Riparian vegetation provides crucial shelter for resting otters in a human-dominated landscape

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Abstract

In many anthropogenic landscapes, the riparian vegetation belt is one of the few remaining covered structures for wildlife. It provides shelter for many species and functions as corridor. However, this landscape is increasingly used by humans for their leisure activities. The loss of riparian vegetation with a concurrent increase of human disturbance in these habitats can pose a serious threat to wildlife.

One of the species potentially affected is the Eurasian otter (*Lutra lutra*). In the Alps, otters are nocturnal and rest during the day when human activity is high. To study the impact of human presence on resting site selection of otters we radio-tracked nine otters for up to 30 months from 2010 to 2013 in the eastern Central Alps in Austria. We analysed resting site selection in relation to human disturbance.

Altogether, we identified 285 resting sites. They were scattered throughout the territories of the individual otters. The average distance between the resting sites was 144 m. 95% of the resting sites were situated in the riparian vegetation, stressing the natural riparian vegetation as an important variable. We found evidence that human disturbance shapes resting site selection. While otters rested in small riparian strips when there was no human presence, they selected areas with a wider vegetation belt when the disturbance level increased. Outside the vegetation period, animals rested below ground more often than above, indicating that vegetation functions as visual cover.

Our study highlights the importance for wildlife to restore riparian stretches where human activities are intense. A combination of spatial distribution of resting sites and the habitat requirement under human disturbance provides information for effective conservation measures for otters of which also other wildlife may benefit.

Key words

Resting site selection, *Lutra lutra*, human disturbance, conservation, riverine landscape, radiotracking

Introduction

The availability and quality of resting sites is a crucial component for the occurrence of a species (Manning et al., 2013) as it affects individual fitness and survival (Lutermann, Verburgt, & Rendigs, 2010). Besides thermoregulatory benefits and protection from adverse weather conditions, resting sites provide shelter from predators (Semeniuk & Dill 2005). Although the use of resting sites against predation is most accentuated in prey species (Martín and López, 1999), predators also make use of safe habitats for rest (Llaneza et al., 2016; Oriol-Cotterill et al., 2015).

In many anthropogenic landscapes the riparian vegetation belt is one of the few remaining structures that provide cover for wildlife. But riparian areas are also highly attractive landscapes for human leisure activities (Kienast et al., 2012), with a preference for stretches of natural habitat (McCormick et al., 2015). Human disturbance is one of the determinants for the distribution of many species (Murphy and Romanuk, 2014), e.g. by eliciting a strong anti-predator response that exceeds the reaction to natural predators (Ciuti et al., 2012). The loss of riparian vegetation with a concurrent increase of human activities may pose a serious threat to the survival of widlife in these habitats.

One of the semi-aquatic species potentially affected is the Eurasian otter (*Lutra lutra*). Populations of this species have declined in the last century due to habitat fragmentation, persecution and pesticides (Foster-Turley et al., 1990). Slow recovery of some populations have been observed in the last few decades (e.g. Janssens *et al.* 2006; Prigioni, Balestrieri & Remonti 2007).

Otters are able to persist in anthropogenic landscapes (Madsen and Prang, 2001; Marcelli et al., 2012; Weinberger et al., 2016), but human disturbance remains a major concern (Barbosa et al., 2001; Loy et al., 2009). Riparian vegetation is a key landscape feature in determining the presence of otters (Kruuk, 2006). Besides a positive effect on fish biomass (Gregory et al., 1991), riparian vegetation may provide important cover for resting otters as shown for other carnivores (Santos et al., 2011).

Due to their secretive and nocturnal lifestyle, few studies have investigated resting site selection of otters in freshwater systems and information remains scarce (e.g. Green, Green & Jefferies 1984; Beja 1996; Durbin 1998). These studies have found that resting sites are mostly situated close to water bodies. They can be located either above ground (“couches”) or in cavities below ground (“holts”) and are found in reeds, brambles, under trees, or in boulders (Beja, 1996; Durbin, 1998; Green et al., 1984; Kruuk, 2006). Otters use several resting sites within their territories (Beja, 1996; Green et al., 1984; Libois and Rosoux, 1991), and resting sites are thought to be clustered within the territory (Green et al., 1984).

In other mustelid species, adverse weather conditions have been shown to influence resting site selection (Baghli and Verhagen, 2005; Slauson and Zielinski, 2009). Alternatively, humans may shape resting site selection. It has been proposed that otters may prefer holts over couches in areas with human disturbance, in contrast to areas where human activity is low (Libois and Rosoux, 1991; Loy et al., 2009; Ruiz-Olmo et al., 2005). So far the impact of human activities on resting site selection remains inconclusive (Beja, 1996; Durbin, 1998; Green et al., 1984).

With an increasing human impact on riparian habitat, the availability of suitable resting sites could be a limiting factor for otter occurrence. Thus, information is required on resting site, selection in areas with human pressure in order to facilitate recovery and persistence of otter populations. Detailed knowledge about habitat requirements and the spatial distribution of resting sites can provide guidance for conservation measures and mitigate conflicts.

In this study, we analysed resting site selection of otters in relation to riparian habitat and human disturbance in an anthropogenic landscape in the Alps. Here, the riverine landscapes have changed massively in the past 50 years due to an increase of industry, tourism and other human activities (Comiti, 2012). Today, many watercourses are channelized and their riparian vegetation belts are reduced or lost (Comiti, 2012; Ewald and Klaus, 2009). Human pressure is high: roads in the valleys are often built close to the watercourses while a multitude of paths within the original riparian vegetation is used for leisure activities like jogging, hiking or fishing. People are often accompanied by dogs, which could increase anti-predator responses of otters (Blanc et al., 2006; Kruuk, 1995). Nevertheless, otter populations in France (Dauverine and Chasserieau, 2012), Austria (Kranz and Poledník, 2015, 2012), Italy (Pavanello et al., 2015) and Switzerland (Weinberger, 2017) are expanding into the Alpine Arc again.

