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Original investigation

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

Irene C. Weinberger[a,*], Stefanie Muff[a,b], Andreas Kranz[c], Fabio Bontadina[d,e]

[a] *Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstr. 190, 8057 Zurich, Switzerland*
[b] *Epidemiology, Biostatistics and Prevention Institute, University of Zurich, Hirschengraben 84, 8001 Zurich, Switzerland*
[c] *alka-kranz Ingenieurbüro für Wildökologie und Naturschutz, Am Waldgrund 25, 8044 Graz, Austria*
[d] *SWILD – Urban Ecology & Wildlife Research, Wuhrstr. 12, 8003 Zurich, Switzerland*
[e] *Swiss Federal Research Institute WSL, Biodiversity and Conservation Biology, 8903 Birmensdorf, Switzerland*

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ABSTRACT

The riparian vegetation belt is one of the few remaining structures that provide coverage for wildlife in many anthropogenic landscapes. It provides shelter for many species and functions as corridors for dispersal. However, this landscape is increasingly utilised by humans for 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 in otters, we radio-tracked nine otters for up to 30 months in the eastern Central Alps of Austria. We analysed resting site selection in relation to human disturbance.

Altogether, we identified 285 resting sites scattered throughout the territories of the individual otters at an average distance of 144 m between sites. Almost all the resting sites (95%) were located in the natural riparian vegetation, making this the most important habitat for resting otters. We found evidence that human disturbance within these riparian habitats shapes resting site selection. Otters preferred narrow riparian strips when there was no human presence, but selected areas with a wider vegetation belt when the disturbance level increased. Outside the vegetation period, animals rested below ground more often than above, which suggests that vegetation also functions as visual cover.

Our study highlights the importance of the restoration of the natural riparian vegetation belt for the protection of wildlife, particularly where human activities are intense. We provide information for the effective conservation management of otters considering the combination of spatial distribution of resting sites and specific habitat requirements in the presence of human disturbance. Areas of conservation importance chosen in this way are likely to benefit other wildlife that utilise the riparian vegetation belt.

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Introduction

The availability and quality of resting sites affects individual fitness and survival (Lutermann et al., 2010; Matthews et al., 2019) and is thus a crucial determinant of species occurrence (Manning et al., 2013). Besides thermoregulatory benefits and protection from adverse weather conditions, resting sites provide shelter from predators (Semeniuk and 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. However, 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 has a major effect on the distribution of many species (Murphy and Romanuk, 2014), e.g. by eliciting a strong antipredator response that exceeds the reaction to natural predators (Ciuti et al., 2012). The loss of riparian vegetation with the concurrent increase of human activities may pose a serious threat to the survival of wildlife in these habitats.

* Corresponding author at: Wasserwerkgasse 2, 3011 Bern, Switzerland.
E-mail address: i.weinberger@quadrapoda.ch (I.C. Weinberger).

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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 et al., 2007). Otters are able to persist in anthropogenic landscapes (Madsen and Prang, 2001; Marcelli et al., 2012; Weinberger et al., 2016), but the effect of human disturbance remains of major conservation 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 also provide 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 et al., 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 activity on resting site selection remains inconclusive.

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 how otters select resting sites in relation to riparian habitat and human disturbance in an anthropogenic landscape in the Alps. Here, riverine landscapes have changed massively in the past 50 years due to an increase in industry, tourism and other human activities (Comiti, 2012). Today many watercourses are channelized and the riparian vegetation belt is often reduced or lost (Comiti, 2012; Ewald and Klaus, 2009). Human pressure is high: roads in the valleys are often built close to 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, 2012, 2015, 2017), 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. The riparian vegetation strip is lost or reduced to a width of one to eight meters along much of the watercourses. People often practice outdoor activities such as jogging, cycling and fishing along the river banks.

