

Differences in Flight-Initiation Distance Between Forest Birds in Anthropogenically Disturbed and Undisturbed Forests

ABSTRACT

Any prey is always trying to avoid predation and tries to survive as long as possible. Human disturbance was equalized with predation risk and because of the increasing human density the habitats overlapping between wildlife and humans and the negative impacts on wildlife rises steadily. We studied the adaptation which takes place in birds in highly disturbed forests compared to undisturbed forests while taking the flight-initiation distance (FID) as a metric for predation risk assessment. This distance describes where the bird flees from an approaching predator. Fleeing is costly and uses energy which otherwise would have been spent on tasks essential for survival and contribution to future fitness. Nine bird species were observed in three different forests. Two in Switzerland are suffering from high human disturbance (Allschwiler Wald near Basle 47°32'N 7°32'E and Sihlwald near Zurich 47°16'N 8°33'E) and one in France experiences almost no disturbance (Forêt de Chaux near Dole 47°5'N 5°41'E). It was found that all nine tested species in the highly disturbed forests Allschwiler Wald and Sihlwald showed shorter flight-initiation distances than in the undisturbed Forêt de Chaux. Many variables have been demonstrated to influence FID leading to inter- and intraspecific differences within an area of the same disturbance level. An increased starting distance of the approaching human and body weight of the species, a greater height above the ground and feeding as current occupation are leading to a greater FID. The location on the paths or off the paths, daytime and date were not found to have an impact on FID. To protect the animals and secure their continued existence such studies are important to build a base for management implications like determining buffer zones based on the measured FID in undisturbed areas or even creating wildlife reserves for very sensitive species.

SEMESTERWORK

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INTRODUCTION

As all animals are part of a food chain and everything is about eating or being eaten, most animals evolved anti-predator responses through evolution [1].

Genetic basis is the precondition that evolution respective natural selection can affect the anti-predator behavior. Thus when removing the predator pressure through isolation of the prey on an island the anti-predator behavior disappears at least to a certain extent [2]. This implies that anti-predator responses are dictated by the level of predator pressure acting on a population [3]. Moreover these findings can be underlined when thinking of young animals first encountering a predator. It is absolutely essential for survival to have an innate recognition ability of potential predators[1].

The other part influencing the behavior is learning by means of experiences. This part can clarify why some phenotypic plasticity in behavior exists [2]. Both aspects, heredity and learning from experiences, leads amongst other aspects to inter- and intra-specific differences in predatory responses [3, 4].

Walther was the pioneer in equalizing human disturbance with predation risk and quite recent his study got support by Alejandro Frid and Lawrence Dill [5]. They postulate that “nonlethal disturbance stimulus caused by humans are analogous to predation risk” because in both circumstances it leads to a distraction from fitness augmenting activities.

The increasing density of humans leads to accretive intersections of birds’ and humans’ habitats connected with more direct and indirect disturbances of life-sustaining activities of the birds. Direct impacts describe an intervention and modification of a habitat, e.g. by removing trees or draining wetlands. These activities lead to the removal of potential habitat and force the animals to migrate to other habitats of probably lower quality. Indirect disturbances caused by recreational activities are not removing habitats but lower the quality of them and animals can respond by either altering their behavior or by leaving their favored habitat [6].

Indirect effects caused by humans recreational activities can have numerous negative impacts on birds and also on other wildlife organisms (e.g. [5], [7], [8]). That’s why it is important to do some research about how strong humans disturb wildlife and how they respond to this impact.

A common metric in science for evaluating predation risk is the flight-initiation distance (e.g. [9], [10]) because one of the many options for a predatory response is flight [1]. The flight-initiation distance (FID), also called “flush distance” [11] or “escape flight distance” [12], describes in general the distance at which an animal flees from an approaching threat [9]. The flight-initiation distance is not fixed for an individual but is variable [13]. Every time when a prey is facing an approaching predator it has to balance between the costs of giving up its ongoing activity like feeding or looking for mating opportunities and the consequences of fleeing too late and getting caught by the predator. Hence what determines the flight-initiation distance is on the one hand the cost of disturbance that probably alleviates the reproductive success and on the other hand the risk of losing life when fleeing was not successful. Animals therefore always face a trade-off and have to find an optimized strategy to ensure the greatest contribution to future fitness [9] [14]. For example the cost of disturbance for a hungry individual that just found a good food source can be very high compared to a well-fed individual. In this case the benefit of taking the risk and waiting longer till flight than normal is bigger and therefore the flight initiation distance decreases [15].

According to different meta-analyses the predator’s and the prey’s characteristics as well as the environment can have an impact on the flight-initiation distance [16] [17] [18].

