Snakes and Monocultures: Habitat Selection and Movements of Female Grass Snakes (*Natrix natrix* L.) in an Agricultural Landscape

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Abstract.—We investigated habitat selection and movement patterns of female Grass Snakes (*Natrix natrix helvetica*) in an agricultural landscape where cropping is the dominant farming practice. The aims were to estimate the relative importance of monoculture as habitat for these snakes and to assess its functional relevance to the snakes. Radiotelemetry was used to measure movements by snakes, and the locations of animals were used as sampling points to examine patterns of habitat use. In the course of the tracking period, all females used monocultures. Because of a combination of suitable basking sites, favorable foraging opportunities, and low pressure from avian predators, monocultures may provide at least temporary advantages over more natural habitats, with a seasonal shift in functional relevance induced by the time of oviposition. Overall, the snakes showed a marked preference for edge habitats, which make up only 7% of the study area. At the microhabitat level, a snakes' probability of occurrence was positively correlated with either percentage cover of perennial layer or distance to cereal crop or with both. Our results clearly demonstrate that monocultures are a component of the habitat of female Grass Snakes during their summer activity period in the study area. However, the marked preference for edge habitats, and the response to particular microhabitat features, emphasizes the importance of a mosaic of habitats and structural heterogeneity of edge habitats for the conservation of this snake population.

Agricultural intensification is among the major threats to biodiversity (Foley et al., 2005). Both the conversion of pristine habitats to farmland and efforts at increasing yield of existing crops contribute to a decline in species richness (Donald and Evans, 2006) and often to a replacement of highly adapted specialists by habitat generalists of low conservation concern (Julliard et al., 2004). Among the established predictors of the sensitivity of a species to habitat modification and fragmentation are microhabitat specialization and matrix use (Henle et al., 2004). Studies on the response of vertebrate populations to the effects of agricultural intensification have largely focused on birds (e.g., Donald et al., 2001; Vickery et al., 2001; Verhulst et al., 2004; Atkinson et al., 2005), mammals (e.g., Wickramasinghe et al., 2003), and amphibians (Guerry and Hunter, 2002; Swihart et al., 2003; Gray et al., 2004), whereas reptiles have received considerably less attention (Driscoll, 2004; Berry et al., 2005).

Among reptiles, snakes, as a group of predators with often very specific resource requirements (Reinert, 1993), are expected to be highly sensitive to habitat modifications, which induce changes in thermal environments (e.g., Webb and Shine, 1998) and in the density and distribution of key resources. The spatial ecology of snakes in rural or human-dominated landscapes has been the subject of several recent studies at both the species (e.g., Whitaker and Shine, 2003; Heard et al., 2004; Pearson et al., 2005) and the community level (Kjoss and Litvaitis, 2001). The respective study areas usually contained large proportions of either idle or extensive farmland. Three studies investigating the spatial behavior of Grass Snakes (*Natrix natrix*) by means of radiotelemetry (Madsen, 1984; Mertens, 1992; Nagy and Korsós, 1998) were performed in areas of either extensive farmland or wetland. Therefore, despite past research on Grass Snakes, the impact of agricultural intensification, characterized by monocultures with high pesticide and fertilizer input, repeated disturbance by agricultural machinery, and severe structural modifications within a single season, on their ecology is still poorly understood.

Grass Snakes occur in anthropogenic habitats experiencing a broad range of disturbance levels (Kabisch, 1999). They prey essentially on anurans (Gregory and Isaac, 2004), a food resource that is undergoing decline over much of the species' range. Females depend on suitable nesting sites, which may be in limited supply in many habitats and force gravid snakes to make considerable movements, as suggested by anecdotal reports of communal

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nesting sites with hundreds of eggs (Golder, 1984; Nöllert et al., 1989). In Switzerland, the Grass Snake is the most widespread of the eight native snake species (Guisan and Hofer, 2003), occurring throughout the country between 300 and 1,000 m a.s.l., with exceptional records up to 1,980 m (Hofer et al., 2001). Switzerland is among the most densely populated countries in Europe. The majority of the population lives in the Midlands, the lowland region between the Alps and the Jura mountains, where pristine habitats, wasteland, and unused areas are still converted into intensive farmland, real estate, or motorways. In the Swiss Midlands, the Grass Snake experienced a strong decline during the last century (Hofer et al., 2001). According to the IUCN criteria, the Red List status of the two subspecies occurring in Switzerland is ''vulnerable'' for *N. n. helvetica* and ''endangered'' for *Natrix natrix natrix* (Monney and Meyer, 2005).

The goal of this study was to collect data on habitat selection and seasonal movement patterns of female Grass Snakes in an agricultural landscape where cropping is the dominant farming practice. The specific aims were (1) to assess the proportional importance of monocultures as habitat for these snakes, relative to remnant and more natural landscape elements, and (2) to assess the functional relevance of monocultures for these snakes.