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). Animals were removed from the traps within 30 min of capture. 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 h of capture in close proximity to their capture site. Animals were tracked up to four times a week between sunrise and sunset, with tracking times 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 an animal's activity was deemed 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. No classification was possible in 43 of the 262 resting sites (16%). The type of waterbody closest to the resting site was categorized into three classes: "main riverbed" (used as reference category in all analyses), "abstracted water" (water derived from the main river for electric power generation) and "standing water" (ponds and wetlands, Appendix Fig. A1). Riparian vegetation width was measured at the resting site. The type of vegetation was classified into three categories of naturalness (Appendix Fig. A2). These were "natural" (trees, bushes, reed or herbaceous stretches with at least a tree or bush within

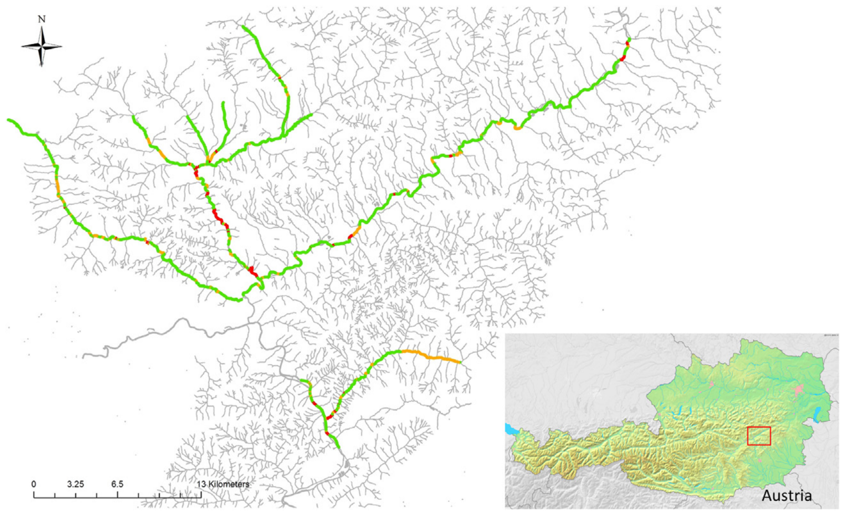

Fig. 1. Study area in the eastern Central Alps in Styria, Austria, defined by the minimum convex polygon for all otters, showing the running waters in grey (with names of main streams). Vegetation type of all main riverbeds within any home ranges was assessed: green = natural (vegetation), orange = modified (vegetation) and red = artificial (no vegetation). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

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 belt is quite fragmented in the study area, thus affecting its potential as a cover. Locally, there is intense land use along the watercourses which reduces 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. by late autumn tall vegetation is flattened and the deciduous trees and shrubs have lost their foliage, resulting in a loss of visual protection. To account for this effect we incorporated a binary indicator for the vegetation period (1 = during vegetation period, 0 = outside vegetation period). Onset and end of the vegetation period vary within the study area and are considered to coincide with the date when the average daily temperature rises above or falls below 10 °C (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 (1) distance to the nearest road or path (whichever was closest), and (2) human disturbance. Anecdotal data by Green et al. (1984) indicated that otters respond only to very close disturbances. Otters also use several resting sites within their territories throughout the year, often switching on a daily basis. We therefore incorporated the likelihood of experiencing disturbances at two different temporal scales: year and day. Alternatively otters may habituate to human disturbance depending on its predictability. In a well-utilised area humans move along the predefined paths that can be anticipated by the local wildlife. This might be contrary to the erratic pathways that free ranging dogs may take. To account for these factors we estimated three types of human 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 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) 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

A set of all known resting sites and an equal number of alternative random locations was drawn for each individual 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 waterbody. 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 disturbance throughout the year, likelihood of 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

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

where $x = (x_1, \ldots., x_n)$ 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

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	Three categories: Couch (resting site above ground, e.g. stick pile, vegetation); Holt (resting site below ground, e.g. boulder, root system) and Unknown (no assignment possible)	Categorical	B
Habitat type	Three categories within the watercourse: Main riverbed; 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) and Standing water (e.g. 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 25 m); Modified (herbacous, meadow, grass) and Artificial (no vegetation)	Ordinal (1-3, with 1 = natural, 2 = modified and 3 = artificial)	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 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 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 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