When considering humans as an approaching predator and birds as prey, it was observed that the higher the speed and the more direct the approach of the human is, the larger gets the flight initiation distance of the bird [19] [20]. But this observation cannot be generalized for

all places where the approach occurs. A study with American Robins could show a greater flight-initiation distance if the approaching human was not on a path [21]. These findings are indications for the habituation of animals that experience high levels of human disturbances [22].

Being off a path means also encountering a different environment. It could be shown that the risk assessment is varying according to shelter and vegetation cover. Prey far away from a shelter showed an increased flight-initiation distance [23] whereas a dense vegetation blocks the sight of an approaching threat and delays the detectability of the closer coming danger [9]. However not only the detectability of the predator but also the visibility from the prey affects the flight-initiation distance. Already early observations reported about the advantage of inconspicuous coloration of birds where not well camouflaged individuals were eaten more often by predators [24]. A cryptic prey has to think about whether it is better to flee when the predator is still at a great distance where flight success is highest or if it is better to remain motionless trusting that the approaching threat doesn't spot the prey and therefore saving the energy otherwise used for fleeing [25]. It is assumed that cryptic species will have a shorter flight-initiation distance than conspicuous species since cryptic animals have lower costs of remaining motionless at a place [9].

Not only coloration has an influence on the prey's flight-initiation distance but also the weight. Because heavier species have a greater inertia it is important to respond and flee earlier compared to lighter species with higher agility [4] [26].

Eventually for all prey, independent of coloration and weight, learning due to lifetime experience plays a central role on the reaction towards predators and comparably towards humans.

The main objective of this study is whether birds adapt to continuous human disturbance (i.e. reduce FID) or whether they increase FID, as has been observed with hunting [27]. I explored whether native forest birds become habituated to indirect human activities in the forest or if they get more sensitive and feel heavily disturbed through increasing levels of persons crossing the forests.

FID can serve as a measure to quantify what indirect influence the humans have on wildlife [28]. It provides information whether anthropogenic stressors impact the behavior and finally the whole ecology of animals. With species-specific flight-initiation distances it is possible to determine buffer zones for wildlife species and define disturbance-free areas to grant a co-existence of wildlife and humans [13].

MATERIAL AND METHODS

Study areas

The flight-initiation distance of native forest birds was measured in three different forests, which experience either a high level of human disturbance by different recreational activities (Allschwiler Wald in Basle and Sihlwald in Zurich, Switzerland) or almost no human disturbance (Forêt de Chaux near Dole, France).

The Allschwiler Wald (47°32'N 7°32'E) has a size of approximately 2.5 km² of which about 2.20 km² belong to the community Allschwil and the remaining 0.30 km² to the community Binningen [29]. The sampling area excluded protected zones and was therefore only about 2.1 km². The forest is dominated by deciduous trees (especially beech and oak) and exhibits often a sparse underground story.

The Sihlwald (47°16'N 8°33'E) has a size of 11 km² and is part of the cantons Zurich, Zug and Lucerne [30]. The sampled area comprises approximately 3.55 km². Zones with conifers

and deciduous trees are alternating where the ground cover is denser in patches with deciduous trees than in patches with conifers.

The Forêt de Chaux (47°5'N 5°41'E) in the department Jura in France measures about 200 km² from which our sampling area included about 2.55 km² [31]. The whole forest is subdivided in many plots, which are managed independently of each other resulting in either a very dense vegetation structure, not usable for data sampling, or quite open plots with dominantly old oaks and hornbeams. Coniferous trees were rather rare.

Data were collected in each forest for 6 days during 6 to 8 hours per day between 11 March 2016 and 11 April 2016. During this time period the trees were still without leaves and the visibility was not restricted. Dense vegetation would limit the sight of the birds and predators could approach closer which would lead to a smaller flight-initiation distance [9].

Study organisms

The selection of the study organisms was based on three criteria. The first requirement was, because of early measurements in the year, that the birds do not migrate in winter to warmer places or at least return back very early. Secondly, the bird species abundance in Switzerland as well as in France was of great importance. To be abundant is at least partly coupled with body weight. Heavier birds rely on more resources which entails larger territories wherefore bird species lighter in weight were chosen [32]. The focus was on the following twelve bird species: blue tit (*Cyanistes caeruleus*), common blackbird (*Turdus merula*), common chaffinch (*Fringilla coelebs*), common chiffchaff (*Phylloscopus collybita*), Eurasian nuthatch (*Sitta europaea*), European robin (*Erithacus rubecula*), great spotted woodpecker (*Dendrocopos major*), great tit (*Parus major*), marsh tit (*Poecile palustris*), short-toed treecreeper (*Certhia brachydactyla*), song thrush (*Turdus philomelos*) and winter wren (*Troglodytes troglodytes*).

Data Collection

Response Variable

FID was only measured in birds which were not affected by other humans or were not disturbed by us before [13]. Birds in groups were not measured because there is some evidence that the flight-initiation distance is influenced by group size [27] [33]. Also individuals engaged in intraspecific behaviors or nesting birds are probably too strongly distracted leading to a remarkably lowered attention. Consequently only single birds were measured for FID.

