Behavior-Based Scale Definitions for Determining Individual Space Use: Requirements of Two Amphibians

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ABSTRACT: Understanding individual space use remains a major issue in ecology, and it is complicated by definitions of spatial scale and the interplay of multiple factors. We quantified the effect of habitat and biotic and individual factors on space use by amphibians (*Bufo bufo spinosus* [BB] and *Bufo viridis* [BV]) that were radio-tracked in their terrestrial summer habitat. We analyzed two spatial scales, 50% core areas and 95% home ranges (excluding 50% core areas), thought to represent resting and foraging areas, respectively. The 50% core area of BB was best explained by habitat structure and prey density, whereas the 50% core area of BV was determined solely by habitat structure. This suggests that the resting and foraging areas of BB are not spatially separated. The 95% home range of BB was determined by prey density, while for BV both habitat structure and prey density determined home range size. We conclude that the terrestrial area requirements of amphibians depend on the productivity and spatiotemporal complexity of landscapes and that differential space use may facilitate their co-occurrence. Behavior-based a priori hypotheses, in combination with an information-theoretic approach and path analyses, provide a promising framework to dis-

entangle factors that govern individual space use, thereby advancing home range studies.

Keywords: *Bufo*, home range size, floodplain mosaic, foraging behavior, habitat structure, path analysis.

Introduction

Home range size, accommodating all behaviors related to reproduction and survival (Burt 1943), has been used as an indicator of energy expenditure (Schoener 1968) and animal performance (Kenward 1985). These factors are in turn linked to key parameters of population dynamics. For example, with decreasing home range size, population density and dispersal rate are predicted to increase (Kjellander et al. 2004; Wang and Grimm 2007). Thus, home range size is a general variable for studying spatially structured populations, and it is informative for population management (Lomnicki 1988).

Among species, variation in home range size is strongly related to body size (McNab 1963; Biedermann 2003). Among individuals, variation in home range size may be influenced by food availability and competition (Ebersole 1980), predation risk (Lima and Dill 1990), cover (Tufto et al. 1996), and differences among individuals (Börger et al. 2006b). Furthermore, habitat structure—for example, habitat composition, configuration, and connectivity—is related to the distribution of resources and shelter (Prohl and Berke 2001). However, the effects of habitat structure and resources on home range size have rarely been untangled (but see Tufto et al. 1996; Lombardi et al. 2007). Habitat structure per se may constrain or facilitate access to resources (Arthur et al. 1996; Revilla et al. 2004), and the distribution of the preferred habitat type may have a dominating effect on space use (Pasinelli 2000; Buner et al. 2005), suggesting a close link between habitat selection and home range size. In this study, we therefore include factors for overall habitat structure (e.g., habitat richness) and partial habitat structure (area of preferred habitat type) and food resources to quantify their separate effects on home range size.

Home range size is usually quantified using a single

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spatial scale, for example, the area including 95% of either raw locations or a calculated utilization distribution (Worton 1989). Animals, however, do not use home ranges uniformly. The intensity of use is higher within core areas than in the peripheral parts of the home range, which may reflect the spatial segregation of behaviors (Marzluff et al. 2001). Consequently, the ecological relevance of the key underlying factors may vary with spatial scale (Börger et al. 2006b). Hence, we need multiple spatial scales when quantifying variation in home range size. We propose to define the spatial scales at which to study variation in home range size by the behaviors they probably integrate. This novel approach allows the formulation of a priori hypotheses on how the impact of factors is expected to vary with scale and behavior, facilitating our understanding of spatially structured populations.

Dynamic floodplains comprise a spatially complex habitat mosaic (Naiman et al. 2005) and are therefore good model systems to study the impacts of habitat factors (e.g., habitat richness, temperature) and biotic factors (food resources) on individual space use. We used two amphibian species (common toad *Bufo bufo spinosus* and green toad *Bufo viridis*), differing in life history and ecology, to shed more light on the processes structuring terrestrial summer home ranges. The two toad species co-occur within the active tract of a naturally dynamic floodplain (Tockner et al. 2006). Our main goal was to quantify direct and indirect effects of habitat, biotic, and individual factors on the sizes of 50% core areas and 95% home ranges.

We focus on the terrestrial summer period because of its importance for the viability of amphibian populations (Trenham and Shaffer 2005; Rittenhouse and Semlitsch 2007) and because it narrows the set of factors that influence space use. During the summer period, amphibians need abundant food to build up fat reserves for maintenance and future reproduction (Wälti and Reyer 2007) as well as refugia from desiccation (Schwarzkopf and Alford 1996; Seebacher and Alford 2002). Hence, resting and foraging are the dominating behaviors in summer that may segregate spatially. We therefore expect that toads use the 50% core areas within home ranges for resting while they use the peripheral areas of 95% home range (excluding 50% core areas) for foraging. Based on these assumptions we formulated three hypotheses that are expected to apply to both species.

1. Habitat factors (habitat structure, home range temperature) control the size of 50% core areas. We expect the 50% core areas to decrease with increasing habitat structure (e.g., area of large wood, habitat richness; Kie et al. 2002; McLoughlin et al. 2003; Buner et al. 2005), as well as to decrease with increasing temperature (Schwarzkopf and Alford 1996; Seebacher and Alford 2002).

2. Biotic factors (prey density and competition) control

the size of 95% home ranges. We expect the size of 95% home ranges to decrease with increasing food density and competition (McNab 1963; Hixon 1980).

3. The effects of individual factors (body mass, sex, animal identity) on 50% core areas and 95% home ranges are predicted to be outweighed by habitat and biotic factors. Body mass is likely a poor explanatory factor as fluctuations in body mass are primarily caused by evaporation and adsorption of water rather than by food intake. The reproductive status (sex; Lombardi et al. 2007) and differences among individuals (Steury and Murray 2003) are considered less important during the nonbreeding season.

Our emphasis on behavior-based a priori hypotheses for determining space use by individuals contributes to a better grounding of home range studies in theory. The statistical approaches applied here provide a promising analytical framework to untangle the web of factors that govern space use, thereby advancing our understanding of spatially structured populations.

Methods

Study Site

The study was conducted from mid-June until the end of September in 2005 and 2006, along the seventh-order Tagliamento River in northeastern Italy (46°N, 12°30'E). The Tagliamento (catchment area: 2,580 km²) originates at 1,000 m asl in the southern fringe of the European Alps and flows almost unimpeded for 172 km to the Adriatic Sea. The river retains its natural morphological and hydrological characteristics.

The main study area was the active tract (1.6 km²) of an island-braided floodplain complex (at river kilometer 79.8–80.8; 135 m asl). This reach contains a spatially complex and temporally dynamic habitat mosaic embedded in an extensive matrix of exposed riverine sediments (Petts et al. 2000; fig. A1, in app. A in the online edition of the *American Naturalist*).

The 800-m-wide active tract is bordered by riparian forest on the north bank and the steep slope of Monte Ragogna on the south bank. Further detailed information on the Tagliamento catchment and the main study area can be found elsewhere (Ward et al. 1999; Arscott et al. 2002; Tockner et al. 2003).

Study Species

Bufo bufo spinosus is a generalist species associated with densely vegetated habitats, while *Bufo viridis* is a pioneer species of the continental and Mediterranean steppes (Giacomina and Castellano 2006). *Bufo viridis* is a quick colonizer of pioneer habitats and far more versatile than *B. b. spi-*

nosus. Both toad species may burrow to withstand harsh environmental conditions and for hydration (Hoffman and Katz 1989). *Bufo b. spinosus* is considered less tolerant of high temperature than *B. viridis* (Degani et al. 1984; Meek and Jolley 2006).