MATERIALS AND METHODS

Study Area.—The study was conducted on the northeastern edge of the Grosses Moos, a former wetland of about 90 km^2 in the Swiss Midlands, which has been drained and gradually converted into an agricultural plain in the last century. Today, the main component of the study area (37°03'N, 07°12'E, Fig. 1) is intensively managed agricultural land dominated by monocultures of cereals and root crops, which surround a hill covered by beech grove. Sections of the forest edge are lined with a shrub layer. To the south and west, the area is bordered by the main drainage channel (75–90 m wide) of the plain, its benching, and the adjacent dam that only holds water at high watermark. The dam is covered by grass interspersed with a few shrubs and linked with the beech grove by a narrow strip of windbreak forest. A network of unpaved roads intersecting the study area is regularly used by farmers and by the local population for leisure activities. The distance from the center of the study site to the nearest main road and nearby village is 1.5 km.

Data Acquisition and Radiotelemetry.—For the study, we investigated the subspecies *N. n. helvetica*. Ten females were captured by hand in the core area and equipped with radiotransmit-

FIG. 1. Home ranges (thick black lines, 95% MCP) of eight radiotracked female *Natrix natrix helvetica*. Dark grey surfaces: forest, light grey surfaces: agricultural land, hatched: village zone, thin black lines: road network, white: channel network.

ters. The transmitters (model SB-2T, Holohil Systems Ltd. Carp, ON, Canada) weighed 5.25 g with a mean ratio of transmitter mass to snake body mass of 2.1% (range: 1.4–2.8%). The radiotransmitters were sterilized with ethylene oxide and implanted into the body cavity through a small vertical incision of about 15 mm laterally in the posterior third of the snake. All snakes were released within 24 h after surgery at the original capture site. Positions of the snakes were located by ''homing-in'' on the animals (White and Garrot, 1990) with a portable receiver (model Australis 26 k, Titley Electronics, Ballina, Australia) and a hand-held H-antenna (model RA-14K, Telonics, Inc., Mesa, AZ). Coordinates of the locations were taken with GPS (model eTrex Geko, Garmin Int., Inc., Olathe, KS). Whenever possible, the snakes were located visually. A minimal distance of 2 m to the animals was then kept to avoid disturbance.

We conducted the study from April to August 2005. The detection of a mass oviposition site with a low hatching rate (< 30%) in the study area (UH, pers. obs.) indicated that suitable nesting sites may be scarce and, thus, have a strong impact on the spatial behavior of gravid females. To account for this and to base corresponding recommendations for conservation measures on the largest sample possible within the logistic constraints, we restricted this study to the female population.

Macrohabitat Selection.—For habitat selection analysis, the snakes were located three times a week during the summer activity period from May until the end of August, with a minimum of 24 h between consecutive locations. Each location was assigned to one of 14 macrohabitat types (Table 1), predefined by the authors using

TABLE 1.   Habitat types (1–15) mapped within home ranges, and their aggregation to the habitat categories (I–V) used in compositional analyses.

Habitat type	Habitat category
1 Deciduous forest	I. Closed-canopy forest
2 Windbreak forest	
3 Coniferous forest	
4 Forest edge with shrubs	II. Forest edges or windfalls
5 Forest edge with grass	
6 Forest edge with bare soil or leaf litter	
7 Windfall	
8 Canal bank wetland	III. Riparian zone
9 Canal bank grass	
10 Canal bank shrubs and trees	
11 Dam embankment	
12 Drainage channel	
13 Wheat (barley/rye/maize)	IV. Monocultures of cereal
14 Potatoes/sugar-beet/grass	V. Monocultures of root crop or grass

shape (surface or edge), area (farmland or forest), and type of dominant vegetation layer as an initial differentiation. Coordinates of the locations served as references to delimit the home ranges (95% minimum convex polygon for each animal; MCP, Biotas 1.03; ESS Ecological Software Solutions, Sacramento, CA). To ensure that the size of the MCP did not depend on the number of locations, the home ranges were tested for the relationship between size and number of locations. The latter should approximate an asymptote when the maximum area is reached. This asymptote was achieved for each individual. With the animal movement extension on ArcView (Environmental Systems Research Institute, Inc., Redlands, CA), we set random points within each individual's home range outside a buffer radius of 1 m around a location. The number of random points corresponded to the number of locations. The random points were assigned to the same macrohabitat categories as the locations and were later used as a basis for estimating habitat availability within home ranges. Compositional analysis (Aebischer et al., 1993) was performed to test for differences between the distribution of actual locations and random points with respect to macrohabitat categories. The advantage of this nonparametric technique is that it accounts for the lack of independence between the proportional uses of habitat types. Results are yielded at the level of the study population. By using the single animal instead of the locations as sample unit, however, pooling data across individuals is avoided. Compositional analysis requires a number of habitat types equal or smaller than the number of individuals analyzed. Therefore, we aggregated the 14 macrohabitat types to five categories for this analysis (Table 1). Statistics were computed

with an Excel macro (P. Smith, pers. comm., E-mail: pgsmith@aber1.fsnet.co.uk, beta version, unpubl.), which also carried out the randomization procedure recommended by Aebischer et al. (1993).