When a bird was localized and identified the starting distance was measured (distance between measuring person and bird after first detection) and afterwards I walked as straight as possible at a steady pace of approximately two steps per second towards the bird until it flushed [13]. Escaping is defined as flying or running away from the measuring person and this includes also moving to higher branches. The winter wren (*Troglodytes troglodytes*) was the only bird species where also moving to the ground was interpreted as fleeing because this species is jumping more likely in the brushwood on the ground than flying in the tree crowns. Due to its small body size it can perfectly hide in the undergrowth [34].

When the bird escaped I stopped immediately and measured the horizontal FID and the height above ground where the bird was sitting just before flight. The Pythagorean theorem can then be used to calculate the beeline FID [10].

To avoid remeasuring twice the same individual, we chose quite large study areas and measures were only done during a short time period (6 days) where each time another path through the forest was chosen. Double measuring of the same individual at two different trials cannot be excluded completely, but if at all, was on a very low level.

Explanatory Variables

The flight-initiation distance could be influenced by the type of the ongoing activity of the bird. Therefore I recorded the behavior of the bird at the moment of the measurement and classified it in three major groups namely singing, feeding or comfort by which resting birds were described.

Furthermore I recorded whether the approaching person had to leave the path or not when walking straight towards the bird, as according to other studies humans on paths might be more predictable than humans off paths why birds may consider humans on paths as less threatening which leads to smaller FID [35].

There are some indications that body mass is increasing during the day and theoretically could affect the flying ability and maneuverability [36] [37] [38]. That is why for every measured bird the time was noted to examine whether daytime affects the flight-initiation distance or not. The same was done for the date, i.e. to observe whether birds measured later in the year reacted differently compared to the birds measured at the beginning of the study.

To observe whether interspecific variation of FID could be influenced by the weight of the species the average of female and male weight of each species was calculated from literature data (see Appendix 1) [39].

Statistical Analysis

Statistical evaluations and graphics were performed in R (Version 3.2.3) with RStudio (Version 0.99.879) [40]. To recognize and explain correlations between the response variable (FID) and explanatory variables a regression analysis was used. These general linear (mixed) models of the lme4 package [41] enable us to estimate effects of the explanatory variables on the response variable [42]. The output of the linear mixed-effects model has to be interpreted with help of a Bayesian inference method where a 95% credible interval of an explanatory variable, which does not include zero, is treated as significant.

In 2015 during the same period of time (13.03.2015 – 18.04.2015) another team measured flight-initiation distances of different bird species in the same forest in France. To increase sample size, especially for the blackbird, the data from France from 2015 and 2016 were pooled. To control for the possible effects of the year and the observer, we included both as random factors in the linear mixed-effects models. In all models, general linear or linear mixed-effects models, starting distance and height were included as additive factors because significant effects on FID have been observed in earlier studies [43] [44].

Five models were fitted to test our hypothesis and to explain how variation in flight-initiation distances can be further explained (Table 2). The assumption of linearity between regressand and regressors as well as the audited normal distribution of errors allowed using general linear models and linear mixed-effects models [42].

A linear mixed-effects model was used to represent the overview model with data from 2015 and 2016 where the regressors starting distance, height, time and date were included as additive factors, species and forest were put in interaction to evaluate species-specific differences between the forests and, because of the pooled data sets, year and observer were added as random factors.

Following the main model, four further models were fitted to examine the effects of different factors on FID.

The difference between the starting distance and the flight-initiation distance, called buffer, was calculated for all measurements. In that way on the one hand a complicated three way interaction between species, forest and starting distance could be avoided and on the other hand this calculated buffer displays if the starting distance dissimilar influences the FID of the different bird species in all three forests. The fitted model was a linear mixed-effects model with the buffer zone as dependent variable. The height and forest in interaction with species were used as explanatory variables. Due to the pooled data observer and year were added as random factors.

To observe whether different activities have varying effects on FID again a linear mixed-effect model was fitted. This model included the additive effect of the activity and a random effect for species. Because the description of behavior differed between 2015 and 2016 only the data from 2016 were analysed.

With another general linear model we tested the effect of the location (on the path or off the path) on the FID of the different species. This could only be done for birds measured in Allschwiler Wald and Sihlwald because in France we could never measure any bird on the path. With a linear mixed effects model we looked at the effect of body weight of the different species in the three forests on the FID, including year and the observer as random factors.

Table 2

Five models either linear mixed-effects models or general linear models with all or a selection of data were fitted. The main model served to examine our hypotheses and the other four models were used to explain the remaining variation in FID.