Habitat Mapping

In 2005 and 2006, the entire study area was mapped in detail at base flow (about $20 \text{ m}^3 \text{ s}^{-1}$) using a differential global positioning system (GPS) device (Trimble GeoXT, Zurich), and data were processed using ArcView GIS 9.0 (ESRI, Redlands, CA). Seven habitat types were discriminated: exposed gravel sediments (63.9 ha; averaged values for both years), water (13.5 ha), established islands (woody vegetation $>2 \text{ m}$ tall, topographically elevated, $\geq 1 \text{ m}^2$; 8.3 ha), open pioneer vegetation (cover 10% to $\leq 50\%$; 6.3 ha), dense pioneer vegetation (cover $>50\%$; 3.9 ha), large wood deposits ($\geq 0.5 \text{ m}^2$; 1.2 ha), and eroded banks (ecotones of established islands providing many earth holes as refuges, with slopes between 45° and 90° ; 0.3 ha).

Radio Telemetry

Adult toads were caught during random searches at night, weighed, and fitted with radio transmitters LT2-351 (2 g) or LT2-392 (5 g; Titley Electronics, Ballina, Australia). Transmitters were tightly fitted around the toads' waists and secured with an aluminum beaded-chain belt (Ball Chain Manufacturing, Mount Vernon, NY; Rathbun and Murphey 1996; fig. A2).

The mass of the transmitter, including the belt, did not exceed 10% of the body mass (mean $\pm$ SD: *B. b. spinosus*, $4.32\% \pm 1.51\%$; *B. viridis*, $6.86\% \pm 0.94\%$), as recommended by Richards et al. (1994). At the start of the study, all toads were sexed and photographed to allow individual identification if a transmitter tag was lost. All toads were reweighed to the nearest 0.1 g at weekly to biweekly intervals during the study period to monitor individual body condition. Neither transmitter mass nor duration of the tracking period negatively affected changes in the toads' body mass (Indermaur et al. 2008).

Scanning receivers (Australis 26k) and handheld antennas (Yagi AY/C, Yagi collapsible) were used for tracking the toads (Titley Electronics, Ballina, Australia). We followed each of 56 radio-tagged *B. b. spinosus* and 59 *B. viridis* for 1–3 months (*B. b. spinosus*: mean 44.5 days, range 13.4–99.5 days; *B. viridis*: mean 33.1 days, range 13.5–71 days). The exact position of each toad was recorded 6 days per week, once daily and once nightly, using a GPS device (average tracking resolution: 1 m). Two observers simultaneously located toads in different parts of the study area, randomly varying the tracking time and

the sequence of tracked animals. For more details on the telemetry methods, see appendix B in the online edition of the *American Naturalist*.

Estimation of Home Range Size

For home range estimation, a total of 3,079 locations of *B. b. spinosus* and 2,545 locations of *B. viridis* were collected (mean number of locations $\pm$ SD: *B. b. spinosus*, 55 ± 27.6 ; *B. viridis*, 43 ± 16). A preliminary analysis (incremental plots; Hayne 1949) of the relationship between the number of locations and home range estimates showed that 20 locations of *B. b. spinosus* and 25 locations for *B. viridis* were required to obtain robust individual home range size estimates. Because the number of locations was at least twice as high as the calculation locations, we consider that our estimates were robust.

Fixed-kernel home ranges were calculated with Ranges 7 software (grid: 160×160 cells; cell size: 1 m^2), using the 50% or 95% contours of the density distribution (South et al. 2005). We omitted the outer 5% of the data. Their inclusion would have extended contours into areas that were not used repeatedly for daily activities but rather for explorative behavior, thereby introducing bias in home range size estimates (Kenward 2001). Toads were considered to use the interior core of home ranges for resting and their periphery for foraging, depicted by the 50% and 95% contours, respectively. These spatial scales were discriminated for each species separately by applying a regression of probability of use against the proportion of total area (fig. A3; Clutton-Brock et al. 1982; Powell 2000).

The average smoothing factor ($h = 0.3$) was least-squares cross-validated using Ranges 7, validated by our field observations, and applied to all individuals of both species. Because *B. viridis* avoided established islands and the riparian forest, we fitted the 95% contours of *B. viridis* as they touched the boundaries of these habitat types, and we compared the congruency of the empirically fitted contour with the analytically derived one using Ranges 7. The contours were entirely congruent, therefore justifying the applied smoothing factor.

Determinants of Home Range Size

Home range size was predicted using three habitat factors (habitat richness, area of large wood deposits, home range temperature), two biotic factors (prey density, competition), and three individual factors (body mass, sex, animal identification [identity]; tables 1, B1). By applying a principal component analysis, we a priori omitted additional explaining factors reflecting habitat structure because of redundancy or the lack of additional variance explained (table B2). Home range temperature was quantified using

Table 1: Habitat, biotic, and individual factors used for predicting home range size

Code	Factor
Habitat factors:	
T	Home range temperature (°C)
Ri	Habitat richness ^a
Wood	Area of large wood deposits ^{a,b}
Biotic factors:	
Co	Intra- and interspecific competition (m)
Prey	Prey density
Individual factors:	
M	Body mass of animals at the beginning of the tracking period
Sex	Sex (integer)
A	Animal identity (integer)

Note: All factors were standardized before analysis.

^a Habitat richness and the area of large wood deposits were surrogates for habitat structure. Highly structured habitats were considered to provide more refuges for protection from harmful environmental conditions than would weakly structured habitats.

^b Large wood deposits was the preferred habitat type within home ranges (see analysis of habitat selection, table B1 in the online edition of the *American Naturalist*).

temperature loggers (Thermochron iButton DS1921G, 0.5°C resolution). We employed 67 loggers in 2005 and 57 loggers in 2006 and used an hourly logging interval to record temperatures at the sediment surface, with locations distributed in proportion to the aerial cover of individual habitat types. Average home range temperature within a home range was calculated as the area-weighted mean of all habitat types within a specific home range.

Prey density was quantified in 2006 by setting up 100 pitfall traps (diameter 9 cm, depth 12 cm, volume 0.5 L) randomly along three transects perpendicular to the river corridor. The pitfall traps were opened (set) at twilight (8:00–9:30 p.m.) and closed at sunrise (5:00–7:00 a.m.), and the traps were sampled three times (July 21–22, August 8–9, September 7–8). Average prey availability (number of prey items m⁻²) within the active tract of the floodplain was calculated by applying the inverse distance-weighted interpolation method in ArcGIS 9.0 using log-transformed prey densities (fit of interpolation: $R^2 = 0.466$). Competition (intra- and interspecific) was calculated by buffering the kernel center of a home range with a diameter of 19 m (average 50% core area) or 45 m (average 95% home range) and summing the weighted inverse distances to all other kernel centers within the buffer. The buffer distance was chosen to allow for home range overlap between individuals.

Statistical Analysis

Modeling strategy. We used an information-theoretic approach (model selection) proposed by Burnham and An-

derson (2002) and path analysis (Mitchell 1993) to quantify variation in home range size. The information-theoretic approach was used to fit a set of 11 candidate models from which we derived model-averaged effect sizes to evaluate the importance of explaining factors. Each of these models reflects a hypothesis with a sound basis in the literature (table B3). In contrast to the information-theoretic approach, path analysis is helpful in quantifying both the direct effects of factors on a response variable and their indirect effects on a response variable via intermediary factors. Hence, we quantified the indirect and direct effects of the most important home range size determinants out of the information-theoretic approach, using path analysis to better understand the interrelatedness of factors. The information-theoretic approach therefore served to set the theoretical background for the path models. To avoid redundancy, we focus on the path analysis and refer to appendixes for methods and results out of the information-theoretic approach (tables B4–B6). We assumed that the interior 50% core areas were used mainly for resting, while the peripheral areas of the 95% home range were used mainly for foraging. For modeling, we therefore removed the 50% core area from the 95% home range to avoid confounded results.