Relationships with Habitat Features.—For a detailed description of the habitat structure at each location and each random point, a series of 11 variables known to be of potential relevance to the habitat selection and spatial behavior of snakes (Reinert, 1993) were recorded within 1-m radius of each location: slope (0–90°); aspect (° deviation from north, clockwise 0–359°); bare soil (% cover); organic litter (% cover); fallen logs (log > 10 cm in diameter, % cover); herb layer (height < 20 cm, % cover); perennial layer (height 20–100 cm, % cover); distance to next cereal crop (height > 1 m); distance to next shrub or tree layer (height > 1 m); distance to the main drainage channel; and distance to next road (unpaved, width 3 m). All distance measures were assigned to one of three classes (0 m < C1 ≤ 1 m; 1 m < C2 ≤ 5 m; C3 > 5 m). Because the random points were sampled at the end of the radiotelemetry period, we had to account for those variables that experienced seasonal changes. For these variables (e.g., percentage cover of herb and perennial layers and of organic litter), representative pictures of each habitat type were taken weekly during the whole study period. Each random point was then randomly assigned to a snake location, and the picture of the corresponding habitat type taken in the week of the snake location was used for estimates of percentage cover. Variables expected to experience no seasonal changes were recorded on-site for each random point.

Relationships between snake locations and variation in habitat features were modeled by bimodal logistic regression. The selection of

TABLE 2. Monitoring period and duration (days), number of locations, and size of the 95% minimum convex polygon (MCP) encompassing all locations of a given female *Natrix natrix helvetica*.

Individual #	Period	Monitoring days	Number of locations	95% MCP (ha)
1	May 16–Aug 29	105	50	044.96
2	May 12–Aug 29	109	50	120.54
3	May 11–Aug 29	110	52	043.62
4	May 25–Aug 29	96	44	029.56
5	May 25–Aug 29	96	43	024.12
6	May 26–Aug 29	95	41	017.49
7	Jun 8–Aug 29	81	34	015.10
8	Jun 18–Jul 31	43	20	021.87

variables for individual modeling was performed with a backward stepwise procedure. We performed the statistical analyses with the program JMP5 (SAS Institute Inc., Cary, NC, 2005). The significance level for variables to be kept in the model was set at $P < 0.05$.

Monitoring of Short-Term Movements.—Each snake was intensively surveyed on three days each month in June, July, and August, with a minimum of five days between two consecutive monitoring days. On a monitoring day, the position of an individual was determined eight times at intervals of at least one hour, the length of an interval depending on the amount of time required for a single location. The coordinates of each location were recorded with a GPS. Because only in a few cases was it possible to directly observe snakes on the move, distance covered was operationally defined as a straight line linking two consecutive locations. Moves were defined as distances of ≥10 m between two consecutive locations. For analyses of moves with respect to time of day, locations before 1200 h were assigned to the morning, those between 1200 h and 1500 h to midday, and those after 1500 h to the afternoon. Mean numbers of moves per period and mean distances covered per hour were calculated for each animal. To test for differences in distance covered and in number of moves among months and among daytime periods, the data were subjected to a nonparametric longitudinal analysis, a procedure which accounts for nonindependence of time series data (Brunner et al., 2002), applying SAS Macro LDF2 (available from: www.ams.med.uni-goettingen.de/de/sof/ld/makros.html).

Resource Use.—Except for the days of monitoring of short-term movements, when unintentional release of moves had to be avoided, attempts were made to visually locate radiotracked snakes using binoculars. Individuals with prey items in their stomach (indicated by abdominal swelling), individuals basking (defined as lying motionless with the whole body or parts of it exposed to the sun), and those with clear signs of upcoming ecdysis (opaque eyes) were recorded accordingly. Prey items were only identified in untagged snakes by forced regurgitation.

RESULTS

Radiotelemetry enabled tracking the activities of eight mature female Grass Snakes during four months. In total, 334 locations from eight females were recorded. The monitoring duration varied between 43 and 110 days per animal, and the number of locations per animal ranged from 20–52 (Table 2). Individual home-range size (95% MCP) ranged from 15.1–120.5 ha, with a mean home-range size of 39.7 ± 34.5 ha (mean ± SD). Relative size and position of the home ranges are shown in Figure 1.

Macrohabitat Selection.—In the total study area, the habitats available were monocultures of cereal (40.9% of all random points), closed-canopy forest (26.1%), and monocultures of root-crop or grass (25.8%). Only 7.2% of the random points were located in edge habitats, which consisted of forest edges or windfalls (4.5%), and riparian zone (2.7%; Fig. 2).

The pattern of habitat use varied among individuals. The main habitats used by snakes were forest edges and windfalls (9.3–79.6%, $N = 8$) and monocultures (2.3–58.9%). Five individuals were located 34.1–58.9% (mean 42.2%) of the time within monocultures. Only two individuals were recorded in all five habitat categories. One female showed the least diverse habitat use, because she was detected in forest edges and windfalls and in monocultures only (Fig. 3). The proportional distribution of locations with respect to habitat categories varied among months: The majority of locations were within riparian zones in May and August, within forest edges and windfalls in June, and within monocultures in July (Table 3).