	Main model	Buffer zone model	Activity model	Location model	Weight model
Fitted model	Linear mixed-effects model	Linear mixed-effects model	Linear mixed-effects model	General linear model	Linear mixed-effects model
Response variable	FID _{Horizontal}	Difference between starting distance and FID _{Horizontal} = Buffer zone	FID _{Horizontal}	FID _{Horizontal}	FID _{Horizontal}
Explanatory variables	Starting Distance Height Species*Forest Daytime Date	Height Species*Forest	Activity Starting Distance Height	Starting Distance Height Location*Species (Location = on/off path)	Starting Distance Height Weight*Forest
Random factors	Observer Year	Observer Year	Species		Observer Year Species
Data used	all	all	Without 2015	Allschwiler Wald and Sihlwald	all

RESULTS

Overall 644 measurements of FID from nine species have been collected in 2015 and 2016. Sample size varied between species because of variable abundance and detectability (Table 1). Because of small sample sizes great spotted woodpecker, blue tit and common chiffchaff were removed as test species.

Table 1

The sample sizes of measured FID by site and species. We excluded the following three species from the analysis due to too low sample sizes: blue tit, common chiffchaff and great spotted woodpecker.

Species	Allschwiler Wald 2016	Sihlwald 2016	Forêt de Chaux 2016	Forêt de Chaux 2015
Blackbird	12	49	1	11
Common chaffinch	34	37	27	22
Eurasian nuthatch	25	8	20	9
European robin	40	24	18	12
Great Tit	47	14	41	30
Marsh Tit	12	8	12	7
Short-toed treecreeper	6	5	9	3
Song thrush	4	11	7	4
Winter wren	25	20	20	9
Blue tit	6	3	17	7
Common chiffchaff	2	3	0	9
Great spotted woodpecker	24	3	5	5
Total	235	182	177	119

Main Model

The main model revealed that averaged over all bird species the FID in the undisturbed Forêt de Chaux was significantly larger compared to the FID in the Allschwiler Wald and Sihlwald. The flight-initiation distance in the Allschwiler Wald and Sihlwald did not differ significantly between each other. Almost all species showed a significant larger FID (interaction species*forest) in the Forêt de Chaux than in the other two forests, except the marsh tit and the song thrush (see Appendix 2 and 3).

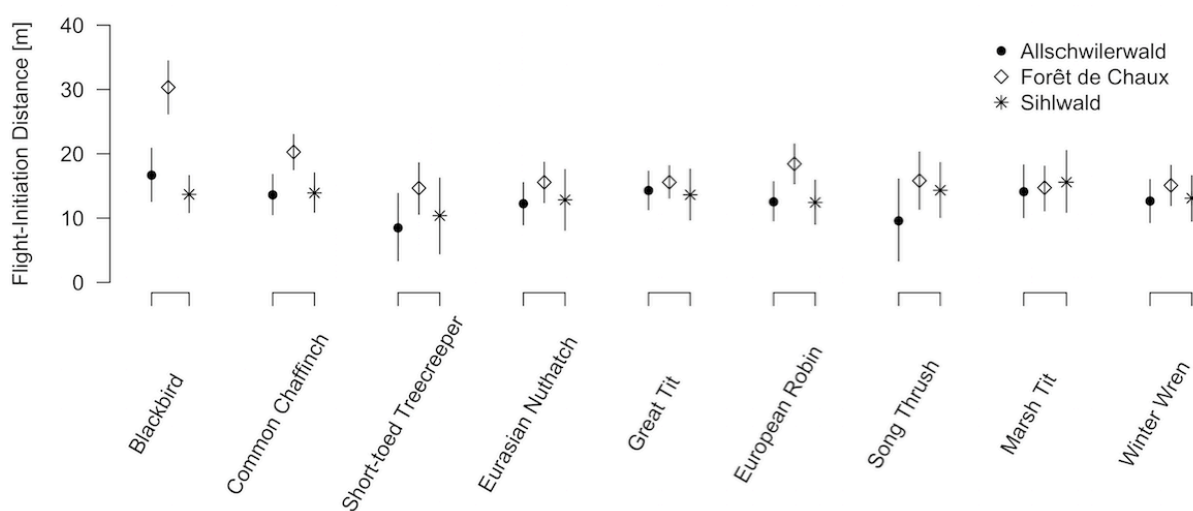


Figure 1. Model predictions of the flight initiation distances of the different bird species in the three forests. Represented are the mean estimates with 95% credible intervals for a starting distance set to 30m, for a mean height, mean date and mean daytime.

According to the main model also height had a significant effect on the flight-initiation distance the FID decreases by 0.50 m per meter higher above ground a bird is sitting. This value is averaged over all species at the 50% quantile.

Another explanatory variable was the starting distance. This variable had a significant effect on FID. Averaged over all bird species and all three forests the flight-initiation distance increased by about 0.50 m per additional meter of starting distance.

Not significant were the effects of time and date on FID.