Path analysis. We fitted path models (AMOS 7.0, SPSS, Chicago) separately per species and spatial scale (50% core area, 95% home range). The direct effects were measured by the standardized partial regression coefficient between Y and X_j by holding all other factors constant. The direct effects were the path coefficients relating Y to X_j . This way, the path models controlled for nuisance correlations among factors typical in field studies. In this study, we accepted a priori the correlation between habitat richness, area of large wood deposits, home range temperature, and prey density (table B7) because each factor may have its own merit. For modeling, we used data from 2006 because prey density was not sampled in 2005. All factors were z standardized before analysis. Home range size was log transformed to assure normally distributed residuals. One outlier (Cook's distance >1) was removed.

Results

Home range use. The percentage of locations where toads were observed moving (= foraging) was consistently lower within the 50% core areas than within the 95% home ranges (number of locations as percent of total locations in 50% core areas/95% home ranges: *Bufo bufo spinosus*, 5.4/17.2; *Bufo viridis*, 9.3/40.2; table B8). However, the percentage of total locations animals were seen moving during the day was higher in the 50% core areas of *B. b. spinosus* than in those of *B. viridis*. These results indicate that the interior core areas were used primarily for resting

and that the peripheral areas of the 95% home range were used mainly for foraging but also that *B. b. spinosus* may forage to some extent in 50% core areas. However, our data do not allow further behavioral detail, such as commuting movements between resting and foraging areas, to be resolved.

Home Range Size, Shape, and Overlap

The mean 50% core area and 95% home ranges of *B. b. spinosus* were 48 and 570 m², respectively, and those of *B. viridis* were 295 and 2,456 m², respectively (table 2). The differences between the two species were statistically significant (50% core areas, univariate ANOVA: $F = 9.054$, $df = 1, 109$, $P = .003$, mean squared error [MSE] = 0.46; 95% home ranges, univariate ANOVA: $F = 10.23$, $df = 1, 109$, $P = .002$, MSE = 0.433). Median home range size was consistently smaller than mean home range size (right-skewed distribution), hence few individuals had very large home ranges (table 2).

The 50% core areas were not significantly different between sexes ($F = 0.186$, $df = 1, 109$, $P = .667$, MSE = 0.46), and there was no interaction between species and sexes ($F = 0.180$, $df = 1, 109$, $P = .672$, MSE = 0.46). Similarly, the 95% home ranges were not significantly different between sexes ($F = 1.713$, $df = 1, 109$, $P = .193$, MSE = 0.433), and there was no interaction between species and sexes ($F = 1.694$, $df = 1, 109$, $P = .196$, MSE = 0.433).

For each species, virtually all 95% home ranges were multinuclear; that is, they consisted of spatially separated areas (*inset*, fig. 1). The relative (%) overlap of home ranges between species was small (mean $\pm$ SD: 50% core areas, $0.33\% \pm 0.20\%$; 95% home range, $2.67\% \pm 1.81\%$), as was the relative overlap of home ranges among individuals of a species (50% core area: *B. b. spinosus*, $0.34\% \pm 0.39\%$,

B. viridis, $3.10\% \pm 2.86\%$; 95% home range, *B. b. spinosus*, $2.75\% \pm 1.88\%$, *B. viridis*, $11.24\% \pm 6.18\%$).

Determinants of Home Range Size

The most important home range size determinants out of the information-theoretic approach were habitat richness, area of large wood deposits, and prey density (confidence intervals of regression coefficients did not include 0), all related to home range temperature (tables B4–B6). Individual factors and the biotic factor competition (table 1) were considered unimportant (confidence intervals included 0; see tables B5, B6). Hence, we used all habitat factors (habitat richness, area of large wood deposits, home range temperature) and the biotic factor prey density to establish a path model, integrating the interrelatedness of factors, to explain variation in home range size (fig. 2). Via the direct path, we predicted that all habitat factors (habitat richness, area of large wood deposits, temperature) and the biotic factor prey density per se may affect home range size. Via the indirect path, we predicted that habitat richness and the area of large wood deposits alter habitat temperature and, therefore, prey density, which in turn might indirectly affect home range size. Factors reflecting habitat structure (habitat richness, area of large wood deposits) explained most variation in log-home range size followed by prey density and temperature (table 3).

Both direct and indirect effects controlled log-home range size of both species (fig. 2). The 50% core areas and 95% home ranges of both species increased with the direct effect prey density (table 3; fig. 2). The direct effect of habitat richness was positively related to home range size, except for the 95% home range of *B. b. spinosus*. Home range size decreased with the area of large wood deposits and temperature, except for the 50% core area of *B. viridis*.

Table 2: Home range size estimates and body mass (mean $\pm$ SD) for both toad species

Species, year	Sex	n	50% core area (m ²)				95% home range (m ²)				Body mass (g)	
			Median	Mean	SD	Range	Median	Mean	SD	Range	Mean	SD
<i>Bufo bufo spinosus</i> :												
2005	M + F	25	44	70	104	3–406	305	675	986	32–3,620	123.4	51.9
2006	M + F	29	19	29	37	3–191	160	480	766	6–3,345	126.7	50.0
2005/2006	M	11	26	37	32	3–104	533	1,164	1,354	32–3,620	52.0	13.3
2005/2006	F	43	24	51	86	3–406	210	418	638	6–3,526	143.3	38.1
2005/2006	M + F	54	24	48	78	3–406	230	570	872	6–3,620	125.1	50.5
<i>Bufo viridis</i> :												
2005	M + F	23	95	124	130	4–568	820	1,074	992	36–3,899	30.8	5.8
2006	M + F	36	86	404	1,016	1–5,000	1,472	3,339	4,810	27–17,248	28.0	4.6
2005/2006	M	20	84	466	1,126	1–5,000	1,337	3,028	4,470	36–13,781	26.6	3.4
2005/2006	F	39	91	208	578	1–3,633	1,109	2,162	3,677	27–17,248	30.5	5.6
2005/2006	M + F	59	91	295	806	1–5,000	1,204	2,456	3,946	27–17,248	29.1	5.3

Note: M = males, F = females, n = number of animals.

Figure 1: Part of the distribution of home ranges (95% contours) of both species in the study site (2006 data). Riparian forest fringes the active tract, which is mainly composed of exposed gravel sediments (white), the river network (dark gray), and vegetated islands (pale gray). The inset shows the multinuclear structure of one *Bufo bufo spinosus* home range (50% core area = thin line; 95% home range = thick line) and the distribution of locations.

Temperature decreased with home range size, except for the 50% core area of *B. b. spinosus*.

For *B. b. spinosus*, habitat richness and the area of large wood deposits had a significant effect on prey density, while for *B. viridis*, only the area of large wood deposits had a significant effect on prey density (fig. 2). Prey density increased with increasing habitat structure and temperature, except for the 95% home range of *B. viridis*, where prey density was inversely related to temperature.

In the 95% home ranges, prey density and the area of large wood deposits varied less for *B. b. spinosus* than they did for *B. viridis* (fig. 3). Average prey density in densely vegetated habitats (established islands, dense pioneer vegetation), mainly occupied by *B. b. spinosus* (fig. 1), was about twice as high ($359 \text{ individuals m}^{-2} \text{ day}^{-1}$ vs. $183 \text{ individuals m}^{-2} \text{ day}^{-1}$) as in open habitats (exposed gravel sediments) that were mainly occupied by *B. viridis*.

Prey availability was dominated by ground-dwelling insects (percent insect density for densely vegetated habitats/exposed gravel sediments: *Coleoptera*, 38.4/24.3; *Arachnidae*, 21.5/38.2; *Acarina*, 8.8/0; *Collembola*, 7.0/7.7), while

exclusively flying insects (*Hymenoptera*, 7.4/7.2) contributed marginally to total density.

Hypothesis 1: Habitat Factors Control the Size of 50% Core Areas

For *B. b. spinosus*, the significant direct effects of both habitat factors (area of large wood deposits, temperature) and the biotic factor prey density determined its 50% core area (fig. 2A), thereby partly supporting our hypothesis. The size of the 50% core area decreased with increasing area of large wood deposits (fig. 2A). The biotic factor prey density had the strongest direct effect on the size of 50% core areas.