Compositional analysis of habitat use versus availability within individual home ranges revealed forest edges and windfalls and ripar-
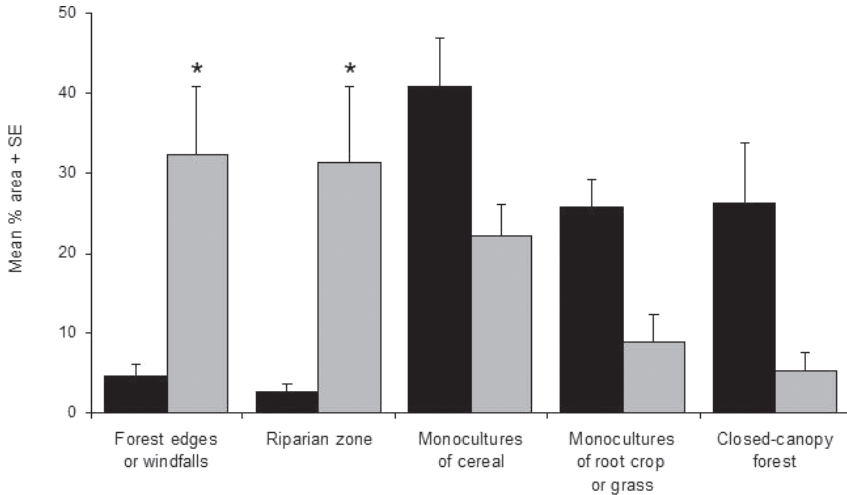
FIG. 2. Macrohabitat selection: comparisons of habitat used (grey) versus habitat available (black) within eight snakes' home ranges (mean percentage area ± SE, $N = 8$). Categories are ranked from most to least used. Forest edge and windfall and riparian zone (marked with an asterisk) are selected over the remaining three categories ($P < 0.05$, compositional analysis).

ian habitats to be selected over both categories of monocultures and closed-canopy forest (χ^2_4 = 13.18, $P < 0.05$). The ranked variables from most to least used were forest edges and windfalls > riparian zone >>> monocultures of cereal > monocultures of root-crop or grass > closed-canopy forest ("$>>>$" denotes a significant difference between two consecutively ranked series of variables; Fig. 2).

Relationships with Habitat Features.—The logistic regression models of seven individuals were significant ($P < 0.01$), with R^2-values between 0.30 and 0.47 and a single R^2-value of 0.1. For the snake with the smallest number of locations (20), no variable was kept in the model. Estimates and standard errors of the six variables kept in at least one model and the R^2-values for each model are given in Table 4. The number of significant variables in the individual models ranged from one to four. The variable "distance to cereal crop" was retained in six models and the variable "percentage cover of perennial layer" in four models. The percentage cover of herb layer, bare soil, perennial layer, and the distance to cereal crop were positively correlated with the
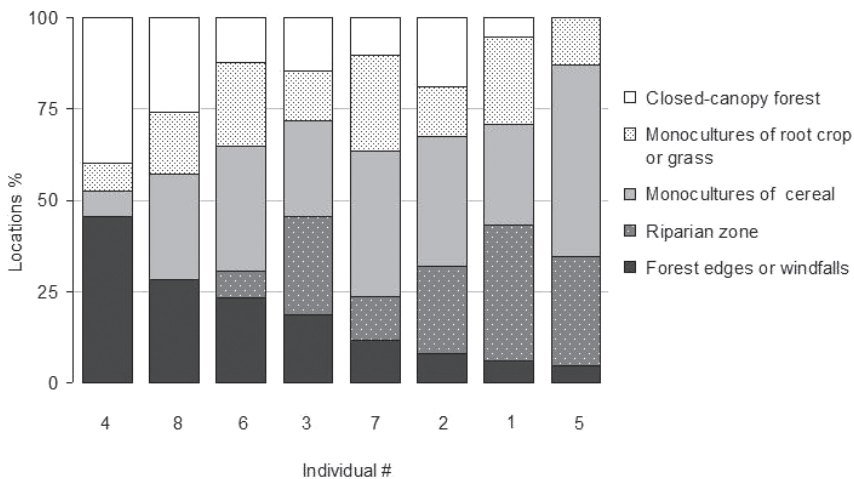

FIG. 3. Percentages of locations in different macrohabitat categories for eight female *Natrix natrix helvetica*, showing individual heterogeneity in habitat use. Categories are stacked in the same order as in Figure 2, and females are ranked in decreasing order according to the proportional use of forest edges and windfalls.

TABLE 3. Shifts in habitat use during summer months. Proportions (%) of locations in different habitat categories. Monthly mean values of eight female *Natrix natrix helvetica*. The range of individual proportions is given in parentheses.