To test the hypothesis that otters minimize human disturbance by avoiding resting near roads or paths, we used an extensive set of radio tracking data of wild otters collected in the Alpine Arc. Additionally, we investigated if otters show a preference for resting sites hidden within a large riparian vegetation belt or for resting sites below ground depending on human disturbance. Following Green et al., 1984, we also predicted resting sites to be clustered within each territory.

Methods

Study area

The field study was conducted from May 2010 to March 2013 in the eastern Central Alps in Styria, Austria (N47°24’36”, E15°16’7”). The study area covered approximately 1760 km^2, with about 3090 km of streams and rivers (Fig. 1). All watercourses belong to the catchment basin of the river Mur (mean annual discharge of approx. 110 m^3/s). The river Muerz (mean annual discharge of 20 m^3/s), forms the main valley of the study area. The elevation of the valley floor ranges from 458 to 974 m, with the surrounding mountains up to 1850 m. Urban areas, intensive agriculture, and iron industry dominate the lower valleys. Agriculture, forestry, and small settlements contribute to the landscape in the higher valleys. Many stretches of the watercourses are modified or regulated for electrical power exploitation. In many parts, the riparian vegetation strip is lost or reduced to a width of one to eight meters. Along river banks, people often practice outdoor activities such as jogging, cycling and fishing.

Capture and radio tracking

Captures took place in spring and autumn between 2010 and 2012. Otters were trapped with soft-catch traps with rubber pads (No. 3, Oneida Victor Inc., Cleveland, Ohio) coupled with GSM trap alarms (Ó Néill et al., 2007). Within 30 minutes of capture, animals were removed from the traps. After the intraperitoneal implantation of the transmitter (model 325/L, model 400/L, Telonics Inc., Mesa, Arizona) in a vet-ambulance, the animals were released within 24 hours of capture in close proximity to their capture site. Animals were tracked up to four times a week between sunrise and sunset, spaced out over the day. Initially, the animals were tracked several times during the day in order to ascertain the use of a single resting site per day. Tracking of otters in resting sites was conducted by a single person by foot using a receiver (Sika, Biotrack Ltd, Dorset UK) and a handheld 3-element Yagi-antenna. The activity of the animals was deduced from the variation in signal strength and classified into three categories: (1) active, (2) passive, and (3) unknown when the activity could not be determined. When passive, the resting site was identified by homing-in to an accuracy of <5 m. All resting sites were georeferenced using a portable GPS (Etrex 10, Garmin Ltd.). Animals were tracked until the transmitter failed, the animal disappeared, or until the end of the field study in March 2013. Data for the first ten days after surgery were discarded.

Habitat variables

Environmental parameters of newly identified resting sites were assessed at a later date when the animal was absent. The type of resting site was categorized into one of the three following classes: “couch” (above ground, in the vegetation, or in a structure such as a stick pile), “holt” (below ground) and “unknown” (no clear assignment possible). The type of resting site could often be attributed to the presence of a single structure where the resting site was located, e.g. stick pile or crevice in the river bank. Only in 43 out of 262 resting sites (16%) no classification was possible. The type of water body closest to the resting site was categorized into three classes: a) “main riverbed” (used as reference category in all analyses), b) “abstracted water” (water derived from the main river for electric power generation) and c) “standing water” (ponds and wetlands, Appendix Fig. 1). Riparian vegetation width was measured at the resting site. The type of vegetation was classified into three categories of naturalness (Appendix Fig. 2), namely “natural” (trees, bushes, reed or herbaceous stretches with at least a tree or bush within 25 m along the bank side; used as reference categories in all analyses), “modified” (grass or herbaceous plants, no trees within 25 m along the bank side), or “artificial” (no vegetation).

The riparian vegetation can function as a visual protective cover. In the study area, the riparian vegetation belt is quite fragmented and its potential as a visual cover is reduced. Locally, the land use along the watercourses is very intense, reducing the width of the natural riparian belt to less than 1 m. The visual cover provided by the vegetation also changes throughout the year, e.g. tall vegetation is flattened and the deciduous trees and shrubs have lost their foliage, resulting in a loss of visual protection. To acknowledge for this effect, we incorporated a binary indicator for the vegetation period (1 = during vegetation period, 0 = outside vegetation period). Onset and end of this period varied within the study area and are considered to coincide with the date when the average daily temperature rose above- or felt below 10°C, respectively (data provided by the GIS office in Styria, Austria). Local temperature and snow cover data were provided by the meteorological stations in Styria, Austria.

Assuming that otters flee into the water only when the source of disturbance is on their bank side, we calculated the distance to the nearest disturbance on the bank side of the resting site. Disturbances included a) distance to the nearest road or path (whichever was closer), and b) human disturbance. Anecdotal data by Green *et al*. (1984) indicated that otters respond only to very close disturbances. Also, otters use several resting sites within their territories throughout the year, sometimes switching them daily. We therefore incorporated the likelihood of experiencing disturbances at two different temporal scales: year and day. Alternatively, otters may habituate to human disturbances depending on their predictability. In a working area, humans move along the predefined paths which can be anticipated by the local wildlife. This might be contrary to the erratic pathways, free ranging dogs may take. To take these considerations into account, we estimated human disturbance for three types of disturbances within 15 m of the resting site (Table 1): 1. Likelihood of disturbance over the year categorised as “none” (area not accessible; reference category), “occasionally” (in proximity to farmland but no path), or “daily” (close to roads or houses). 2. Likelihood of human disturbance throughout the day, estimated by the existence and use of paths or roads: “none” (not accessible or no path discernible; reference category), “once” (rarely used hiking paths), “every few hours” (cycling paths and tracks), or “permanent” (working sites or in settlements). 3. The predictability of the daily disturbance classified into four categories with decreasing predictability of their movements: “none” (no activity; reference category), “working” (industrial zones, settlements and farmland), “spare time” (people jogging, hiking, or fishing), and “dogs” where dogs were taken for walks or lived (spare time, house, or farming). When several categories were present, the one with the lowest level of predictability was used (spare time with dogs < spare time < working < none). All habitat variables were then attributed to the locations using ArcMap 10 (ESRI, 2011).