For *B. viridis*, the direct effect of the habitat factor area of large wood deposits controlled its 50% core area (fig. 2C), which is in line with our hypothesis. Other biotic, habitat, and individual factors were considered unimportant (tables 3, B5; confidence intervals include 0). Unexpectedly, the size of the 50% core area increased with increasing area of large wood deposits.

Figure 2: Path diagrams relating the factors habitat richness (*Ri*), area of large wood deposits (*Wood*), home range temperature (*T*), and prey density (*Prey*) to log-home range size (*log-HRS*), separately per species, 50% core area, and 95% home range. The values for standardized direct effects (**bold text**) and indirect effects (*plain text*) are given adjacent to the arrows. The thickness of arrows is proportional to the effect size of factors. Significant effects are underlined (see table 3 for significance levels). Negative relationships are shown with broken lines. Single-headed arrows represent causal effects; double-headed arrows represent correlations.

Hypothesis 2: Biotic Factors Control the Size of 95% Home Ranges

For *B. b. spinosus*, the biotic factor prey density solely determined its 95% home range (fig. 2B). Hypothesis 2 was partly supported, because the biotic factor competition poorly explained variation in its 95% home range and the size of the 95% home range increased with increasing prey density (table 3; fig. 2B).

For *B. viridis*, the direct effects of the factors habitat richness and prey density controlled the size of its 95% home range, thereby partly constituting our hypothesis (table 3; fig. 2D). The 95% home ranges were largest when both habitat richness and prey density were high.

Hypothesis 3: The Effects of Individual Factors Are Outweighed by the Effects of Habitat and Biotic Factors

All individual factors were poorly supported, as indicated by the results of the information-theoretic approach, thereby confirming our hypothesis (tables B4, B5). Sampling bias, expressed by either the number of locations

collected (table B5) or the number of weeks that toads were tracked (table B6), poorly explained variation in home range size (confidence intervals included 0). The direct effect sizes evaluated using path analysis (table 3; fig. 2) were similar to those evaluated with the information-theoretic approach (table B5).

Discussion

Our main goal was to quantify the separate direct and indirect effects of habitat, biotic, and individual factors on summer home range size of amphibians (*Bufo bufo spinosus* and *Bufo viridis*) at biologically relevant spatial scales, namely, 50% core areas that are the interior areas of home ranges with the highest intensity of use and 95% home ranges that include large peripheral areas (about 10 times the size of 50% core areas). We hypothesized (hypothesis 1) that the 50% core areas are mainly used for resting and therefore controlled by habitat factors reflecting refuge density (habitat richness, area of large wood deposits), while (hypothesis 2) the 95% home ranges (excluding the 50% core areas) are used for foraging and therefore are

Table 3: Effect sizes (β) and variances (R^2) with standard errors for the path models (see fig. 2)

Factors	50% core area					95% home range				
	β	SE	P	R^2	SE	β	SE	P	R^2	SE
<i>Bufo bufo spinosus</i> ($n = 23$, GFI = .345):						<i>Bufo b. spinosus</i> ($n = 22$, GFI = .356):				
Direct effects:						Direct effects:				
Ri	.030	.017	.078	.762	.023	-.018	.027	.501	.754	.233
Wood	-.074	.110	<.001	.523	.158	-.017	.035	.634	.406	.125
T	.052	.017	.002	.114	.034	-.045	.041	.269	.160	.049
Prey	.409	.014	<.001	.071	.021	.493	.028	<.001	.255	.079
e3				.001					.004	.001
Indirect effects:						Indirect effects:				
Ri $\rightarrow$ T	.087	.115	.452			.119	.135	.379		
Ri $\rightarrow$ prey	.788	.092	<.001			.577	.174	<.001		
Wood $\rightarrow$ T	.020	.139	.883			.079	.184	.667		
Wood $\rightarrow$ prey	.301	.110	.006			.646	.234	.006		
T $\rightarrow$ prey	.421	.168	.012			.754	.275	.006		
<i>Bufo viridis</i> ($n = 24$, GFI = .318):						<i>B. viridis</i> ($n = 28$, GFI = .489):				
Direct effects:						Direct effects:				
Ri	.057	.067	.393	.990	.292	.258	.076	<.001	.905	.242
Wood	.597	.103	<.001	.788	.233	-.042	.093	.648	.828	.221
T	-.073	.144	.614	.094	.028	-.217	.295	.462	.042	.011
Prey	.123	.091	.176	.235	.069	.435	.085	<.001	.489	.131
e3				.045	.013				.099	.027
Indirect effects:						Indirect effects:				
Ri $\rightarrow$ T	.088	1.925	.054			.100	.044	.024		
Ri $\rightarrow$ prey	.151	.946	.344			.206	.165	.211		
Wood $\rightarrow$ T	.099	1.723	.085			.039	.046	.395		
Wood $\rightarrow$ prey	.167	4.853	<.001			.682	.161	<.001		
T $\rightarrow$ prey	.331	.438	.661			-.462	.648	.476		

Note: See table 1 for abbreviations of factors. All factors were standardized before analysis. P = P value for significance level .001, e3 = unexplained variance in log-home range size, and GFI = goodness-of-fit index for the most constrained model. Values <0 and >1 indicate that the data do not fit the model, while values close to 1 indicate good fit (Jöreskog and Sörbom 1984). The true model fit here lies somewhere between the reported GFI values and 1.

controlled by biotic factors (prey density, competition). Furthermore (hypothesis 3), the impacts of individual factors on 50% core areas and 95% home ranges were hypothesized to be marginal compared to habitat and biotic factors.

Our results demonstrate that a web of habitat and biotic factors determines summer home range size of both species. However, the two species responded differently to the same web of factors when using 50% core areas and 95% home ranges.

The Impact of Direct and Indirect Effects of Habitat and Biotic Factors on Space Use

Direct effects. Our results demonstrate that the sizes of the 50% core areas and 95% home ranges of two amphibian species, differing in life history and ecology, were primarily governed by habitat structure (habitat richness, area of large wood deposits) and prey density (food resources; table 3; fig. 2). However, the generalist species *B. b. spinosus* responded to the area of large wood deposits and prey

density within its 50% core area (table 3; fig. 2A), while the pioneer species *B. viridis* solely responded to the area of large wood deposits (table 3; fig. 2C). These results suggest that *B. b. spinosus* may rest and forage within 50% core areas while *B. viridis* rests only within core areas, in line with behavioral field data (table B8). Furthermore, these results demonstrate the dominating effect of single habitat structures on space use, which has been shown for other animals, such as birds (Pasinelli 2000; Buner et al. 2005) and bears (McLoughlin et al. 2003).

For both species, the 50% core areas increased with increasing habitat structure (surrogate for refuge density), except for *B. b. spinosus*, where the 50% core area decreased with increasing areas of large wood deposits (fig. 2A, 2C). Hence, individuals may increase their core areas to include multiple habitat types (*B. b. spinosus*; table B5) or large wood deposits (*B. b. spinosus*, *B. viridis*) that are patchily distributed. A similar relationship was found by Tufto et al. (1996) and Rosalino et al. (2004) for roe deer and badgers. These results are in line with the resource-dispersal hypothesis (Macdonald 1983), which predicts that

Figure 3: Relationships between log-home range size (95% home range) and prey density (A), number of habitat types (habitat richness; B), and area of large wood deposits (C). Standardized values are shown. The relationships in figure 3 deviate partly from those in figure 2 due to the exclusion of other explaining factors and their interrelatedness.

home range size increases when resources are patchily distributed. Hypothesis 1 was partly supported because both habitat and biotic factors determined the size of the 50% core areas of *B. b. spinosus*.