Habitat category	Month			
	May	Jun	Jul	Aug
Riparian zone	64.8	38.9	10.6	45.6
	(0–87.5)	(0–68.7)	(0–42.8)	(0–100)
Monocultures of cereal	3.7	9.3	50.0	8.8
	(0–25.0)	(0–33.3)	(7.1–70.0)	(0–40.0)
Monocultures of root-crop or grass	3.7	0.9	14.4	11.8
	(0–25.0)	(0–11.1)	(0–38.5)	(0–50.0)
Forest edges or windfalls	22.2	44.4	20.2	29.4
	(12.5–75.0)	(6.2–100)	(0–57.1)	(0–100)
Closed-canopy forest	5.6	6.5	4.8	4.4
	(0–50.0)	(0–21.4)	(0–35.7)	(0–18.2)

probability of a snake's presence. Percentage of organic litter cover and distance to the next unpaved road were negatively correlated with a snake's presence.

Monitoring of Short-Term Movements.—For the analyses of movement patterns, 546 locations were recorded from eight individuals. After exclusion of the first location of each day, which served only as a starting point for distance measures, 112 of the remaining 477 locations indicated moves. Distances covered per hour differed significantly among months ($F_{2, 7}$ = 8.07, $P < 0.01$) but not among the morning, midday, and afternoon periods ($F_{2, 7} = 0.23, P = 0.74$). Mean distances covered per hour were 16.6 m in June, 34.8 m in July, and 3.2 m in August. Mean number of moves per individual differed significantly among months ($F_{2, 7}$ = 4.12, $P = 0.02$), with more moves in July. Moves were also more frequent at midday ($F_{2, 7}$ = 9.20, $P < 0.01$, Table 5). The 112 recorded moves were unequally distributed across habitat categories ($\chi^2_4 = 26.84, P < 0.01$): 46.4% of all moves were recorded within monocultures, 23.2% within forest edges and windfalls, 11.6% within riparian zone, and 0.9% within closed-canopy forest. In the remaining 14.3%, snakes moved from one habitat category to another.

Resource Use.—Radiotracked animals were sighted in 74 cases. In 82.4% of these sightings, the snakes were basking, with 44.6% of the corresponding basking sites located in forest edges and windfalls, 27.7% in riparian zone, 20% in monocultures, and 7.7% in closed-canopy forest. Indications of a first ecdysis were recorded at the end of June for five radiotagged animals. The four individuals for whom a second ecdysis in August was recorded were all located in forest edges and windfalls and in riparian zone (three of which occurred at the same site).

Six radiotagged individuals were located at the same oviposition site between 28 and 30

TABLE 4. Estimates (SE) of the variables included in the logistic models regarding the relationship between the probability of individual Grass Snakes' presence and biophysical features. Only significant models are specified ($N = 7$). R^2 indicates the proportion of variance explained by the model. Only significant variables as retained by the models are shown (*: $P < 0.05$, **: $P < 0.01$).

Variable	Individual number						
	1	2	3	4	5	6	7
Bare soil (%)			2.36*				
			(1.20)				
Organic litter cover (%)		−4.22*		−1.79*			
		(1.99)		(0.75)			
Herb layer cover (%)							5.34*
							(2.02)
Perennial layer cover (%)		5.73**	3.89**	3.06**		8.35**	
		(1.68)	(1.05)	(0.91)		(2.78)	
Distance to cereal crop	1.40**	2.80**	2.61**	2.65**	2.81**	1.85**	
	(0.32)	(0.80)	(0.63)	(0.63)	(0.73)	(0.63)	
Distance to unpaved road		−2.51*					
		(1.01)					
R^2	0.30	0.44	0.36	0.30	0.47	0.40	0.10

TABLE 5. Mean (±SD) distance (m) covered per hour, and mean number (± SD) of moves in relation to time of the day and month, for eight female *Natrix natrix*. The range of distances covered per hour is given in parenthesis. Only distances of ≥ 10 m were defined as moves.

Month	Daytime	Distance covered per hour	Number of moves
Jun	morning	9.46 ± 9.92 (0–95.13)	0.16 ± 0.12
	midday	16.51 ± 32.20 (0–278.73)	0.15 ± 0.21
	afternoon	23.43 ± 32.03 (0–608.12)	0.25 ± 0.24
Jul	morning	46.15 ± 75.70 (0–992.80)	0.27 ± 0.18
	midday	26.63 ± 16.43 (0–102.03)	0.54 ± 0.27
	afternoon	31.19 ± 35.34 (0–358.00)	0.27 ± 0.28
Aug	morning	1.21 ± 2.64 (0–36.11)	0.05 ± 0.09
	midday	2.43 ± 3.30 (0–24.86)	0.14 ± 0.18
	afternoon	5.36 ± 10.45 (0–216.33)	0.06 ± 0.09

June, a compost pile on a forest edge that has been used by >20 females in previous years (UH, pers. obs.). On the days before that period, some females moved directly to the compost pile, and others moved in steps with resting periods in nearby places. Females covered distances of up to 500 m to reach the oviposition site. Aggregations of two to six tagged and untagged female Grass Snakes were observed at the oviposition site during the egg laying period in late June.