Selection of resting sites

For each individual, a set of all known resting sites and an equal number of alternative random locations was drawn from the available area. This area was defined for each individual by a buffer around the waterbodies within its home range, excluding the tributaries. Home range size was estimated with a 95% fixed kernel (for details see Weinberger *et al.* 2016 and Fig. 2). The width of the buffer around the waterbodies was calculated to be 24 m, which equals the mean + 2 SD of the distance of all tracked resting sites to the nearest water body. Where riparian vegetation was missing, e.g. within settlements or along roads, we added a buffer of 1 m to ascertain that all types of vegetation were included in the available area without forcing an over-representation of the type “artificial”. For all those locations, habitat type, vegetation width, vegetation type, distance to the nearest path, likelihood of human disturbance throughout the year, likelihood of human disturbance throughout the day and predictability of the daily disturbance were estimated (Table 1, “A”). All continuous variables were centred and scaled (mean of 0, variance of 1). A standard logistic regression model was fitted with a binary response variable as indicator for available (0) or used (1) locations. All variables were first included as fixed effects, plus a random intercept for the individuals. The model with the lowest AICc was selected (Burnham and Anderson, 2002). Given the slope coefficients $\beta_1, \ldots, \beta_n$,a Resource Selection Function (RSF) is obtained from

$$RSF = w(x) = \exp(\beta_1 x_1 + \ldots + \beta_n x_n),$$

where x = (x_1, …., x_n) are the predictor variables included as fixed effects (Manly et al., 2002). For any value of the independent variables, w(x) corresponds to the respective proportion between the frequency of use (f_u) and the availability (f_a), and reflects the preference for a habitat with covariates x compared to its availability. Values of w(x) > 1 represent habitats that were over-proportionally used by the animal with respect to their availability and w(x) < 1 represents habitats that over-proportionally used.

Selection of the type of resting site

Otters use either holts or couches as resting sites. This selection may be driven as protection either to adverse weather conditions or to disturbance elicited by humans. In order to identify the driving force of this selection, we carried out a complementary analysis focussing on the type of resting site. We used the complete data set of all individuals throughout the tracking period. We discarded all data where the type of resting site could not be attributed to either holt or couch. This resulted in 1720 data points (mean = 191 per animal, range = 18 - 441). A logistic regression was applied with the resting site type encoded as binary response variable (0 = below, 1 = above ground) and the variables habitat type, vegetation width, vegetation type, vegetation period, temperature, snow cover, distance to the nearest path and human disturbance throughout the year, human disturbance throughout the day and predictability of the daily disturbance (Table 1, “B”) as explanatory variables.

Distribution of resting sites within the home range

Otters use multiple resting sites throughout the year. Location and distribution of good quality habitat for resting sites may be crucial for the establishment of a territory. We therefore measured the distances between the resting sites along the main watercourses and calculated the 50% and 95% quantiles of the respective distribution in order to obtain an estimate of both typical and limiting distances.

Results

Between May 2010 and March 2013, 13 otters were captured. Of those, nine otters (three males and six females) were radio tracked for an average of 655 days (range = 229 - 1032). Their resting sites were successfully located on 1814 days (mean = 208, range = 65 - 399), excluding 60 occasions (3.2%) when individuals were not found. The animals were nocturnal and they remained in their chosen resting site throughout the day. Only in July and August, rare diurnal sallies were noted. Animals were tracked at a total of 305 distinct resting sites, with an average number of 33 resting sites per individual (range = 14 - 54, Fig. 2 and Appendix Table 1). Nine resting sites were used by two different individuals. The composition of the individuals involved varied depending on the resting site but were always of opposite sex. Descriptive data could be obtained for 285 resting sites. Of those, 271 (95%) were within the riparian vegetation and eight (3%) were either situated in the riparian vegetation but disconnected by a hiking path from direct access to the water or were holts in revetments with no vegetation. Only six resting sites (2%) were outside the riparian vegetation, all above ground.

Selection of resting sites

The dataset for this analysis included a total of 285 resting sites, plus the same number of random locations. The model with the lowest AICc included the variables habitat type, vegetation width, vegetation type, distance to the nearest path, likelihood of human disturbance throughout the day, the predictability of the daily disturbance, the interaction between vegetation width and the likelihood of human disturbance throughout the day, plus the animal-specific random slope for distance to path (Table 2). Vegetation type was included in all three models with lowest AICc (Appendix Table 2), and the best model indeed provides very strong evidence that it is an important explanatory variable ($p<0.001$). Compared to random locations, animals preferred resting sites in areas with a natural vegetation type (estimates for the categories *modified* and *no vegetation* were both clearly negative, with $p<0.001$ and $p = 0.005$, respectively). There is some evidence that resting sites are selected further away from paths (estimate = 0.39, $p = 0.05$). Besides vegetation type, likelihood of human disturbance throughout the day was retained in all three models with the lowest AICc. Human disturbance was associated with the choice of resting site locations in dependence of the vegetation width ($p<0.001$ for the respective interaction term, see Fig. 3 for a graphical representation). In the absence of daily human disturbance, animals over-proportionally used resting sites with riparian strips up to 10 m wide (Fig. 3a). However, this preference changed when there was a high frequency of daily human disturbance, with otters then preferring areas with larger vegetation width, although the uncertainty in the RSF was large (Fig. 3d). In the presence of intermediate disturbances, the otters showed no clear preferences on vegetation width (Fig. 3b and c).

