, 2287–2294.

Stier, K.S., Almasi, B., Gasparini, J., Piault, R., Roulin, A. & Jenni, L. (2009) Effects of corticosterone on innate and humoral immune functions and oxidative stress in barn owl nestlings. *Journal of Experimental Biology*, **212**, 2085–2091.

Strasser, E.H. & Heath, J.A. (2013) Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology*, **50**, 912–919.

Sutter, G.C., Devis, S.K. & Duncan, D.C. (2000) Grassland songbird abundance along roads and trails in southern Saskatchewan. *Journal of Field Ornithology*, **71**, 110–116.

Tablado, Z. & Jenni, L. (2017) Determinants of uncertainty in wildlife responses to human disturbance. *Biological Reviews*, **92**, 216–233.

Tarjuelo, R., Barja, I., Morales, M.B., Traba, J., Benítez-López, A., Casas, F., Arroyo, B., Delgado, M.P. & Mougeot, F. (2015) Effects of human activity on physiological and behavioral responses of an endangered steppe bird. *Behavioral Ecology*, **26**, 828–838.

Taylor, A.R. & Knight, R.L. (2003) Wildlife responses to recreation and associated visitor perceptions. *Ecological Applications*, **13**, 951–963.

Thiel, D., Jenni-Eiermann, S., Braunisch, V., Palme, R. & Jenni, L. (2008) Ski tourism affects habitat use and evokes a physiological stress response in capercaillie *Tetrao urogallus*: a new methodological approach. *Journal of Applied Ecology*, **45**, 845–853.

Thiel, D., Ménoni, E., Brenot, J.-F. & Jenni, L. (2007) Effects of recreation and hunting on flushing distance of capercaillie. *The Journal of Wildlife Management*, **71**, 1784–1792.

Thompson, B. (2015) Recreational trails reduce the density of ground-dwelling birds in protected areas. *Environmental Management*, **55**, 1181–1190.

Trombulak, S.C. & Frissell, C.A. (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, **14**, 18–30.

Trzcinski, M.K., Fahrig, L. & Merriam, G. (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications*, **9**, 586–593.

Vincze, E., Papp, S., Preiszner, B., Seress, G., Bókony, V. & Liker, A. (2016) Habituation to human disturbance is faster in urban than rural house sparrows. *Behavioral Ecology*, doi:10.1093/beheco/arw047.

Virkkala, R. (1987) Effects of forest management on birds breeding in northern Finland. *Annales Zoologici Fennici*, **24**, 281–294.

Waldstein Parsons, A., Bland, C., Forrester, T., Baker-Whatton, M.C., Schuttler, S.G., McShea, W.J., Costello, R. & Kays, R. (2016) The ecological impact of dogs on wildlife in protected areas in eastern North America. *Biological Conservation*, **203**, 75–88.

Walker, B.G., Dee Boersma, P. & Wingfield, J.C. (2006) Habituation of adult Magellanic Penguins to human visitation as expressed through behavior and corticosterone secretion. *Conservation Biology*, **20**, 146–154.

Ware, H.E., McClure, C.J.W., Carlisle, J.D. & Barber, J.R. (2015) A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 12105–12109.

Weston, M. a., McLeod, E.M., Blumstein, D.T. & Guay, P.J. (2012) A review of flight-initiation distances and their application to managing disturbance to Australian birds. *Emu*, **112**, 269–286.

Whittingham, M.J., Butler, S.J., Quinn, J.L. & Cresswell, W. (2004) The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos*, **106**, 377–385.

Wilkes, B. (1977) The myth of the non-consumptive user. *The Canadian Field-Naturalist*, **91**, 343–349.

Wilson, D.S. (1998) Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **353**, 199–205.

Wilson-Aggarwal, J.K., Troscianko, J.T., Stevens, M. & Spottiswoode, C.N. (2016) Escape distance in ground-nesting birds differs with individual level of camouflage. *The American Naturalist*, **188**, 231–239.

Young, J.K., Olson, K.A., Reading, R.P., Amgalanbaatar, S. & Berger, J. (2011) Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. *BioScience*, **61**, 125–132.

Van der Zande, A.N., Berkhuizen, J.C., Van Latesteijn, H.C., ter Keurs, W.J. & Poppelaars, A.J. (1984) Impact of outdoor recreation on the density of a number of breeding bird species in woods adjacent to urban residential areas. *Biological Conservation*, **30**, 1–39.

Zanette, L.Y., White, A.F., Allen, M.C. & Clinchy, M. (2011) Perceived predation risk reduces the number of offspring songbirds produce per year. *Science*, **334**, 1398–1401.

Zaradic, P.A., Pergams, O.R.W. & Kareiva, P. (2009) The impact of nature experience on willingness to support conservation. *PLoS ONE*, **4**, 10–14.

# ACKNOWLEDGMENTS

First of all I want to thank you, Lukas Jenni and Zulima Tablado, for the great support and motivation during the entire PhD project. It was a great opportunity and finally success for me to carry out this PhD project in the Forêt domaniale de Chaux. I profited a lot from your experience in designing the study, leading through and successfully complete it and finally publish the findings. I would like to thank Lukas Keller and Alain Jacot, which formed my PhD committee together with Lukas Jenni. The committee meetings were always very fruitful and helped a lot to focus on a few targeted aims, which finally succeeded.