The 95% home range of *B. b. spinosus* was solely determined by the biotic factor prey density, which implies that this species forages in the peripheral areas of its home range (table 3; fig. 2B). For *B. viridis*, habitat richness and prey density controlled the size of its 95% home range (table 3; fig. 2D). *Bufo viridis* may therefore forage in more diverse habitats because of their higher productivity and/or because predatory shelters are located close to foraging areas in exposed gravel sediments. For example, rodents and ungulates reduced predation risk by decreasing distances between foraging places and shelters (Lagos et al. 1995; Hamel and Cote 2007). The patchy distribution of predatory shelters and prey as well as the depletion of food patches may have forced toads to extend their foraging areas, thereby increasing 95% home ranges. The resulting multinuclear home range structure (*inset*, fig. 1) is most likely a general phenomenon in pond-breeding amphibians (Semlitsch 1981; Forester et al. 2006). In addition, large home ranges are considered to mitigate the impacts of fluctuating environmental conditions (Ferguson et al. 1999), which are characteristic of dynamic floodplains (Arscott et al. 2001; Naiman et al. 2005). In contrast, small home ranges (table 2) might have resulted from the occasional spatial aggregation of food resources and refuge. Toads may stop adding areas to their home ranges when minimum requirements are met. Therefore, increasing home range size does not necessarily result in higher prey and refuge density.

The generalist species *B. b. spinosus* occupied densely vegetated habitats where prey density was about twice as high as in habitats mainly occupied by the pioneer species *B. viridis* (fig. 1). The habitats of both species differed little in prey composition, implying rather indiscriminate feeding habits of the two toads. Indeed, a number of studies showed prey selection by amphibians to depend on prey availability rather than prey size (Smith and Bragg 1949; Berry 1970). In addition, individuals of the same amphibian species that differed largely in body size selected prey items of all sizes (Inger 1969). Hence, *B. viridis* might have increased its 95% home range much more than *B. b. spinosus* to compensate for low prey density. This may explain the large differences in home range size among species (table 2) and suggests pioneer species may be more limited by prey density than generalist species.

Hypothesis 2 was partly supported, as the 95% home range of *B. viridis* was determined by both prey density and habitat richness. However, competition was a poor predictor, although juveniles and undetected adults were excluded from our studies. Nevertheless, we consider our results robust. First, competition is most likely low under harsh environmental conditions (intermediate disturbance hypothesis; Connell 1979). Second, we radio-tracked a representative sample of the reproductive population (about 30% of *B. b. spinosus* and 60% of *B. viridis*), an estimate that is based on all individuals that were ever caught (app. B) on egg clutch counts over 2 years (L. Indermaur, unpublished data) and by assuming equal sex ratios.

Indirect effects. Prey density increased with increasing habitat structure (habitat richness, area of large wood deposits) and mostly with increasing temperature (fig. 2).

However, prey availability for the generalist species *B. b. spinosus* was determined by overall habitat structure (habitat richness, area of large wood deposits), while prey availability for the pioneer species was determined by a single habitat structure (area of large wood deposits). Hence, both species used highly structured habitats because of their expected high productivity, as well as of their role as potential thermal and predatory refugia.

In general, home range size decreased with increasing temperature, except for the 50% core area of *B. b. spinosus*, where home ranges were largest when temperature was high (fig. 2). *Bufo b. spinosus* was exposed to moderate temperature in densely vegetated habitats (maximum 33.5°C), whereas *B. viridis* was exposed to highest temperature in open habitats (maximum 43°C). Hence, at high temperature, *B. b. spinosus* may move and therefore may forage more actively in its 50% core area (table B8). For *B. viridis*, which mainly rests in large wood deposits (mean maximum 27.2°C), leaving thermal shelter may increase the desiccation risk, thereby decreasing movement activity and home range size.

The Impact of Individual Factors on Space Use

As expected (hypothesis 3), individual factors poorly explained variation in 50% core areas and 95% home ranges (tables B4–B6). The weak impact of body mass on 50% core areas and 95% home ranges is in accordance with previous studies on deer (Relyea et al. 2000; Said and Servanty 2005) and bears (Dahle and Swenson 2003). We argue that in the amphibian body, mass strongly fluctuates due to evaporation and hydration, thereby masking changes in body fat. Furthermore, in patchy environments such as dynamic floodplains, metabolic requirements may not depend linearly on home range size. Differences among individuals, expressed by the animal identity factor, were far less important than habitat and biotic factors (tables B4–B6), in contradiction to experimental data on *Tribolium* beetles that were kept in microlandscapes of varying complexity but stable environmental conditions (Morales and Ellner 2002). We expect that differences among individuals might be more important in less variable environments (Klopfer and MacArthur 1960).

Conclusions

We demonstrated that the summer home range size (50% core areas and 95% home ranges) of two pond-breeding amphibians was a function of prey density and habitat structure (habitat richness, area of large wood deposits). Habitat factors affected home range size directly, probably by increasing refuge density, or indirectly, by increasing prey availability. This finding implies that the terrestrial

area requirements of amphibians depend on the productivity and spatiotemporal complexity of the landscape. Reducing habitat complexity may therefore impede resting and foraging behaviors, which are both paramount for survival and future reproduction (Wälti and Reyer 2007). The relative importance of the same factors varied between species and across spatial scales (50% core areas, 95% home ranges). Therefore, differential space use facilitates the coexistence of the two toad species in the terrestrial summer habitat.

Our results did not fully correspond with the assumption that 50% core areas mainly integrate resting behavior, because for *B. b. spinosus*, the habitat factor area of large wood deposits (surrogate for refuge) and the biotic factor prey density determined the 50% core area. This suggests that resting and foraging behaviors may not be spatially separated. The use of behavior-related scale definitions therefore contributes to our understanding of spatially structured populations, regardless of whether underlying assumptions are met. Behavior-based scale definitions, applying an information-theoretic approach, and path analysis provide a promising framework to disentangle the web of factors governing space use and hence advance home range studies.

Further research should focus on the relationships between habitat structure, resource density, and population dynamics. A number of empirical studies have shown that home range size depends on habitat structure and/or resource density (Ebersole 1980; Prohl and Berke 2001; Buner et al. 2005; our study). Home range size is generally predicted to decrease when population density increases (Kjellander et al. 2004; Wang and Grimm 2007). However, we lack empirical evidence that home range size and population dynamics are similarly controlled by the interplay of habitat structure and resource density. Approaching this topic would require an experimental setup where levels of habitat structure and resource density are easily manipulated and the response (home range size, population density) can be quantified. Another research direction should focus on the effect of qualitative differences (physiological state, tolerance to environmental factors) among individuals on home range size in relation to environmental stability. As previously argued, theory predicts individual differences to be more important in stable rather than in dynamic environments (Klopfer and MacArthur 1960). As dynamic floodplains become more and more regulated and, therefore, habitat stability increases, differences among individuals might become more important in controlling home range size. Furthermore, if there is evidence for individual differences, it is important to determine whether these are related to survival and passed on to offspring.

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Appendix A from L. Indermaur et al., “Behavior-Based Scale Definitions for Determining Individual Space Use: Requirements of Two Amphibians”

(Am. Nat., vol. 173, no. 1, p. 60)

Supplemental Figures

Figure A1: Overview of the study site from Monte Ragogna (Indermaur et al. 2008).

Figure A2: Toads with externally fitted radio transmitters. A, *Bufo bufo spinosus* with a 5-g transmitter; B, *Bufo viridis* with a 2-g transmitter.

Figure A3: Estimates of percent of core areas are plotted in 5% intervals against the percent area of the largest home range for 2005 and 2006. The increase of the regression line after the 50% core area (*dashed line*) denotes increased foraging activities.

Appendix B from L. Indermaur et al., “Behavior-Based Scale Definition for Determining Individual Space Use: Requirements of Two Amphibians”

(Am. Nat., vol. 173, no. 1, p. 60)

Evaluation of Tracking Success and Failure

We conducted a pilot study in 2004 on 10 individuals of *Bufo bufo bufo* that were radio-tracked from the end of June until the beginning of September and were located once each day and night to evaluate the performance of transmitters. Adult toads were fitted with radio transmitters LT2-351 (2 g) or LT2-392 (5 g; Titley Electronics, Ballina, Australia). The life spans of transmitters were about 10 weeks and 6 months, respectively. The detection range varied between 10 and 400 m, depending on the terrain topography and the animals' hiding places. When animals were buried underneath stones and fitted with transmitter LT2-351, the detection range was minimal. Signals of transmitters LT2-392 were consistently stronger than signals of transmitter LT2-351.