Selection of the type of resting site

The type (couch or holt) could be assessed for 262 resting sites. 102 resting sites (40%) were situated above ground and 160 below ground. For 43 resting sites a clear classification was not possible. They were omitted from this analysis. The model with the lowest AICc included riparian vegetation width, vegetation period, temperature, distance to nearest path, likelihood of human disturbance throughout the day, and the interaction of vegetation width and likelihood of human disturbance throughout the day (Table 3; for the three models with lowest AICc, see Appendix Table 3). Given the very similar AICc value for the first two models, we also present the results of the model with the second lowest AICc in Appendix Table 4 to illustrate the robustness of the main findings. There was very strong evidence that the likelihood of human disturbance in combination with vegetation width shapes the selection of resting site structures (interaction $p<0.001$). At sites without daily human disturbance, sites were more likely to occur above ground than below where vegetation was wider (estimate 0.37, $p = 0.001$). However, for human disturbance once a day, no clear preference can be seen (estimate for the regression slope for vegetation width is not directly visible from Table 3; it is the sum of the reference category= 0.37 and the respective interaction -0.31, thus $0.37 - 0.31 = 0.06$). Surprisingly, disturbances every few hours seem to invert this preference, that is, animals then are more likely to sleep below ground with increasing vegetation width and above ground at small vegetation width. The opposite is indicated for permanent disturbance, where again wider vegetation width correlates with more resting sites above ground. Outside of the vegetation period, animals tended to sleep below ground more often than during the vegetation period (estimate = -0.86, p<0.001).

Distribution of resting sites within the home range

Resting sites were distributed throughout the territory (Fig. 2). Distances between the resting sites varied between a few meters and up to 5000 m. The median showed that half of the resting sites were located within a distance of 144 m. 95% of all resting sites where spaced within 1755 m.

Discussion

Our study illustrates the influence of human presence on resting site selection of a nocturnal carnivore in a modified landscape. It also highlights the importance of natural riparian vegetation cover as a habitat requirement for resting sites of otters. This is contrary to the foraging habitat selection where the species appears to be largely indifferent to the naturalness of the watercourses (Weinberger et al., 2016).

In anthropogenic landscapes, human presence is a driving factor for resting site selection. At low levels of daily human presence, riparian vegetation width plays a marginal role. However, once humans move around a resting site regularly throughout the day, the animals seem to require a wide riparian vegetation strip. This suggests that otters perceive humans as a threat. However, resting site selection may not entirely be driven by human disturbance, but may also be influenced by fine scale habitat conditions or distances to foraging sites. At the same time, resting sites could also be traditional sites: some of the resting sites found could have been used by otters since decades as shown in Wales (Chanin, 2013) and thus before the increased presence of humans.

Studies investigating the effect of human presence on habitat selection (Baltrūnaitė et al., 2009; Barbosa et al., 2001; Durbin, 1998; Juhász et al., 2013; Weinberger et al., 2016), and resting site selection (Beja, 1996; Green et al., 1984; Libois and Rosoux, 1991) of otters have led to controversial results. Those studies used different variables to measure human disturbance, usually with a proxy: e.g. roads (Durbin, 1998; Weinberger et al., 2016), houses (Baltrūnaitė et al., 2009; Juhász et al., 2013), or human and road densities (Barbosa et al., 2001). However, the substitution of a variable that is difficult to measure entails the risk that the outcome of the analysis does not represent the actual influence of the variable of interest . By estimating human disturbance in close proximity to the resting site, we measured its immediate impact on the selection of resting sites. Whereas this variable is of limited use for large-scale habitat suitability modelling due to the lack of available information on fine scale disturbances, the results are highly informative to guide conservation management.

Otters use resting sites above and below ground. The selection of these sites might be driven either by adverse weather conditions or as a protection against disturbances. We show that vegetation cover had a stronger effect on resting site type selection than temperature, indicating indeed a relationship of the vegetation and its function as a visual protection from predators. This is different to other studies that stressed the importance of thermal cover characteristics in medium sized mammals (Baghli and Verhagen, 2005; Brainerd et al., 1995; Weber, 1989). While holts are preferred resting sites in winter, presumably due to a lack of vegetation cover, holts were used also in summer. Especially during hot weather thermal insulation might be an important driver. Dense fur can result in overheating, because otters dissipate heat only through the small body surface of their feet (Kuhn and Meyer, 2009). Within holts the temperature might be more stable and cooler in summer than the temperature in couches. Thus, holts can also be important structures during peaks of hot weather.

Altogether, our findings support other studies on different animal species where the riparian vegetation is of major importance (Bennett et al., 2014; Matos et al., 2009; Medina Vogel et al., 2003; Naiman et al., 1993; Semlitsch and Bodie, 2003; Sepulveda et al., 2007). In areas otherwise devoid of natural vegetation, the riparian landscape provides the only remaining cover structure for wildlife. Exactly this vegetation belt is disappearing in many areas due to intensification in agriculture, flood management, and urbanization (Comiti, 2012). Our results stress the need for conservation action to protect riparian vegetation and thus facilitating the recovery of this semi-aquatic carnivore. Beside good foraging habitat and an unpolluted environment, safe resting sites are crucial requirements for the long-term recovery of otters. Especially for reproducing females, resting sites with no disturbance are of high importance (Beja, 1996; Durbin, 1996). Information on key habitat features of the focal species are therefore important, particularly in the light of limited financial funding for conservation measures. Using the information on the number and the spacing of resting sites of otters within the watercourses, management plans for otter conservation can be efficiently addressed. In riverine landscapes where human pressure is high, we believe that the establishment of riparian vegetation refuges with restricted access for humans provides a feasible solution. These refuges ideally encompass a vegetation belt of at least 15 m width. They should be spaced along any waterbodies, with an ideal interval of 140 m. Such small stretches of natural riparian vegetation left exclusively for wildlife along the human-dominated watercourses may be necessary for otters to be able to persist in such a landscape.

By combining resting site selection with the spatial distribution of those sites, a holistic approach along the watercourses is feasible. While thus targeting otter conservation, such refuges will be beneficial to numerous other species.