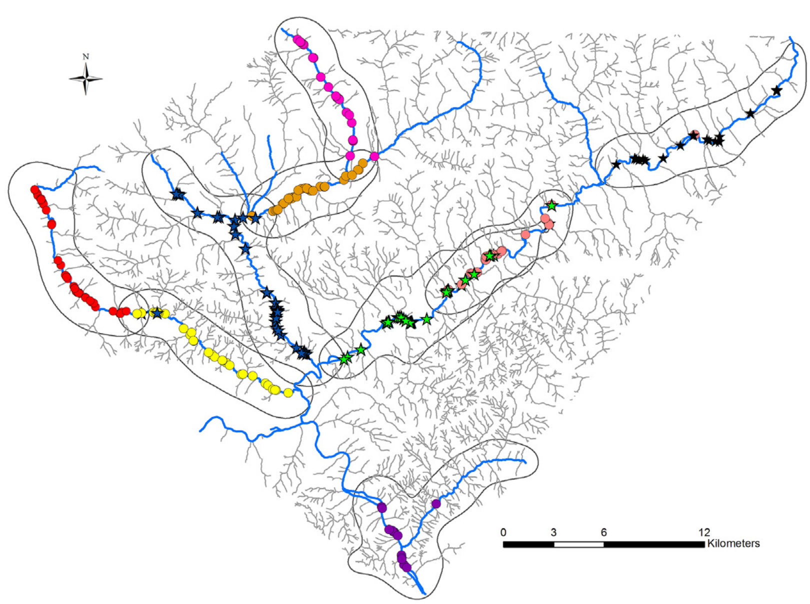

Fig. 2. Distribution of resting sites for all nine radio-tracked otters. Colours indicate individuals, circles indicate resting sites of the females, stars indicate the resting sites of the males. Each individual's home range was estimated using fixed kernel estimator at 95% of all locations and is shown as a black line surrounding their resting sites. Blue lines indicate the main streams in the valleys, while grey lines indicate the tributaries. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

used by the animal with respect to their availability and $w(x) < 1$ represents habitats that were under-proportionally used.

Selection of the type of resting site

Otters use either holts or couches as resting sites. The choice between them may be driven by seeking protection against either adverse weather conditions or human disturbance. 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

Table 2
Summary of the model used for selection of resting sites at the local scale. Categorical variables are italicised, where the respective p values belong to the χ^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: "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 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 daily disturbance (p = 0.04)				
(Reference category: "None")				
Working	−0.15	0.46	−0.33	0.74
Spare time	−0.91	0.55	−1.66	0.10
Dog	−0.88	0.56	−1.57	0.12
Interaction Vegetation width: Likelihood of disturbance throughout the day (p < 0.001)				
(Reference category: "Vegetation width:none")				
Vegetation width:once a day	0.73	0.24	3.08	0.002
Vegetation width:every few hours	0.66	0.32	2.05	0.04
Vegetation width:permanent	2.14	0.69	3.13	0.002

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 likelihood of disturbance throughout the year, likelihood of 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

A total of 13 otters were captured between May 2010 and March 2013. Nine of these otters (three males and six females) were radio-tracked for an average of 655 days (range = 229–1032). 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 resting site throughout the day. Rare diurnal activities were noted only in July and August. 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 A1). While most resting sites were used by only one individual, nine resting sites of females were also used by the male otter in their vicinity. 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 within bank reinforcements with no vegetation. Only six resting sites (2%) were outside the riparian vegetation and all of these were above ground.