Small scale differences in FID within forests due to different human disturbance intensities could not be analyzed properly due to missing measures for some species in some regions.

Buffer zone

When testing the buffer zone as response variable, no significant difference was ascertainable between the different forests and no species-specific discrepancies were detectable.

Activity

Birds feeding had a significantly shorter FID compared to birds in the comfort status (Figure 2). Comfort and singing did not differ significantly.

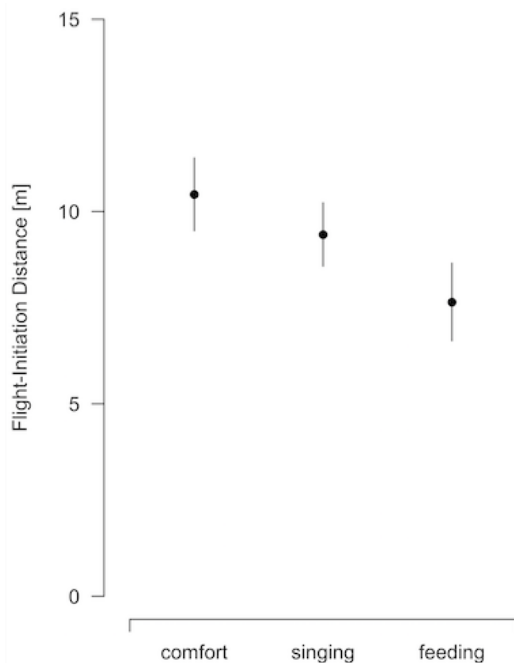


Figure 2. The computed flight-initiation distances where the species-specific effect is a random variable and not correlated with the explanatory variables shows that birds in a comfort condition have the largest flight-initiation distance. Singing leads to a not significant decrease in FID. Feeding on the other hand is the only activity which distinguishes itself significantly from the reference status comfort. Represented are the mean estimates with 95% credible intervals for a starting distance set to 30m and for a mean height.

Location

When approaching birds on the path, FID was significantly longer (~2.95 m) compared with birds approached off the path ($p < 0.05$).

However this result cannot be generalized and is not applicable to all species (Figure 3). Out of the nine species tested five (common chaffinch, short-toed treecreeper, Eurasian nuthatch, European robin and song thrush) showed a larger FID when the approach occurred on the path compared to off the path. But only the common chaffinch and the Eurasian nuthatch achieved a significantly different FID between the locations (interaction species*location, $p < 0.05$).

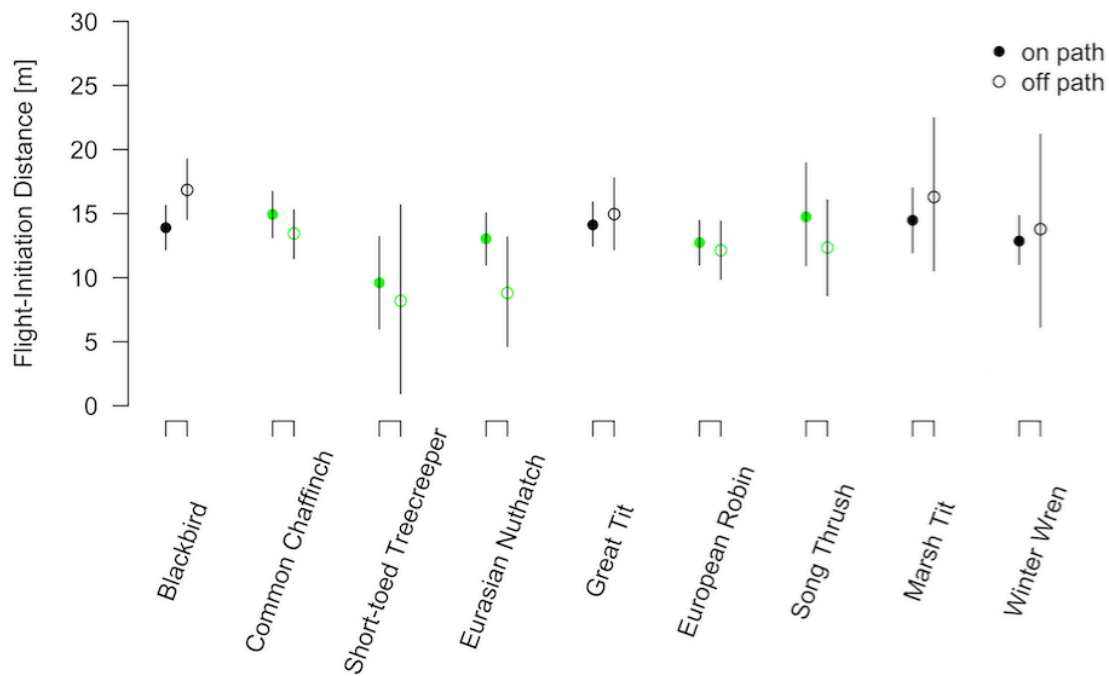


Figure 3. For every single species the average flight-initiation distance is shown in pairwise comparison between the two possible locations where the bird was measured, on the path or off the path. The black data points show those species that have a longer FID when measured off the path. The green data points in contrary show the bird species having a longer FID on the path. Shown are the mean estimates with 95% credible intervals represented for a starting distance set to 30m and for a mean height.