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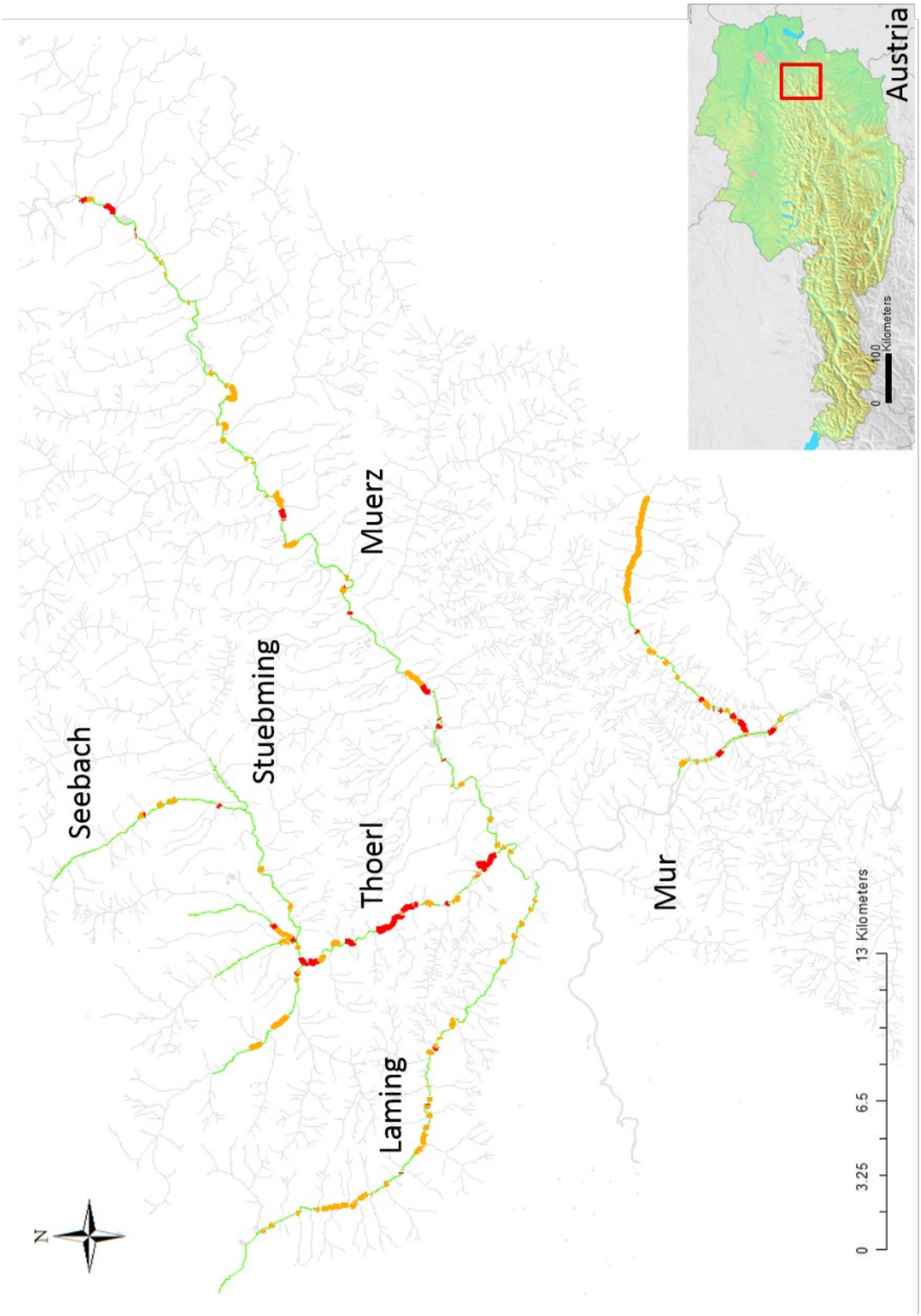


Figure 1. Study area in the eastern Central Alps in Styria, Austria, defined by the minimum convex polygon for all otters, showing the running waters (with names of main streams). Vegetation type of all main riverbeds within any home ranges was assessed: green = natural (vegetation), orange = modified (vegetation) and red = artificial (no vegetation).