On warm days, some snakes remained active in the late afternoon until dusk, but no activity was observed after sunset. Two additional radiotracking sessions on the warmest nights of the season showed that the snakes were inactive at nighttime, sheltered in edge habitats (dense vegetation, tree trunks, stumps, underground, fallen logs, organic piles) or in rodent burrows in monocultures.

Because we tried to avoid disturbing the snakes while radiotracking, detection of individuals with prey items in their stomach was infrequent and concerned mostly non-tagged individuals: Observations were recorded in forest edges ($N = 4$), maize ($N = 1$), potatoes ($N = 1$), and grassland ($N = 1$). Prey items of nontagged Grass Snakes were eight Common Toads (*Bufo bufo*), one Slow-Worm (*Anguis fragilis*), and one Common Frog (*Rana temporaria*).

DISCUSSION

Our data obtained from eight radiotracked female Grass Snakes in an area of intensive agriculture demonstrate that monocultures are a component of snake habitat. This is a striking difference to the Swedish population studied by Madsen (1984), where the snakes generally only traversed arable land to move between edge habitats and did not stay for long in monocul-

tures. In the second half of July, we recorded the highest proportions of locations, as well as the greatest percentage of moves, within monocultures. Consecutive locations of an individual within the same crop occurred over time spans of up to 27 days. The 74 sightings of snakes revealed some behavioral adaptations to conditions prevailing within these habitat types. From direct observations of the tracked animals, it was clear that, in maize, the snakes selectively used spots where sunlight reached the ground, whereas in cereals, they were often located basking adjacent to or within machine tracks. Deep soil cracks in crops and meadows were used both for moving and as retreat sites.

When comparing proportional habitat use to availability within individual home ranges, the snakes showed a clear preference for the edge habitats in the study area (i.e., embankments, dams, forest edges, and riparian zones). Similar preferences of Grass Snakes for edge habitats, mostly dense stands of blackberry bushes (*Rubus fruticosus*) in close proximity to stone fences, were recorded by Madsen (1984) in a rural landscape. Mertens (1992) identified thorny shrub and forest edges, windfalls, and light forest as the preferred habitat of the Grass Snakes in the surroundings of a botanical garden. Thermal gradients determine the spatial behavior of snakes (Peterson et al., 1993; Reinert, 1993; Blouin-Demers and Weatherhead, 2001, 2002). Forest edges facing east, west, and south show strong edge-oriented thermal gradients on a small spatial scale (Matlack, 1993), which may allow snakes to adjust their body temperature with minimal effort. In the five most significant of our logistic regression models, the snakes' probability of occurrence was positively correlated with either percentage cover of perennial layer or distance to cereal crop or with both. Perennial vegetation is the dominant vegetation layer of edge habitats in

the study area, and the snakes tended to avoid stretches of edge habitat frequently overshadowed by adjacent crop vegetation.

The snakes in our study area tended toward a unimodal daily movement pattern, with the highest number of moves recorded at midday. According to Mertens (1994), body temperatures allowing for optimal locomotion in Grass Snakes range from 32–34°C. In dense vegetation of edge habitats or in the dappled shade of monocultures, such temperatures are probably not achieved before midday.

Our findings suggest a seasonal shift in functional relevance of monocultures as a component of snake habitat. Twenty-five percent of all locations in monocultures fell within the preoviposition period, when many gravid females select sites where they can maintain a high and stable body temperature during gestation (Reinert 1993). Monocultures may provide suitable basking sites at this time of the year. The remaining 75% of locations in monocultures occurred after 10 July (i.e., the approximate date of oviposition for Grass Snakes in this study area), when the females postoviposition have high energy requirements and, thus, seek an optimal foraging environment. For both foraging and basking snakes, crops such as maize and cereals may provide extensive protection from several avian predators at this time of the season, because, according to our observations, hawks, kites, and Gray Herons (*Ardea cinerea*), known to feed on snakes in the study area, seem to avoid cereal crops of a given height. The principal prey of Grass Snakes are anurans (Gregory and Isaac, 2004), especially Common Toads (Madsen, 1984; Mertens, 1992; Reading and Davies, 1996), which also dominated our small sample of regurgitated prey items ($N = 10$). However, the radiotracking data are insufficient to determine whether the use of monocultures is linked to foraging activities. It is possible that in these locations snakes forage for rodents, which are most abundant in midsummer (K. Krähenbühl and R. Arlettaz, unpubl. data), and perhaps monocultures provide female snakes postgestation with prey that is energetically superior to frogs.