The transmitters were tightly fitted with an aluminum beaded-chain belt (Ball Chain Manufacturing, Mount Vernon, NY) around the waist (Rathbun and Murphey 1996; fig. A2). Animals either accepted the transmitter or tried to get rid of it by moving with outstretched legs. In the latter case, we quickly removed the transmitter. The beaded-chain belt caused lateral abrasions on every second animal during the pilot study. When the abrasions did not heal after loosening the belt, we removed the radio transmitter. In 2% of the relocations, the antenna was entangled in dense vegetation and animals had to be manually released. The radio transmitters were modified in this respect for the main study; that is, we attached less flexible antennas to avoid tangles in dense vegetation.

For the main study in 2005 and 2006 in Italy, the belt was coated with black Plasti Dip (Plasti Dip, Blaine, MN), a silicon-like substance, to avoid lateral abrasion and to be more cryptic to predators. Coating the belt clearly prevented abrasions: out of 114 individuals of *Bufo bufo spinosus* and 134 individuals of *Bufo viridis* that were ever fitted with a radio transmitter, 1 individual of *B. b. spinosus* (1%) and 5 individuals of *B. viridis* (4%) had lateral abrasions. We removed the transmitters from these animals and excluded them from analyses. Three individuals of *B. viridis* became snagged on vegetation by the belt and were manually released. We lost the signal of three individuals of *B. b. spinosus* and two individuals of *B. viridis*, probably due to transmitter failure. We removed the transmitters from all animals at the end of the study period.

The transmitter did not limit the toads' ability to access narrow shelters (mouse holes), to bury themselves up to 30 cm deep in the sand, or to shed skin. No other effect on the toads' behavior was observed. To avoid stress and bias in movements, animals were not dug out to verify their presence when hidden under shelter for less than a week.

Over 2 years (2005–2006), 7,417 locations of 114 *B. b. spinosus* and 134 *B. viridis* were gathered. For estimation of home range size, we used 6,071 locations of 67 *B. b. spinosus* and of 59 *B. viridis*. Thus, 41% of all radio-tracked individuals of *B. b. spinosus* and 56% of *B. viridis* were omitted for analyses because they lost the transmitter before a sufficient number of locations was collected to robustly estimate home range size. Sixteen animals that lost the transmitter were recaptured and fitted again with radio transmitters. These animals were identified by individual photos that were taken at first capture.

Predation among all animals tracked in 2 years was low: out of 114 tracked *B. b. spinosus*, 3 individuals (2.6%) were probably killed by herons or minks, whereas out of 134 tracked *B. viridis*, 8 individuals (5.9%) were killed by snakes (*Natrix natrix*). Two individuals of *B. viridis* died, probably due to desiccation.

Background and Results of the Information-Theoretic Approach Used

Eleven candidate models were formulated based on previous studies and our present field observations to address the three hypotheses (table B3). Models 1–3 hypothesized that habitat factors (habitat richness, area of large

wood deposits, home range temperature) determine home range size (hypothesis 1). Model 7 hypothesized that biotic factors (prey density, competition) determine home range size. Models 5, 6, and 8 hypothesized that both habitat and biotic factors determine home range size (hypothesis 2). Models 9–11 hypothesized that individual factors (body mass, sex, animal identity) determined home range size (hypothesis 3).

Models 1 and 2 were nested within model 3 to evaluate the relative contribution of the preferred habitat type (area of large wood deposits; see table B1), habitat richness, and home range temperature to variance in home range size. Each model, except model 10, included the number of locations to correct for sampling bias. We preferred to use the number of locations as a covariate instead of estimating home ranges with equal numbers of randomly selected locations, as proposed by Börger et al. (2006a) and Fieberg (2007). The former approach allowed us to quantify the separate effect of sampling bias. In each model, sex was used as a factor to correct for its potential effect on home range size. Emphasis was put on minimizing the set of factors and number of models to avoid bias in model selection. Interactions between factors were excluded because of the rather small sample size and to avoid overfitted models.

For home range calculation, we used data of both years, taking individuals as sample units. For model selection, we used data from 2006 because prey density was not sampled in 2005. Candidate models were fitted with general linear models (family = Gaussian, link = identity) in R, version 2.4.0 (R Development Core Team 2005), separately per species and scale using the same sample size (Anderson and Burnham 2002). All factors were z standardized before to analysis. Home range size was log transformed to assure normally distributed residuals. One outlier (Cook’s distance >1) was removed.

Hypothesis 1: Habitat Factors Control the Size of 50% Core Areas

For *B. b. spinosus*, the three top-ranked models that were best supported by the data included the factors habitat richness, home range temperature, and prey density (table B4). The top-ranked model (no. 6) was twice as well supported as the second-ranked model (no. 5) and seven times better supported than the third-ranked model (no. 4; see evidence ratios, table B4). The effect of prey density on its 50% core area was almost six times larger than was the effect of habitat richness (table B5). For *B. b. spinosus*, hypothesis 1 was partly supported, because both habitat factors (habitat richness) and biotic factors (prey density) determined the 50% core area. For *B. viridis*, the best selected model (no. 1; $\omega_i > 0.9$) contained the factor area of large wood deposits (table B4), which solely determined its 50% core area (table B5), partly supporting hypothesis 1. For both species, the factor home range temperature was poorly supported (confidence intervals included 0; table B5), contrasting with our hypothesis.

Hypothesis 2: Biotic Factors Control the Size of 95% Home Ranges

For *B. b. spinosus*, although the three top-ranked models (4, 5, and 7; sum of $\omega_i > 0.9$) contained the factors home range temperature, prey density, and competition (table B4), prey density alone determined the 95% home range (table B5), partly supporting hypothesis 2. In contrast, for *B. viridis*, the three top-ranked models (2, 3, and 6) contained habitat richness, area of large wood deposits, home range temperature, and prey density ($\omega_i > 0.9$; table B4). For *B. viridis*, hypothesis 2 was partly supported as both habitat factors (habitat richness) and biotic factors (prey density) predicted the size of the 95% home ranges (table B5), though confidence intervals included 0. Competition poorly explained the variation in 95% home ranges of both species (confidence intervals included 0; table B5), contrasting with our hypothesis.

Hypothesis 3: The Effects of Individual Factors Are Outweighed by the Effects of Habitat and Biotic Factors

All individual factors (models 9–11) poorly predicted variation in the size of 50% core areas and 95% home ranges (confidence intervals included 0; tables B4, B5), fully supporting hypothesis 3. Results were consistent when using the number of weeks instead the number of locations to correct for sampling bias (table B6). In summary, the most important home range-size determinants were prey density, habitat structure (habitat richness and area of large wood deposits), and temperature.

Table B1

Ranking order of preferred habitat types from compositional analysis separated for both species and the 50% core area (50) and the 95% home range (95)

Species, scale	1	2	3	4	5	6	7	<i>n</i>	λ	χ^2	<i>P</i>	df
<i>Bufo bufo spinosus</i> :												
50	ERO >	ISL-E =	ISL >	LWD =	PD >	GRA >	PL	54	.27	70.3	<.001	6
95	LWD >	ISL-E >	ERO >	GRA >	PD >	ISL >	PL	54	.39	50.9	<.001	7
<i>Bufo viridis</i> :												
50	LWD >>>	GRA =	ISL-E =	RIP-E >	PL >	PD >	ERO	59	.16	110.0	<.001	6
95	LWD >>>	GRA >	RIP-E >	ISL-E >	ERO >	PL >	PD	59	.12	96.8	<.001	6

Note: λ = Wilks's lambda, χ^2 = chi square statistics, >>> = a significant deviation, and > = a nonsignificant deviation from proportionality at $P < .05$. ERO = eroded banks, GRA = exposed gravel sediments, ISL = established islands, ISL-E = island edge (5-m buffer around established islands), LWD = large wood deposits, PD = dense pioneer vegetation, PL = open pioneer vegetation, and RIP-E = riparian edge (5-m buffer along river network).