I would like to thank the entire “Fachbereich 6” headed by Susi Jenni-Eiermann, for the discussions and inputs which brought the entire project one step further.

I thank Susi Jenni-Eiermann, Bettina Almasi and Juanita Olano Marin for their guidance and help during the lab work; it was very pleasant to work in the Vogelwarte lab.

I thank Marc Kéry for his local knowledge of the French Jura region, which helped a lot to counteract certain reservations against our project. Thanks a lot for your visit on terrain.

I thank Renaud Scheifler and Bruno Dorbani for introducing us into the local affairs and for their help in obtaining permissions from the authorities in Franche-Comté.

Many thanks to Michel Romanski and Jean-Luc Dessolin from the ONF for their support “sur place”, open-mindedness for our project and finally the approval.

I thank Christian Stauffer and Ronald Schmidt who allowed us to collect data in the Sihlwald and provided the number of visitors.

I thank all field assistants and trainees who helped during the field work in France which laid the basis to the experimental study; in alphabetical order: C. Arnace, R. Baffoin, M. Crespo Ballester, S. Bühler, B. Garde, L. Gillespie, M. Hitt, F. Le Bagousse, F. Leugger, N. Mortier, J. Nouri, M. Quetstroey, A. Rouméas, J. Vasseur.

Thanks for statistical support go to Bettina Almasi, Marc Kéry and Fränzi Korner-Nievergelt.

I thank the two students Daniel Scherl (Bachelor thesis ZHAW) and Selina Gugelmann (Semester work ETH) for their efforts during field work in their own projects. The findings of these projects added a lot to this thesis.

Big thanks go to the entire staff at the Vogelwarte Sempach, the working environment was always very comfortable.

I thank all my friends and my parents Stephanie and Manfred for their support in different domains and the visits in France.

Finally I want to express my great gratitude to you, Hella, for your immense support during the two main field work seasons, where you collected a lot of the data. I could profit from your fieldwork experience not only with birds but also with field assistants, which facilitated for me the realisation of this project.

# CURICULUM VITAE

Name: Yves BÖTSCH

Date of birth: 14th October 1986

From: Wängi TG, Switzerland

Education:

2002-2005 Highschool at the “Mathematisch-Naturwissenschaftliches Gymansium” Bern-Neufeld, Matura with specialisation in Biology and Chemistry, supervised by Dr. D. M. Moser
Thesis-title: Habitat und Verhalten des Birkhuhns in der Region Lombachalp

2005-2008 University of Bern, Specialisation in Zoology, Bachelor-Thesis at the Division for Conservation Biology, supervised by Dr. P. Patthey and Prof. R. Arlettaz
Thesis-title: Does the black grouse (*Tetrao tetrix*) play the role of an umbrella species for alpine timberline arthropods?

2008-2010 University of Bern, Master-thesis at the Division for Conservation Biology, supervised by PD Dr. M. Schaub and Prof. R. Arlettaz
Thesis-title: Breeding dispersal of hoopoes in relation to reproductive success, sex and age (Bötsch, Arlettaz & Schaub 2012)

2010-2013 Part-time employment at the Swiss ornithological Institute for the Swiss ringing scheme and as scientific collaborator in the Hoopoe-project, in between trainee at the Landschaftswerk Biel-Seeland for several months

2013-2017 PhD-Thesis at the Swiss Ornithological Institute and at the University of Zurich, Institute of Evolutionary Biology and Environmental Studies, supervised by Prof. L. Jenni, Prof. L. Keller, Dr. A. Jacot and Dr. Z. Tablado (Meyrier *et al.* 2017; Bötsch, Tablado & Jenni 2017)

Attended Conferences:

2013: EOU, Norwich, Poster-presentation

2015: ICCB-ECCB, Montpellier, Speed-talk
DO-G, Konstanz, without own contribution

2016: ISBE, Exeter, Talk
DO-G, Stralsund, Poster-presentation

2017: SWIFCOB, Bern, without own contribution
EOU, Turku, Talk

Publications:

**Bötsch, Y.**, Arlettaz, R., & Schaub, M. (2012). Breeding dispersal of Eurasian Hoopoes (*Upupa epops*) within and between years in relation to reproductive success, sex, and age. *The Auk*, *129* (2), 283-295.

Meyrier, E., Jenni, L., **Bötsch, Y.**, Strebel, S., Erne, B., & Tablado, Z. (2017). Happy to breed in the city? Urban food resources limit reproductive output in Western Jackdaws. *Ecology and Evolution*, 7 (5), 1363-1374.

**Bötsch, Y.**, Tablado, Z., & Jenni, L. (2017). Experimental evidence of human recreational disturbance effects on bird-territory establishment. In *Proc. R. Soc. B*, 284 (1858), 20170846.

**Bötsch, Y.**, Tablado, Z., Scherl, D., Graf, R. & Jenni, L. Effect of recreational trails on forest birds: does human presence matter? *Biodiversity and Conservation, under review.*