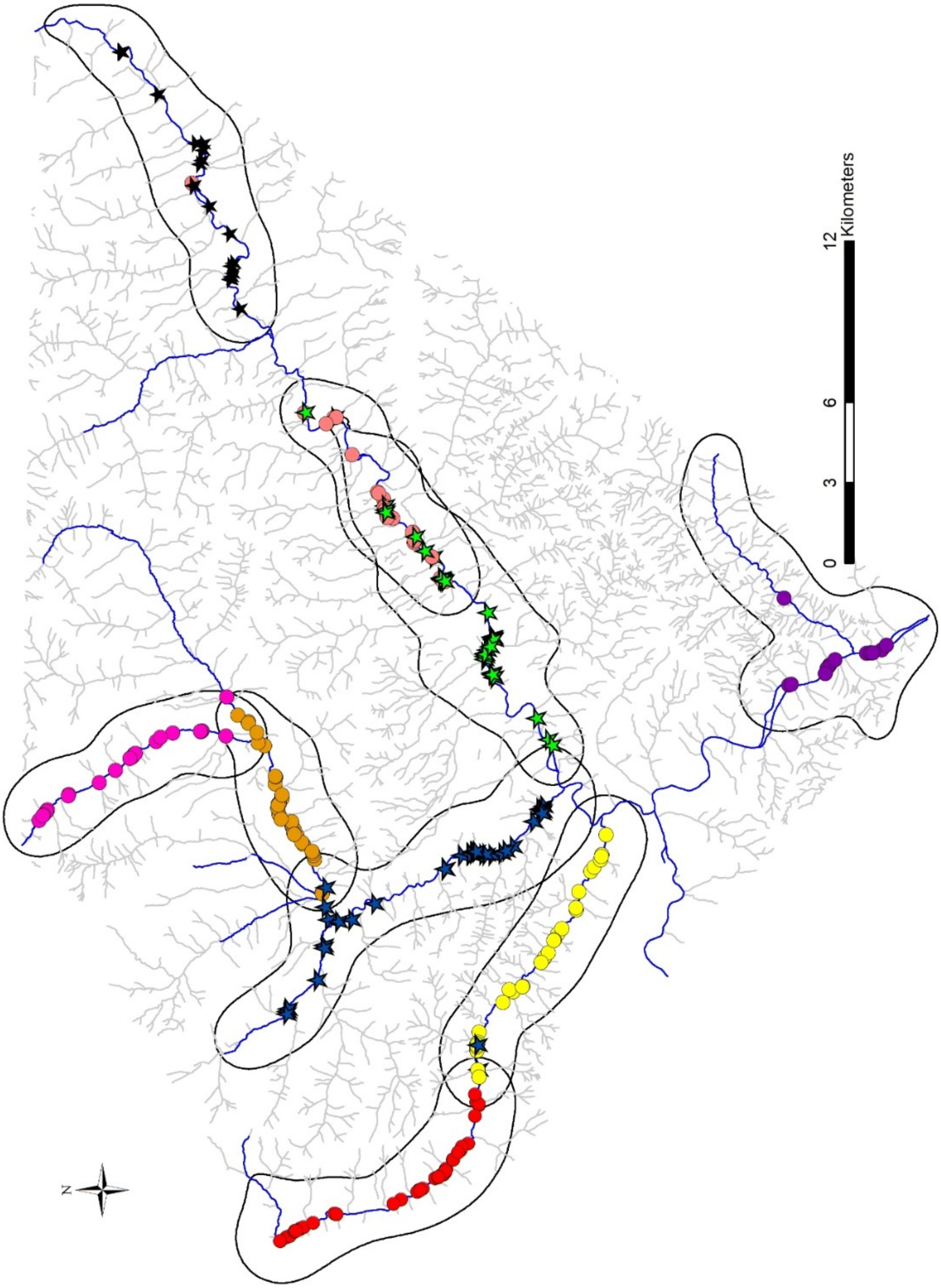


Figure 2. Distribution of resting sites for all radio tracked otters (colours indicate individuals, circles indicate resting sites of the females, stars indicate the resting sites of the males) within their respective home range using fixed kernel estimator at 95%, shown as black lines. Blue lines indicate the main streams in the valleys, while grey lines indicate the tributaries.

Table 1. Day resting sites: Overview of the environmental variables used in the analyses. Variables included in the different analyses are indicated with A) selection of resting sites, and B) selection of the type of resting sites.

Variables	Description	Measurement	Analyses
Resting site type	Couch: resting site above ground (e.g. Stick pile, Vegetation); Holt: resting site below ground (e.g. boulder, root system)	Categorical	B
Habitat type	Four categories within the watercourse: a) Main riverbed b) Abstracted water (Water derived from the dam reservoir to the hydroelectric power station (head water) and from there (tail water) back to the main riverbed c) Standing water such as ponds	Categorical	A, B
Vegetation width	Width of natural or semi-natural vegetation measured from waterside	Continuous	A, B
Vegetation type	Naturalness of the type of riparian vegetation: natural (forest, reed, herbacous stretches with at least 1 tree/bush within 25m), modified (herbacous, meadow, grass) and no vegetation)	Ordinal (1-3, with 1 = natural, 2 = foreign and 3 = no vegetation)	A, B
Vegetation period	Onset and end of the vegetation period	Categorical (0 = outside, 1 = during vegetation period)	B
Temperature	Mean daily temperature from nearest weather station (five stations over the whole area)	Continuous	B
Snow cover	Daily snow cover, data from the nearest weather station (five stations over the area)	Continuous	B
Distance to path	Path or roadlike structure (from hiking path to highway)	Meters	A, B
Likelihood of human disturbance throughout the year	General human presence over the year	Ordinal (1-3, with 1 = none, 2 = occasionally and 3 = daily)	A, B
Likelihood of human disturbance throughout the day	Human disturbance throughout the day	Ordinal (1-4, with 1 = none, 2 = once a day, 3 = every few hours, 4 = permanent or min. 1 every 2 hours)	A, B
Predictability of the daily disturbance	Type and intensity of disturbance	Ordinal (1-4, with 1 = none, 2 = working, 3 = spare time and 4 = spare time with dogs)	A, B

Table 2. Summary of the model used for selection of resting sites at the local scale. Variables in italics indicate categorical variables, where the respective p values belong to the chi[2] test of an overall influence of the variable. The p values in the last column can be used to test for the differences between the indicated category and the reference category.

Variables	**Estimate**	**Std. Error**	**z-value**	**Pr(>|z|)**
HABITAT TYPE (p = 0.05) *(Reference category: "Main riverbed")*				
Abstracted water	1.48	0.86	1.72	0.09
Standing water	0.25	0.40	0.62	0.54
Vegetation width	-0.74	0.15	-5.02	<0.001
Vegetation type (p <0.001) *(Reference category is "Natural")*				
Modified	-2.29	0.47	-4.83	<0.001
No vegetation	-1.60	0.57	-2.83	0.005
Distance to path	0.39	0.20	1.97	0.05
Likelihood of human disturbance throughout the day *(p = 0.01)* *(Reference category: "None")*				
Once a day	0.38	0.49	0.84	0.40
Every few hours	-0.48	0.52	-0.92	0.36
Permanent	-0.60	0.62	-0.98	0.33
Predictability of the daily disturbance				