Selection of resting sites

The dataset for this analysis included a total of 285 resting sites and 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 disturbance throughout the day, the predictability of the daily disturbance, the interaction between vegetation width and the likelihood of disturbance throughout the day, and the animal-specific random slope for distance to path (Table 2). Vegetation type was included in all three models with lowest AICc (Appendix Table A2), and the best model provides very strong evidence that it is an important explanatory variable ($p < 0.001$). Animals preferred resting sites in areas with a natural vegetation type, with a significantly negative deviation found from random for the "modified" ($p < 0.001$) and "artificial" ($p = 0.005$) categories. There is some evidence that resting sites are preferred further away from paths (estimate = 0.39, $p = 0.05$). Besides vegetation type, likelihood of 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 depending on the width of the vegetation ($p < 0.001$ for the respective interaction term, see Fig. 3 for a graphical representation). In the absence of daily human disturbance, animals used resting sites with a riparian vegetation belt up to 10 m wide more than expected at random (Fig. 3a). 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). The otters showed no clear preferences on vegetation width in the presence of intermediate disturbances (Fig. 3b and c).

Selection of the type of resting site

The type (couch or holt) could be assessed for 262 resting sites. A total of 102 resting sites (40%) were situated above ground and 160 below ground. Resting sites where no clear classification was possible (n = 43) were omitted from this analysis. The model with the lowest AICc included riparian vegetation width, vegetation period,