Table B2

Results of a principal component analysis summarizing variation in landscape measures, separated by species, the 50% core area, and the 95% home range

Species, factor	50% core area component		95% home range component	
	1	2	1	2
<i>Bufo bufo spinosus</i> :				
Richness	.97	-.04	.94	.05
No. patches	.96	-.13	.91	.05
Edge length	.89	.33	.74	.61
Contagion index	.01	.99	.02	.99
% variance explained	66.45	27.44	63.24	26.85
<i>Bufo viridis</i> :				
Richness	.92		.90	
No. patches	.88		.89	
Edge length	.87		.73	
Contagion index	.45		.71	
% variance explained	64.51		66.25	

Note: All factors were standardized before analysis. For *B. viridis*, only the first component was extracted.

Table B3

Candidate models used for predicting home range size (log-HRS)

Model	Factors	Explanation/key features	Reference
1	Wood + <i>N</i> + sex	Partial habitat structure (area of large wood deposits, which is the preferred habitat)	Pasinelli 2000; McLoughlin et al. 2003; Buner et al. 2005
2	Wood + Ri + <i>N</i> + sex	Total habitat structure (area of large wood deposits plus habitat richness)	Kie et al. 2002
3	Wood + Ri + T + <i>N</i> + sex	Total habitat structure and habitat temperature	Schwarzkopf and Alford 1996; Seebacher and Alford 2002
4	Prey + <i>N</i> + sex	Prey density	McNab 1963; Ebersole 1980
5	Prey + T + <i>N</i> + sex	Prey density and habitat temperature	Pereira et al. 2002
6	Prey + T + Ri + <i>N</i> + sex	Prey density, habitat temperature and habitat structure	Tufto et al. 1996; Lombardi et al. 2007
7	Prey + Co + <i>N</i> + sex	Prey density and competition	Hixon 1980

Table B3 (Continued)

Model	Factors	Explanation/key features	Reference
8	Prey + Co + Ri + N + sex	Prey density, competition and habitat structure	Burt 1943; Kleeberger 1985; Smyers et al. 2002
9	M + N + sex	Body mass not important	Relyea et al. 2000; Said and Servanty 2005
10	N + N + sex	No. locations (sampling bias)	Börger et al. 2006a; Fieberg 2007
11	A + N + sex	Differences in quality among animals not important	Steury and Murray 2003

Note: See table 1 for abbreviations of factors. The number of locations (N) was used as a covariate in every model (except model 10) to correct for sampling bias. Similarly, sex was used in every model to correct for its potential effect on home range size.

Table B4

Model selection results for predicting intraspecific variation in log-home range size, sorted after differences between Akaike's small-sample information criterion (ΔAICc), separately by species, the 50% core area, and the 95% home range

Model no.	Models	R^2	K	LL	AICc	ΔAICc	ω_i	ER
<i>Bufo bufo spinosus</i> , 50% core area ($n = 23$):								
6	Prey + Ri + T	.992	7	45.9	-70.3	.0	.585	1
5	Prey + T	.990	6	43.1	-69.0	1.3	.312	2
4	Prey	.987	5	40.0	-66.4	3.9	.085	7
7	Prey + Co	.987	6	40.0	-62.7	7.6	.013	44
8	Prey + Ri + Co	.989	7	41.1	-60.8	9.5	.005	117
3	Wood + Ri + T	.935	7	21.1	-20.7	49.6	.000	6. E + 10
2	Wood + Ri	.916	6	18.2	-19.2	51.1	.000	1. E + 11
1	Wood	.615	5	.7	12.1	82.4	.000	8. E + 17
10	N	.143	4	-8.5	27.2	97.5	.000	1. E + 21
9	M	.112	5	-8.1	30.2	100.5	.000	7. E + 21
11	A	.150	5	-8.4	30.3	100.6	.000	7. E + 21
<i>B. b. spinosus</i> , 95% home range ($n = 22$):								
4	Prey	.988	6	31.8	-63.4	.0	.599	1
5	Prey + T	.989	7	33.1	-60.8	1.8	.245	2
7	Prey + Co	.984	5	28.3	-60.4	3.1	.125	5
6	Prey + Ri + T	.984	6	28.7	-56.7	6.2	.027	22
8	Prey + Ri + Co	.985	7	29.0	-56.2	10.0	.004	147
2	Wood + Ri	.769	6	-.7	12.8	65.1	.000	1. E + 14
3	Wood + Ri + T	.791	7	.4	14.9	67.3	.000	4. E + 14
1	Wood	.635	5	-5.7	21.3	71.3	.000	3. E + 15
9	M	.352	5	-12.1	33.3	83.9	.000	2. E + 18
11	A	.252	5	-11.7	34.0	84.1	.000	2. E + 18
10	N	.211	4	-14.2	34.5	84.8	.000	3. E + 18
<i>Bufo viridis</i> , 50% core area ($n = 24$):								
1	Wood	.916	5	4.5	4.3	.0	.798	1
2	Wood + Ri	.918	6	4.7	7.5	3.2	.162	5
3	Wood + Ri + T	.922	7	5.4	10.2	6.0	.041	20
4	Prey	.783	5	-6.9	27.1	22.9	.000	9. E + 04
5	Prey + T	.783	6	-6.9	30.7	26.4	.000	6. E + 05
7	Prey + Co	.783	6	-6.9	30.7	26.5	.000	6. E + 05
6	Prey + Ri + T	.794	7	-6.3	33.6	29.3	.000	2. E + 06
8	Prey + Ri + Co	.792	7	-6.4	33.8	29.5	.000	3. E + 06
10	N	.126	4	-23.6	57.3	53.1	.000	3. E + 11
9	M	.166	5	-22.1	57.6	53.4	.000	4. E + 11

Table B4 (Continued)

Model no.	Models	R^2	K	LL	AICc	ΔAICc	ω_i	ER
11	A	.129	5	-23.6	60.5	56.2	.000	2. E + 12
<i>B. viridis</i> , 95% home range ($n = 28$):								
2	Wood + Ri	.784	7	2.8	-4.9	.0	.400	1
3	Wood + Ri + T	.780	7	3.0	-5.2	.6	.290	1
6	Prey + Ri + T	.716	5	1.9	-8.9	1.2	.214	2
8	Prey + Ri + Co	.719	6	1.8	-8.7	4.1	.051	8
1	Wood	.717	6	-3.7	-8.9	4.4	.045	9
4	Prey	.593	6	-5.2	-14.1	14.9	.000	1,741
5	Prey + T	.511	5	-3.7	-16.8	17.1	.000	5,050
7	Prey + Co	.610	7	-4.7	-13.5	17.2	.000	5,343
10	N	.273	5	-14.4	-19.4	22.7	.000	9. E + 04
9	M	.332	4	-13.8	-21.3	23.1	.000	1. E + 05
11	A	.334	5	-14.0	-21.3	26.0	.000	4. E + 05

Note: See table 1 for abbreviations of factors. The top-ranked model, with $\Delta\text{AICc} = 0$, best approximates the data, and models with $\Delta\text{AICc} \leq 2$ are considered to receive substantial support from the data. The number of animals (n), the coefficient of determination (R^2), number of factors (K), log likelihood (LL), model weights (ω_i) and evidence ratios (ERs) are given. When one model receives $\omega_i \geq 0.9$, there is no model selection uncertainty apparent. ERs are the ratio of model weights of a particular model in relation to the top-ranked model. Models in boldface (confidence set: sum of $\omega_i > 0.9$) were used for model averaging.