Weight

The analysis revealed that weight has within Sihlwald and Allschwiler Wald no major effect on FID (interaction forest *weight). However in Forêt de Chaux FID increases with weight what is represented in the visual presentation of the fitted model (Figure 4).

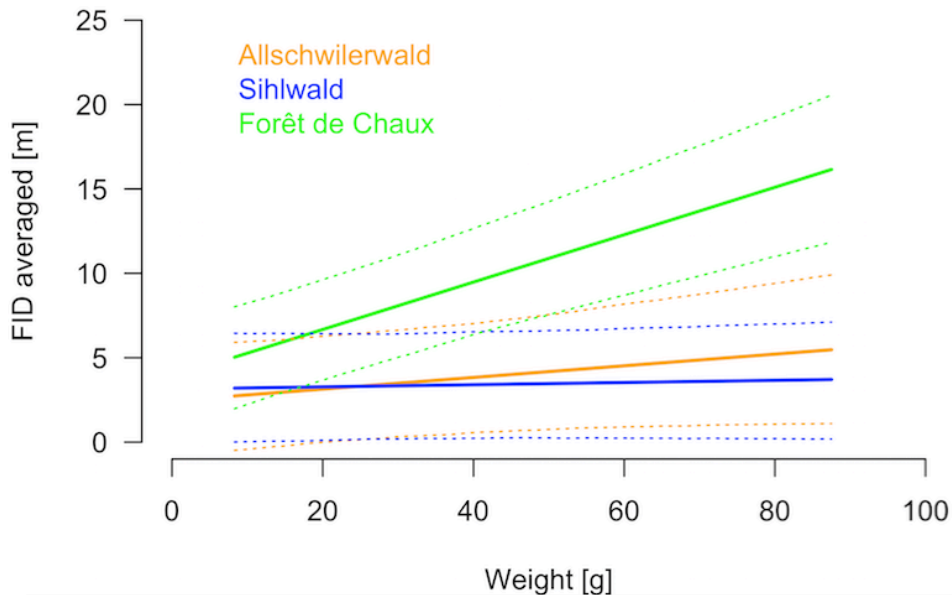


Figure 4. The influence of the weight on the flight-initiation distance and the related 95 % credible intervals for a starting distance set to 10m and a height set to 3m are shown for every forest separately. The influence of the year and the observer was included as random factors. In the Forêt de Chaux the weight has the greatest impact on the FID whereas the Sihlwald and the Allschwiler Wald do not differ significantly from each other. The plotted range of the x-axis was chosen in between the lightest and heaviest bird I measured.

DISCUSSION

In this study it could be clearly shown that birds exposed to a high human disturbance intensity adapt to this kind of disturbance. Almost all tested species had a shorter flight-initiation distance in the highly disturbed forests Allschwiler Wald and Sihlwald compared to the undisturbed Forêt de Chaux. The only bird species showing the largest FID not in the undisturbed Forêt de Chaux was the marsh tit with a minimal larger FID in the Sihlwald although this difference was compared to the Allschwiler Wald not significant. The missing significance and the manually calculated very small larger FID in Sihlwald compared to the Forêt de Chaux led to the assumption that this result is because of few measurements and therefore statistical uncertainty. The only bird species showing no significant result was the song thrush. This is probably again because of very few measurements in Allschwiler Wald and in addition the fact that they were almost always encountered on the ground in the Sihlwald and sitting very high in the tree crowns in the Forêt de Chaux which led to distortion of the measured FID.

Outstanding in the comparison of all species' FID between the three forests is the blackbird with its overall highest FID in Forêt de Chaux and also highest difference in FID between the three forests. Because in Allschwiler Wald and Sihlwald the FID of the blackbird is similar to the other bird species, the weight can't be taken to explain this discrepancy. 150 to 200 years ago the blackbirds began to colonize areas outside of the forest closer to human settlements in Central Europe. The example of the urbanization process of blackbirds shows clearly that adaptation to humans is possible even for this originally shy forest bird. But at places where the birds get hunted the urbanization process and thus the habituation to humans is inhibited [45]. In France every year 5.5 millions thrushes get killed by hunters of which one million are blackbirds [46]. In Switzerland the Regulation concerning hunt and protection of wild mammals and birds provides that self-help measures against the protected blackbird species is only allowed if damage caused by game animals occur [47]. This remarkable difference in hunting culture could be an explanation for the large difference in shyness of blackbirds in France and Switzerland. But nevertheless this explanation could also be used to explain at least partly the overall greater shyness of all bird species in France because also other songbirds get killed and eaten [48]. Another explanation for the larger flight-initiation distance particular for the blackbird could just be explained by the nature of this bird species. In different literature references *Turdus merula* is portrayed as very shy forest inhabitant. This characteristic could be either fully accountable for the observed shyness or at least a supplementary factor contributing to the timid behavior of the blackbird [49] [50] [51].