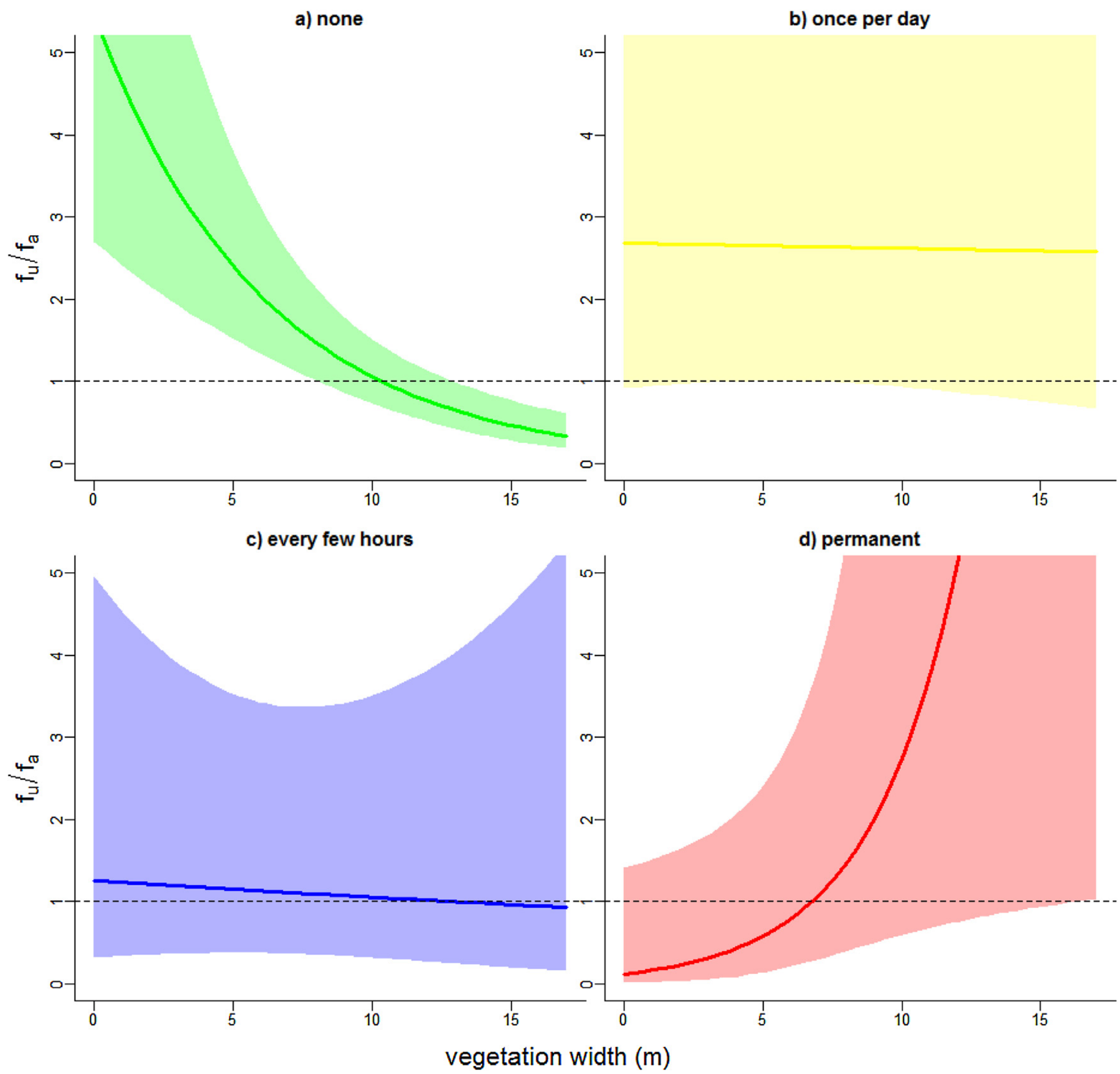

Fig. 3. The influence of vegetation width at resting site locations depending on the likelihood of daily human disturbance in natural riparian vegetation: increasing daily disturbance (a to d). The plots show the regression lines and the 95% confidence bands.

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 χ^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	−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 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 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

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 A3). 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 A4 to illustrate the robustness of the main findings. There was very strong evidence that the likelihood of disturbance in combination with vegetation width shapes the selection of resting site type (interaction $p < 0.001$). At sites without daily human disturbance resting sites were more likely to occur above ground where vegetation was wider than below (estimate 0.37, $p = 0.001$). No clear site preference was found where human disturbance occurred once a day. Note that the 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; here animals selected resting sites that were below ground in regions with increasing vegetation and above ground at sites with narrow vegetation. The opposite is indicated for permanent disturbance, where again wider vegetation 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 distance between resting sites was 144 m, and 95% of the resting sites where spaced within 1755 m of each other.

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 degree of modification of the watercourses (Weinberger et al., 2016).

Human presence is a driving factor for resting site selection in anthropogenic landscapes. Riparian vegetation width plays a marginal role at low levels of daily human presence, but wide riparian vegetation strips were preferred at sites with regular daily human activity. This suggests that otters perceive humans as a threat. However, in addition to human disturbance, resting site selection could also be influenced by factors such as fine scale habitat conditions or the proximity to a rich foraging site. For example, otters are known to use resting sites which have been used by other otters for decades (Chanin, 2013). Those traditional resting sites may thus persist even when the level of disturbance increases.

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 contradictory 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 with a coarser variable 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 for conservation management.

Otters use resting sites above and below ground. The selection of the type of resting sites might be driven either by adverse weather conditions or as protection against disturbances. We show that vegetation cover had a stronger effect on resting site type selection than temperature, supporting 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, they were also used in the summer. Thermal insulation might be a particularly important driver of resting site selection during hot weather. Otters dissipate heat only through the small body surface of their feet (Kuhn and Meyer, 2009) and their dense fur can result in overheating. The temperature in holts is likely more stable and cooler in summer than the temperature in couches, making them important structures during exceptionally hot weather.

Altogether, our findings support other studies on different animal species where the riparian vegetation is of major importance (Bennett et al., 2014; Carrasco-Rueda and Loiselle, 2019; 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 structure as coverage for wildlife. This important 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 and restore riparian vegetation in order to facilitate the recovery of this semi-aquatic carnivore. Besides good foraging habitat and an unpolluted environment, safe resting sites are crucial requirements for the long-term recovery of otters. This applies particularly to reproducing females where successful breeding and raising of offspring depends on access to resting sites with no disturbance (Beja, 1996; Durbin, 1996). Such information on key habitat features of threatened species is of prime importance, particularly in light of the limited financial funding for conservation measures. Management plans for otter conservation will benefit from the information on the number and the spacing of resting sites of otters along watercourses. 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 at least 15 m wide and should be spaced along any waterbodies, ideally at intervals of 140 m. Our results suggest that such small stretches of natural riparian vegetation left exclusively for wildlife along the human-dominated watercourses are important for the persistence of otters in such a landscape.

While our recommendations focus specifically on otters, these measures will benefit the conservation of numerous other species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.mambio.2019.09.001.

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