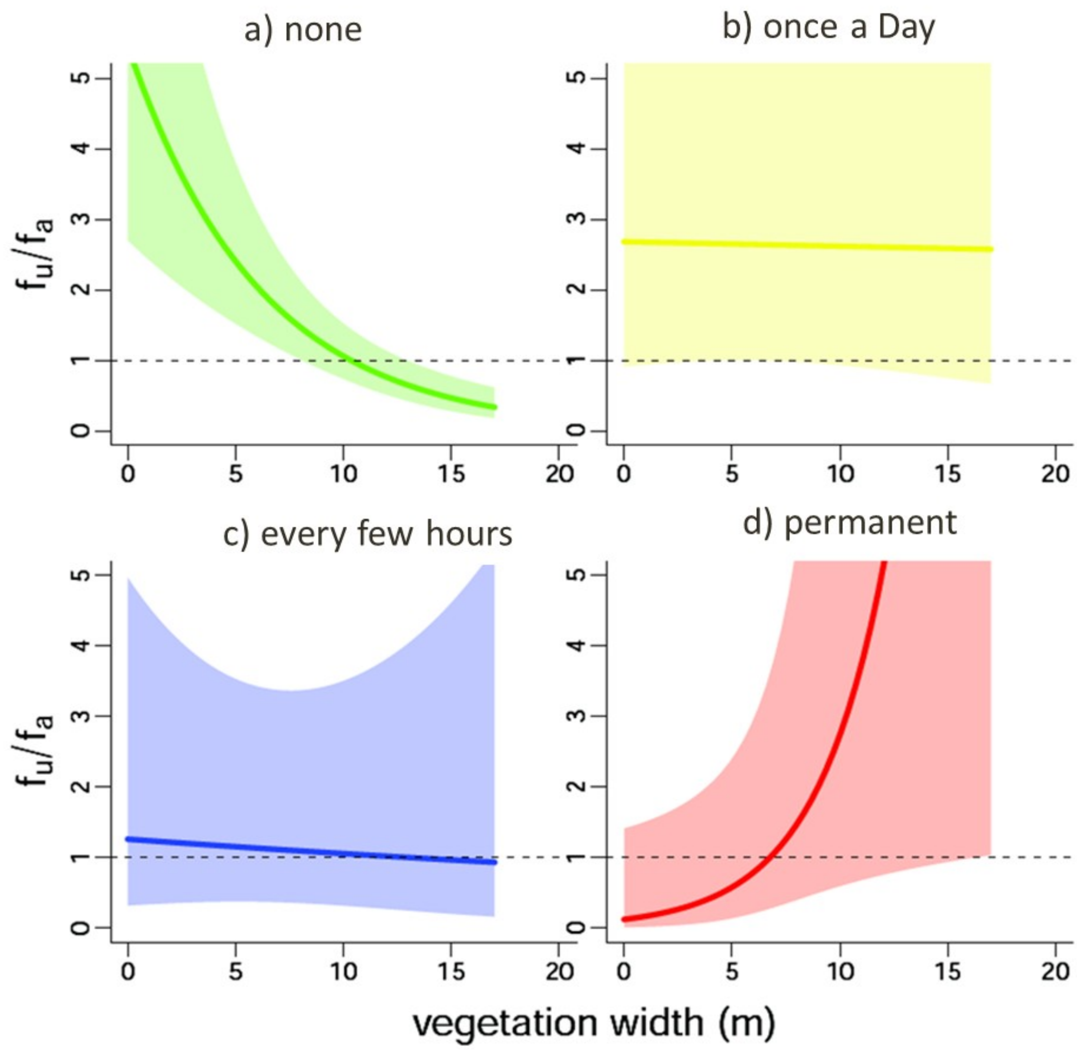


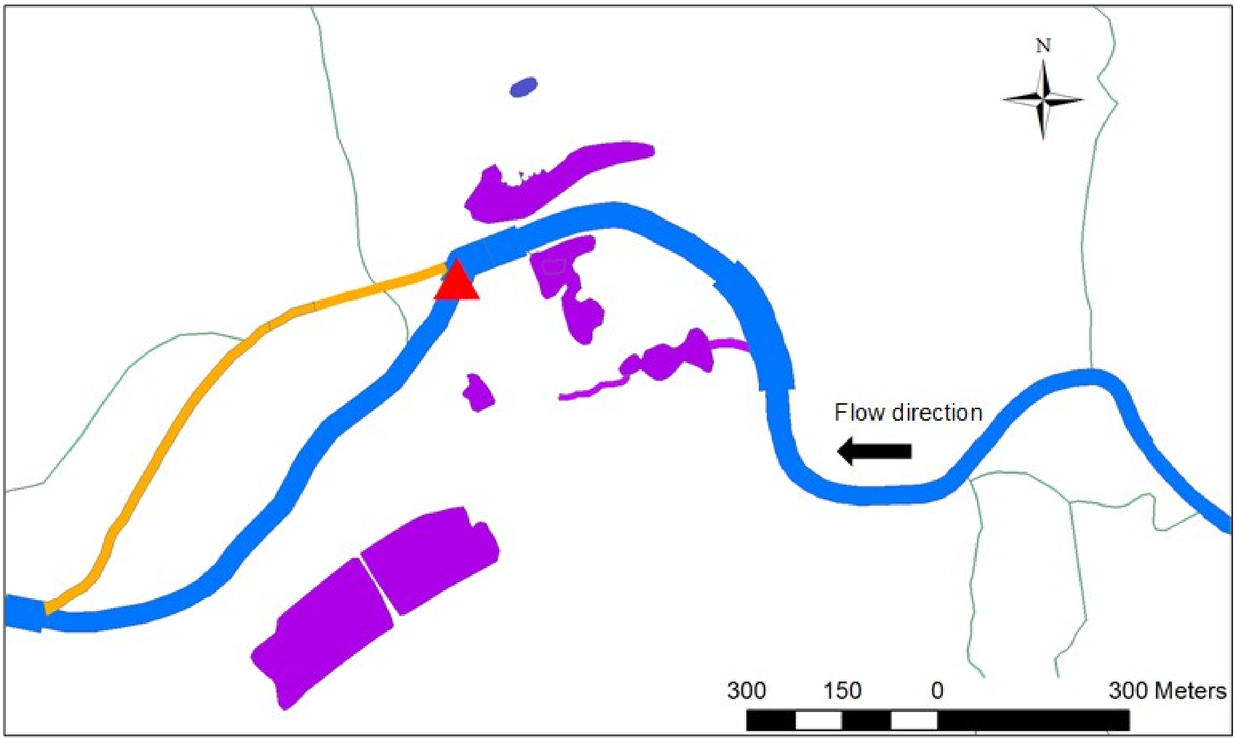
Figure 3. The influence of vegetation width at resting site locations depending on the likelihood of daily human disturbance in natural riparian vegetation: increasing daily disturbance (a to d). The plots show the regression lines and the 95% confidence bands.

Table 3. Summary of the model used for the analysis on resting site type, with resting site type as the response variable (0 = below ground, 1 = above ground resting sites). Variables in italics indicate categorical variables, where the respective p values belong to the chi^2 test of an overall influence of the variable. The p values in the last column can be used to test for differences between the indicated and the reference category of the variable.