Table B5

Model-averaged factors of intraspecific variation in home range size for both species in the 50% core area and the 95% home range

Factors	50% core area					95% home range				
	β	SE	CV	LCI	UCI	β	SE	CV	LCI	UCI
<i>Bufo bufo spinosus</i> :										
Co						-.025	.019	.764	-.063	.012
N	.012	.026	2.132	-.040	.064	-.003	.047	14.450	-.096	.089
Prey	.333	.048	.145	.236	.430	.461	.056	.121	.352	.571
Ri	.059	.028	.468	.004	.114	-.040	.028	.704	-.094	.015
Sex	.039	.065	1.676	-.092	.169	.008	.105	12.392	-.197	.214
T	.090	.063	.696	-.035	.215					
<i>Bufo viridis</i> :										
Co						.032	.180	5.641	-.321	.384
Wood	.705	.125	.177	.456	.954					
N	.146	.137	.942	-.129	.420	.174	.284	1.629	-.382	.730
Prey						.429	.289	.673	-.137	.996
Ri	.038	.065	1.739	-.093	.168	.214	.160	.744	-.098	.527
Sex	-.110	.204	1.851	-.519	.298	-.050	.582	11.590	-1.192	1.091
T						-.057	.069	1.202	-.192	.078

Note: See table 1 for abbreviations of factors. All factors were standardized before analysis. Unconditional effect size (β = slopes of factors in general linear models) with standard error (SE), coefficient of variation ($|CV| = SE/\beta$), and lower (LCI) and upper (UCI) confidence intervals ($\beta \pm 2 SE$). β , SE, and CV are based on a confidence model set (summarized weights ≥ 0.90). Factors not listed (see table 1) or without values were not included in the model set used for model averaging. Factors that did not include 0 in confidence intervals are considered important (bold).

Table B6

Model-averaged factors of intraspecific variation in home range size for both species in the 50% core area and the 95% home range

Factors	95% home range									
	<i>Bufo bufo spinosus</i>					<i>Bufo viridis</i>				
	β	SE	CV	LCI	UCI	β	SE	CV	LCI	UCI
Co	-.026	.019	.720	-.064	.011	-.007	.089	12.535	-.181	.167
Week	.013	.050	3.862	-.086	.112	.175	.211	1.210	-.240	.590
Prey	.453	.058	.129	.338	.568	.414	.203	.491	.015	.814
Ri	-.032	.027	.834	-.086	.020	.247	.155	.628	-.057	.551
Sex	-.001	.102	174.325	-.202	.201	-.079	.434	5.427	-.930	.770
T						-.115	.068	.592	-.250	.018

Note: Here, the number of weeks (Week) was used to correct for sampling bias, while in table B5 the number of locations collected was used to correct for sampling bias. See table 1 for abbreviations of other factors. All factors were standardized before analysis. Unconditional effect size (β = slopes of factors in general linear models) with standard error (SE), coefficient of variation ($|CV| = SE/\beta$), and lower (LCI) and upper (UCI) confidence intervals ($\beta \pm 2 SE$). β , SE, and CV are based on a confidence model set (summarized weights ≥ 0.90). Factors not listed (see table 1) or without values were not included in the model set used for model averaging. Factors that did not include 0 in confidence intervals are considered important (bold).

Table B7

Correlation matrix of factors used in candidate models for predicting log-home range size (HRS), separated by species, the 50% core area, and the 95% home range

Factors	<i>n</i>	log-HRS	Ri	Wood	Prey	Co	M	T	N	Week
<i>Bufo bufo spinosus</i> , 50% core area:										
Log-HRS	54	1.000	.938	.710	.993	-.331	-.047	.432	.345	.272
Ri	54		1.000	.708	.942	-.259	-.068	.262	.181	.141
Wood	54			1.000	.777	-.167	-.113	.180	.016	-.084
Prey	23				1.000	-.343	-.061	.380	.300	.243
Co	54					1.000	-.198	.017	.114	-.007
M	51						1.000	-.450	.169	.101
T	54							1.000	.375	.238
N	54								1.000	.818
Week	54									1.000
<i>B. b. spinosus</i> , 95% home range:										
Log-HRS	54	1.000	.760	.686	.992	-.215	-.265	.549	.261	.408
Ri	54		1.000	.611	.774	-.279	-.101	.306	.081	.216
Wood	54			1.000	.705	-.120	-.265	.274	.011	.163
Prey	22				1.000	-.124	-.284	.560	.259	.414
Co	54					1.000	.094	-.119	.093	.037
M	51						1.000	-.539	.232	.179
T	54							1.000	.141	.323
N	54								1.000	.802
Week	54									1.000
<i>Bufo viridis</i> , 50% core area:										
Log-HRS	59	1.000	.639	.940	.839	-.022	.103	.556	.182	.159
Ri	59		1.000	.614	.596	-.135	.402	.574	.096	-.159
Wood	59			1.000	.834	-.127	.181	.579	.045	.088
Prey	26				1.000	.015	.314	.557	.149	.176
Co	59					1.000	-.213	-.166	-.318	.106
M	57						1.000	.314	-.136	.142
T	59							1.000	.074	.027
N	59								1.000	.490

Table B7 (Continued)

Factors	<i>n</i>	log-HRS	Ri	Wood	Prey	Co	M	T	N	Week
Week	59									1.000
<i>B. viridis</i> , 95% home range:										
Log-HRS	59	1.000	.583	.536	.851	-.005	.003	.239	.538	.343
Ri	59		1.000	.383	.427	-.438	-.048	.552	.287	.138
Wood	59			1.000	.698	.094	.127	.380	.169	.185
Prey	29				1.000	.027	.037	.351	.379	.248
Co	59					1.000	.087	-.308	-.126	.407
M	57						1.000	-.004	.148	.234
T	59							1.000	.140	.064
N	59								1.000	.609
Week	59									1.000

Note: See table 1 for abbreviations of factors. All factors were standardized before calculating Pearson coefficients *n* = number of animals.

Table B8

Distribution of locations, classified as “resting” or “foraging,” in 50% core areas and 95% home ranges

	<i>Bufo bufo spinosus</i>				<i>Bufo viridis</i>			
	<i>n</i>	%	<i>n</i> (% of total <i>n</i>)		<i>n</i>	%	<i>n</i> (% of total <i>n</i>)	
			Core area	Home range			Core area	Home range
Seen	1,116	35.1	13.7	31.7	1,152	45.1	17.4	42.7
Not seen	2,063	64.9	36.7	61.8	1,404	54.9	38.5	54.3
Total	3,179	100.0	50.3	93.6	2,556	100.0	55.9	97.0
Seen at day	406	36.4	16.2	33.2	374	32.5	19.4	31.7
Seen at night	710	63.6	22.7	57.3	776	67.5	19.1	63.0
Total	1,116	100.0	38.9	90.4	1,150	100.0	38.5	94.8
Not seen at day	1,329	64.4	37.0	61.2	985	70.3	49.8	69.5
Not seen at night	734	35.6	19.5	34.0	417	29.7	20.3	29.4
Total	2,063	100.0	56.5	95.2	1,402	100.0	70.0	98.9
Seen moving	156	19.6	5.4	17.2	342	43.1	9.3	40.2
Seen sitting	639	80.4	31.9	72.5	451	56.9	27.7	55.0
Total	795	100.0	37.4	89.7	793	100.0	37.1	95.2
Seen moving at day	23	14.7	6.4	14.1	13	3.8	1.5	3.8
Seen moving at night	133	85.3	21.2	73.7	329	96.2	20.2	89.5
Total	156	100.0	27.6	87.8	342	100.0	21.6	93.3
Seen sitting at day	274	42.9	16.7	38.2	242	53.7	33.0	52.5
Seen sitting at night	365	57.1	23.0	52.0	209	46.3	15.7	44.1
Total	639	100.0	39.7	90.1	451	100.0	48.8	96.7

Note: *n* = number of locations.

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