The starting distance showed a significant enlarging effect on the FID what means that a larger starting distance is coupled with a larger FID and a smaller starting distance with a smaller FID. Because of this positive colinearity the buffer zone was calculated which displays the difference between starting distance and flight-initiation distance [52]. If this buffer zone is not significantly different between the forests or between the species the theory of positive correlation can be supported. Otherwise a significant result would be an indication of independence between starting distance and FID. In our result we couldn't find a significant difference between the different forests nor between the different species what corresponds to the observations in earlier studies. Besides the influence of biological factors the positive relationship between FID and SD could also be caused by a mathematical artefact. This artefact comes about the relative distributions of SD, AD and FID. AD means the alert distance and describes the detection delay. AD is often difficult to measure and due to the assumption that SD and AD are highly correlated it was not measured in this study. If it is expected that $SD \geq AD \geq FID$ the variances of the variables are no longer homogenous and the assumptions of linear regression are not valid anymore. This can be illustrated when arbitrarily values of SD, AD and FID are selected from a uniform distribution the outcome is almost every time statistically significant positive relationships between these three factors [53].

Ydenberg and Dill 1986 postulated a decrease in FID if the cost of flight increases [9]. The result of our study obviously confirms this statement while feeding seems to be the most important activity compared to comfort or singing according to the significant decrease in FID. Feeding is imperative when thinking of future fitness and it looks like even more future contributing than singing which procure perhaps mating opportunities or defending a territory [54]. But singing is a trait of male birds and rather rare by female individuals. This result could therefore be biased by the sex of the birds. The sex was not recorded, because some species are difficult to distinguish from afar. If this would have been done only the males should have been included in this model to receive an unbiased and reliable result.

While the location on the path or off the path was not found to influence FID in this study, the weight of the species on the contrary seemed to have an effect. There's no significant effect of the weight on the FID in Allschwiler Wald and Sihlwald. The graph indicates only in Forêt de Chaux that heavier bird species fly earlier than lighter birds if a threat is approaching. This finding is congruent with the theory that smaller bird species are more agile and faster in reacting than larger species and due to this higher inertia they have to flee earlier which prolongs the flight-initiation distance [4] [26]. This result is strongly dependent on the large FID of the black birds observed in Forêt de Chaux.

Despite of a significant effect of the location on FID it was not considered as significant anymore after regarding the species-specific answers on the location.

This result does not comply with the expectations that a shorter FID was predicted when the approaching person could stay on the path when walking towards a bird. Here the opposite was found for some species with a longer FID on the path than off the path. This significant difference is only true if the result is averaged over all species. Regarding the species-specific outcome only the common chaffinch and the Eurasian nuthatch showed a significantly longer FID when the approach occurred on the path. All the other species' FID were not influenced by the location. Our two Swiss forests have a high network of paths and a lot of fireplaces are localized in the middle of the forest without any footpaths around them. People therefore have to cross through the forest to reach these places. That could be a reason why most bird species are habituated to encounter people everywhere in the forests and the hypothesis of smaller FID on the path is not applicable anymore.

MANAGEMENT IMPLICATIONS

The aim of studies testing the effects of anthropogenic disturbance on wildlife is to have a basis for management implications if a co-existence is endangered.

Based on the obtained results it could be assumed that the birds perfectly adapted to the high disturbance caused by humans. It is true that they adapted to humans but it is not necessarily true that they found an optimized energy-balance. Even though the individuals let the approaching human closer and did not react as sensitive as individuals not adapted to humans, it doesn't mean that they use less energy because of less amounts of flight. Consequences of the high energy loss can be higher disease susceptibility or lowered reproductive success and many more [55] [56]. Another option would be to move to other areas with fewer disturbances and causing a lower population density or even completely disappear [57] [58]. To save the birds from spending unneeded energy when fleeing from forest visitors the measured flight-initiation distances (in this study the one from France) should be used to determine buffer zones through restricting the building of forest fragmenting paths. Not all species are equally sensitive against disturbances why the size of these buffer zones can not be standardized. For individuals not habituating well, including also individuals which potentially already left highly disturbed areas and for this reason can not be measured, it even would make sense to establish wild nature reserve to protect them.