Habitat structure and resource availability are known to have an effect on movement patterns and home-range size (Gregory et al., 1987). With an average of 40 ha, home ranges in our study area were substantially larger than the 25-ha ''total'' home range obtained by Madsen (1984) for gravid females in a Swedish population. The Grass Snakes of this population foraged essentially in unidirectional moves along stone fences, and they made long distance movements to and from manure-hills, which they used as nesting sites. Grass Snakes in a fishpond system in Hungary foraged in a linear movement pattern along embankments separating individual ponds (Nagy and Korsós, 1998) and were highly sedentary during summer, spending most of the time at the same spot with optimal access to prey. The comparatively large home ranges documented in our study may be the result of several factors. We consider low-prey density and nesting-site density to be most likely. For example, the five of the seven gravid females that moved to the same site for oviposition by covering distances of up to 500 m might have responded to a lack of suitable nesting sites. However, regardless of the density and spatial separation of resources in the study area, our findings suggest that monocultures provide at least temporary advantages over more natural habitats to female Grass Snakes. This may be the result of a combination of suitable basking sites, favorable foraging opportunities, and low pressure from avian predators. Whether monocultures are similarly beneficial to nonreproductive females and males remains to be demonstrated.

Implications for Conservation.—The fact that all eight radiotagged individuals monitored in this study used almost all types of crops in a high-intensity agricultural system shows that monocultures can provide suitable habitat for female Grass Snakes. Nonetheless, these snakes clearly preferred remnant edge habitats, suggesting that they are of higher quality than monocultures. Apart from species-specific management interventions, such as the creation of nesting sites and of anuran breeding ponds, the maintenance of a mosaic of habitats and of the structural heterogeneity of edge situations appears the highest priority for the successful management of this snake population.

committee on animal testing of the canton of Berne, Switzerland.

LITERATURE CITED

AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analyses of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

ATKINSON, P. W., R. J. FULLER, J. A. VICKERY, G. J. CONWAY, J. R. B. TALLOWIN, R. E. N. SMITH, K. A. HAYSOM, T. C. INGS, E. J. ASTERAKI, AND V. K. BROWN. 2005. Influence of agricultural management, sward structure and food resources on grassland field use by birds in lowland England. Journal of Applied Ecology 42:932–942.

BERRY, O., M. D. TOCHER, D. M. GLEESON, AND S. D. SARRES. 2005. Effect of vegetation matrix on animal dispersal: genetic evidence from a study of endangered skinks. Conservation Biology 19: 855–864.

BLOUIN-DEMERS, G., AND P. J. WEATHERHEAD. 2001. An experimental test of the link between foraging, habitat selection and thermoregulation in Black Rat Snakes (*Elaphe obsoleta obsoleta*). Journal of Animal Ecology 70:1006–1013.

———. 2002. Habitat specific behavioral thermoregulation by Black Rat Snakes (*Elaphe obsoleta obsoleta*). Oikos 97:59–68.

BRUNNER, E., S. DOMHOF, AND F. LANGER. 2002. Nonparametric Analysis of Longitudinal Data in Factorial Experiments. Wiley, New York.

DONALD, P. F., AND A. D. EVANS. 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. Journal of Applied Ecology 43:209–218.

DONALD, P. F., R. E. GREEN, AND M. F. HEATH. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London (B) 268:25–29.

DRISCOLL, D. A. 2004. Extinction and outbreaks accompany fragmentation of a reptile community. Ecological Applications 14:220–240.

FOLEY, J. A., R. DEFRIES, G. ASNER, C. BARFORD, G. BONAN, S. R. CARPENTER, F. S. CHAPIN, M. T. COE, G. C. DAILY, H. K. GIBBS, J. H. HELKOWSKI, T. HOLLOWAY, E. A. HOWARD, C. J. KUCHARIK, C. MONFREDA, J. A. PATZ, I. C. PRENTICE, N. RAMANKUTTY, AND P. K. SNYDER. 2005. Global consequences of land use. Science 309:570–574.

GOLDER, F. 1984. Ein gemeinsamer Masseneiablageplatz von *Natrix natrix helvetica* und *Elaphe longissima* mit Daten über Eizeitigung und Schlupf. Salamandra 21:10–12.

GRAY, M. J., L. M. SMITH, AND R. I. LAYVA. 2004. Influence of agricultural landscape structure on a southern high plains, USA, amphibian assemblage. Landscape Ecology 19:719–729.

GREGORY, P. T., AND L. A. ISAAC. 2004. Food habits of the Grass Snake in south eastern England: is *Natrix natrix* a generalist predator? Journal of Herpetology 38:88–95.

GREGORY, P. T., J. M. MACARTNEY, AND K. W. LARSEN. 1987. Spatial patterns and movements. *In* R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), Snakes, Ecology and Evolutionary Biology, pp. 366–395. Macmillan Publishing Company, New York.

GUERRY, A. D., AND M. L. HUNTER. 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. Conservation Biology 16:745–754.

GUISAN, A., AND U. HOFER. 2003. Predicting reptile distributions at mesoscale: relation to climate and topography. Journal of Biogeography 30: 1233–1243.

HEARD, G. W., D. BLACK, AND P. ROBERTSON. 2004. Habitat use by the inland Carpet Python (*Morelia spilota metcalfei*: Pythonidae): seasonal relationships with habitat structure and prey distribution in a rural landscape. Austral Ecology 29:446–460.