Variables	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Vegetation width	0.37	0.12	3.10	0.001
Vegetation period (Reference category: "During vegetation period")				
Outside vegetation period (p)	-0.86	0.20	-4.30	<0.001
Temperature	-0.19	0.10	-1.89	0.06
Distance to path	0.57	0.07	8.13	<0.001
Likelihood of human disturbance throughout the day *(p <0.001) (Reference category: "None")*				
Once a day	0.002	0.14	0.01	0.99
Every few hours	-2.51	0.74	-3.41	<0.001
Permanent	0.21	0.62	0.34	0.74
Interaction vegetation width: Likelihood of human disturbance throughout the day (p < 0.001) (Reference category: "Vegetation width:none")				
Vegetation width:once a day	-0.31	0.14	-2.26	0.02
Vegetation width:every few hours	-3.08	0.78	-3.94	<0.001
Vegetation width:permanent	1.37	0.76	1.81	0.07

Appendix:

Riparian vegetation provides crucial shelter for resting otters in a human-dominated landscape



Appendix Figure 1. Classification of the main water bodies. Blue= main riverbed, orange = abstracted water, grey= tributaries, and lilac=standing water. The red triangle signifies the weir where the abstracted water is deviated from the main riverbed

Appendix Figure 2. The three different categories of naturalness of the riparian vegetation. Left: “natural” (trees, bushes, reed or herbaceous stretches with at least a bush or tree within 25m along the bank side). Middle: “modified” (stretch with grass or herbaceaous plants with no trees or bushes within 25m). Right: “artificial” (no vegetation)

Appendix Table 1. Information on number of tracked animals and resting site (RS) over the tracking period. For 20 resting sites, not enough data could be collected, resulting in 285 unique resting sites. Nine resting sites were used by two individuals and were treated independently for each individual for further analyses.

Animal	Sex	Age at Capture	Start Tracking	End Tracking	Successful RS locations	Mean RS locations/week	Total RS (data deficient / shared)	RS analysed (unique RS)
Alena	F	Sub-adult	08/05/2010	05/03/2013	399	3.08	54 (3/0)	51
Baukje	F	Adult	07/11/2010	05/03/2013	279	2.58	36 (2/1)	34
Cleo	F	Sub-adult	10/11/2010	15/06/2012	195	2.58	44 (3/0)	41
Dan	M	Adult	10/11/2010	07/03/2013	233	2.27	44 (2/1)	42
Fee	F	Sub-adult	03/05/2011	21/03/2013	189	2.20	26 (2/0)	24
Gessa	F	Adult	03/05/2011	18/03/2013	181	2.27	33 (2/2)	31
Hans	M	Adult	07/05/2011	09/03/2013	185	2.29	36 (1/5)	35
Ivo	M	Adult	14/04/2012	21/02/2013	88	2.33	27 (4/0)	23
Johanna	F	Adult	14/04/2012	29/11/2012	65	2.14	14 (1/0)	13
Total					**1814**	**2.41**	**314 (20/9)**	**294 (285)**

Appendix Table 2. Lowest AICc models for fine scale resting site selection according to the corrected Akaike's Information Criterion (AICc). K is the number of estimated parameters for each model. The ranking of the models is based on differences in AICc (Delta AICc (wi)).

Models	**AICc (K)**	**Delta AICc (wi)**
Habitat type + Vegetation width + Vegetation type + Distance to path + Likelihood of human disturbance throughout the day + Type of daily disturbance + Vegetation width : Likelihood of human disturbance throughout the day	698.40 (17)	0 (0.59)
Vegetation width + Vegetation type + Distance to path + Likelihood of human disturbance throughout the day + Type of daily disturbance + Vegetation width : Likelihood of human disturbance throughout the day	700.22 (15)	1.83 (0.24)
Habitat type + Vegetation width + Vegetation type + Distance to path+ Likelihood of human disturbance throughout the day + Type of daily disturbance + Vegetation width : Likelihood of human disturbance throughout the day + Vegetation width : Type of daily disturbance	701.05 (20)	2.6 (0.15)

Appendix Table 3. Lowest AICc models for resting site selection above or below ground according to the corrected Akaike's Information Criterion (AICc). K is the number of estimated parameters for each model. The ranking of the models is based on differences in AICc (Delta AICc).

Models	**AIC c (K)**	**AICc (wi)**
Vegetation width + Vegetation period + Temperature + Distance to path + Human disturbance throughout the day + Vegetation width : Human disturbance throughout the day	1908.101 (12)	0.00 (0.50)
Vegetation width + Vegetation period + Temperature + Distance to path + Human disturbance throughout the day + Human disturbance throughout the year + Vegetation width : Human disturbance throughout the day	1908.112 (14)	0.012 (0.49)
Vegetation width + Vegetation period + Temperature + Distance to path + Type of daily disturbance+ Vegetation width : Type of daily disturbance + Vegetation width : Vegetation period	1919.186 (13)	11.09 (0.01)

Appendix Table 4. Summary of the model with second largest AICc weight (given as 0.49), with resting site type as the response variable (0= below ground, 1=above ground resting sites).

Variables	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**
Vegetation width	0.37	0.12	3.10	0.001
Vegetation period *(Reference category: “During vegetation period”)*				
Outside vegetation period	-0.86	0.20	-4.29	< 0.001
Temperature	-0.20	0.10	-1.98	0.05
Distance to path	0.56	0.07	7.84	<0.001
Human disturbance throughout the day *($p < 0.001$)* *(Reference category: “None”)*				
Once a day	0.07	0.15	0.43	0.67
Every few hours	-2.22	0.76	-2.93	0.003
Permanent	0.65	0.64	0.32	0.65
Human disturbance throughout the year *($p = 0.13$)* *(Reference category: “None”)* Occasional (p =)	-0.26	0.19	-1.39	0.16
Permanent (p)	-1.43	0.90	-1.61	0.11
Interaction Vegetation width: Human disturbance throughout the day ($p < 0.001$) *(Reference category: “Vegetation width:none)*				
Vegetation width:once a day	-0.32	0.14	-2.31	0.02
Vegetation width:every few hours	-3.06	0.78	-3.94	<0.001
Vegetation width:permanent	1.18	0.73	1.62	0.11