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Appendix

1) Calculation for the weight for the bird species [39]

<u>Species</u>	<u>Size (cm)</u>	<u>Weight M (g)</u>	<u>Weight F (g)</u>	<u>Average weight</u>
common chiffchaff	10.50	8.2	8.4	8.30
short-toed treecreeper	12.50	8.6	8.2	8.40
winter wren	9.50	10.3	9.7	10.00
marsh tit	11.50	10.5	11	10.75
blue tit	11.50	11.4	13.4	12.40
European robin	14.00	n.a.	n.a.	17.60
great tit	14.00	18.9	17.6	18.25
Eurasian nuthatch	14.00	23.2	21.9	22.55
common chaffinch	14.50	24	23.2	23.60
great spotted woodpeck	22.00	92.25	87.4	55.00
song thrush	23.00	n.a.	n.a.	67.60
blackbird	24-25	91	84	87.50

n.a. = not available

2) Calculation for species-specific flight-initiation distances according to the main model at starting distance an height equal to zero.

	Allschwilerwald	Sihlwald	Forêt de Chaux	
Blackbird	$3.96=3.96$	$3.96-3=0.96$	$3.96+13.64=17.6$	
Common Chaffinch	$3.96-3.08=0.88$	$3.96-3-3.08+3.32=1.2$	$3.96+13.64-3.08-6.97=7.55$	
Short-toed Treecreeper	$3.96-8.09=-4.13$	$3.96-3-8.09+4.82=-2.31$	$3.96+13.64-8.08-7.48=2.04$	
Eurasian Nuthatch	$3.96-4.41=-0.45$	$3.96-3-4.41+3.5=0.05$	$3.96+13.64-4.41-10.27=2.92$	
Great Tit	$3.96-2.41=1.55$	$3.96-3-2.41+2.32=0.87$	$3.96+13.64-2.41-12.34=2.85$	
European Robin	$3.96-4.16=-0.2$	$3.96-3-4.16+2.91=-0.29$	$3.96+13.64-4.16-7.75=5.69$	
Song Thrush	$3.96-7.19=-3.23$	$3.96-2.92-7.19+7.75=1.6$	$3.96+13.64-7.19-7.31=3.10$	n.s.
Marsh Tit	$3.96-2.54=1.42$	$3.96-3-2.54+4.45=2.87$	$3.96+13.64-2.54-13.05=2.01$	
Winter Wren	$3.96-4.06=-0.1$	$3.96-3-4.06+3.51=0.41$	$3.96+13.64-4.06-11.14=2.4$	

3) Complete output of the main model

Model output with Bayesian 95% credible interval (upper and lower limit represented with 2.5% and 97.5%). If 0 is not included in the interval of the tested variables the result is significant.

	Intercept	Forest	Explanatory Variables	Species	Interaction between Forest and Species	
					Forêt de Chaux	Sihlwald
2.5%	-2.212342	Forêt de Chaux 8.746625	Starting Distance 0.4865325	Common Chaffinch -6.8803764	Common Chaffinch -12.369791	Common Chaffinch -1.229144
50%	3.959302	13.653044	0.5292738	-3.0805768	-6.965924	3.323958
97.5%	10.179126	18.653163	0.5708437	0.8179951	-1.220885	7.911275
2.5%		Sihlwald -6.6263093	Height -0.6210942	Short-toed Treecreeper -14.210022	Short-toed Treecreeper -15.238156449	Short-toed Treecreeper -3.161736
50%		-2.9232119	-0.5085884	-8.085237	-7.479655154	4.816167
97.5%		0.7116782	-0.4027111	-2.294789	0.009427245	12.853436
2.5%			Time -0.7043527	Eurasian Nuthatch -8.4925576	Eurasian Nuthatch -16.112285	Eurasian Nuthatch -2.549526
50%			-0.2187781	-4.4078640	-10.273070	3.503613
97.5%			0.2830353	-0.3051747	-4.503218	9.674477
2.5%			Date -0.60194816	Great Tit -6.001862	Great Tit -17.70244	Great Tit -2.860932
50%			-0.008055427	-2.413936	-12.33571	2.321207
97.5%			0.044369346	1.357296	-7.01957	7.375574
2.5%				European Robin -8.0442130	European Robin -13.216881	European Robin -2.007798
50%				-4.1629204	-7.747213	2.911022
97.5%				-0.2413183	-2.138910	7.538761
2.5%				Song Thrush -13.8977626	Song Thrush -15.783267	Song Thrush -0.04165875
50%				-7.1943925	-7.313282	7.75397930
97.5%				-0.4042117	1.358764	15.31854633
2.5%				Marsh Tit -7.322669	Marsh Tit -19.725481	Marsh Tit -1.947277
50%				-2.539266	-13.050572	4.452781
97.5%				2.310673	-6.333969	10.952122
2.5%				Winter Wren -8.0801644	Winter Wren -16.936732	Winter Wren -1.658661
50%				-4.0632403	-11.140534	3.513395
97.5%				0.1155652	-5.305495	8.509474