HENLE, K., K. F. DAVIES, M. KLEYER, C. MARGULES, AND J. SETTELE. 2004. Predictors of species sensitivity to fragmentation. Biodiversity and Conservation 13:207–251.

HOFER, U., J. C. MONNEY, AND G. DUŠEJ. 2001. Die Reptilien der Schweiz. Verbreitung–Lebensräume– Schutz. Birkhäuser, Basel, Switzerland.

JULLIARD, R., F. JIGUET, AND D. COUVET. 2004. Common birds facing global changes: what makes a species at risk? Global Change Biology 10:148–154.

KABISCH, K. 1999. *Natrix natrix* (Linnaeus, 1758)— Ringelnatter. *In* W. Böhme (Hrsg.), Handbuch der Reptilien und Amphibien Europas, Band 3/IIA: Schlangen II, Serpentes II: Colubridae 2 (Boiginae, Natricinae), pp. 513–580. Aula-Verlag, Wiebelsheim, Germany.

KJOSS, V. A., AND J. A. LITVAITIS. 2001. Community structure of snakes in a human-dominated landscape. Biological Conservation 98:285–292.

MADSEN, T. 1984. Movements, home range size and habitat use of radio-tracked Grass Snakes (*Natrix natrix*) in southern Sweden. Copeia 1984:707–713.

MATLACK, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66:185–193.

MERTENS, D. 1992. Ökoethologisch-Radiotelemetrische Untersuchungen an einer Population der Ringelnatter (*Natrix natrix* L.) unter besonderer Berücksichtigung von Populationsstruktur, Aktivität, Ressourcenausnutzung und Thermoregulation. Unpubl. Ph.D. diss. Phillipps-University, Marburg/Lahn, Germany.

———. 1994. Some aspects of thermoregulation and activity in free-ranging Grass Snakes (*Natrix natrix* L.). Amphibia-Reptilia 15:322–325.

MONNEY, J.-C., AND A. MEYER. 2005. Red List of the threatened reptiles of Switzerland. Federal Office for the Environment, and Swiss Amphibian and Reptile Conservation Program. BAFU-Series: Implementation Environment, Berne, Switzerland.

NAGY, Z. T., AND Z. KORSÓS. 1998. Data on movements and thermal biology of Grass Snake (*Natrix natrix* L.) using radiotelemetry. *In* C. Miaud and R. Guyétant (eds.), Current Studies in Herpetology: Proceedings of the 9th Ordinary General Meeting of the Societas Europaea Herpetologica 25–29 August 1998, pp. 339–343. SHE, Le Bourget du Lac, France.

NÖLLERT, A., K-D. STEGEMANN, AND A. RITTER. 1989. Bemerkungen zu einem Massen-Eiablageplatz der Ringelnatter (*Natrix n. natrix*) am Ahlbecker Fenn, Kreis Ueckermünde, Bezirk Neubrandenburg. Jahrbuch für Feldherpetologen 3:107–114.

PEARSON, D., R. SHINE, AND A. WILLIAMS. 2005. Spatial ecology of a threatened python (*Morelia spilota imbricata*) and the effects of anthropogenic habitat change. Austral Ecology 30:261–274.

PETERSON, C. R., A. R. GIBSON, AND M. E. DORCAS. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. *In* R. A. Seigel and J. T. Collins (eds.), Snakes—Ecology and Behavior, pp. 241–307. McGraw-Hill, Inc., New York.

READING, C. J., AND J. L. DAVIES. 1996. Predation by Grass Snakes (*Natrix natrix*) at a site in southern England. Journal of Zoology 239:73–82.

REINERT, H. K. 1993. Habitat selection in snakes. *In* R. A. Seigel and J. T. Collins (eds.), Snakes—Ecology and Behavior, pp. 201–233. McGraw-Hill, Inc., New York.

SWIHART, R. K., T. M. GEHRING, M. B. KOLOZSVARY, AND T. E. NUPP. 2003. Responses of ''resistant'' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions 9:1–18.

VERHULST, A., A. BÁLDI, AND D. KLEIJN. 2004. Relationship between land-use intensity and species richness and abundance of birds in Hungary. Agriculture, Ecosystems and Environment 104:465–473.

VICKERY, J. A., J. R. TALLOWIN, R. E. FEBER, E. J. ASTERAKI, P. W. ATKINSON, R. J. FULLER, AND V. K. BROWN. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. Journal of Applied Ecology 38:647–664.

WEBB, J. K., AND R. SHINE. 1998. Using thermal ecology to predict retreat-site selection by an endangered snake species. Biological Conservation 86:233–242.

WHITAKER, P. B., AND R. SHINE. 2003. A radiotelemetric study of movements and shelter-site selection by free-ranging Brownsnakes (*Pseudonaja textilis*, Elapidae). Herpetological Monographs 17:130–144.

WHITE, G. C., AND R. A. GARROT. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, Inc., San Diego, CA.

WICKRAMASINGHE, L. P., S. HARRIS, G. JONES, AND N. VAUGHAN. 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. Journal of Applied Ecology 40:984–993.