

Habitat selection of three cryptic *Plecotus* bat species in the European Alps reveals contrasting implications for conservation

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Abstract Assessing the ecological requirements of species coexisting within a community is an essential requisite for developing sound conservation action. A particularly interesting question is what mechanisms govern the stable coexistence of cryptic species within a community, i.e. species that are almost impossible to distinguish. Resource partitioning theory predicts that cryptic species, like other sympatric taxa, will occupy distinct ecological niches. This prediction is widely inferred from eco-morphological studies. A new cryptic long-eared bat species, *Plecotus macrobullaris*, has been recently discovered in the complex of two other species present in the European Alps, with even evidence for a few mixed colonies. This discovery poses challenges to bat ecologists concerned with planning conservation measures beyond roost protection. We therefore tested whether foraging habitat segregation occurred among the three cryptic *Plecotus* bat species in Switzerland by radiotracking 24 breeding female bats (8 of each species). We compared habitat features at locations visited by a bat versus random locations within individual home ranges, applying mixed effects logistic regression. Distinct, species-specific habitat preferences were revealed.

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P. auritus foraged mostly within traditional orchards in roost vicinity, with a marked preference for habitat heterogeneity. *P. austriacus* foraged up to 4.7 km from the roost, selecting mostly fruit tree plantations, hedges and tree lines. *P. macrobullaris* preferred patchy deciduous and mixed forests with high vertical heterogeneity in a grassland dominated-matrix. These species-specific habitat preferences should inform future conservation programmes. They highlight the possible need of distinct conservation measures for species that look very much alike.

Keywords Cryptic species · Heterogeneity · *Plecotus* · Radiotracking · Resource partitioning · Switzerland

Introduction

Ecologists have a special interest in the ecological requirements of morphologically similar species and they try to identify the mechanisms that enable coexistence of these species in the community (Schoener 1974; Abrams 1998; Arlettaz 1999). Based on the principle of competitive exclusion (Gause's principle), a stable co-existence of species within a community is only conceivable if the species-specific utilisation of limiting resources is clear-cut (Hutchinson 1978; Ricklefs 1990; Arlettaz et al. 1997; Wang et al. 2005). Previous evidence suggests that the three most important niche dimensions are habitat, food, and foraging time (Pianka 1969; Schoener 1986). Habitat selection is seen as the main mechanism that allows species to coexist within a community (Arlettaz 1999).

Bats are the second largest order of mammals with 1,150 species and a high proportion of threatened species worldwide (IUCN red list 2011). Bat populations are declining as a result of various factors, including habitat transformation, habitat loss, extensive use of pesticides and large-scale agri- and silvicultural intensification, which influence the quality and diversity of the available habitats and thus also prey abundance (Stebbing 1988; Ransome 1990; Walsh and Harris 1996a, b; Wickramasinghe et al. 2004; Bontadina et al. 2008). Studies of habitat selection that clarify the species-specific habitat requirements are therefore an important key for bat preservation and successful management (Walsh and Harris 1996a). Consequently, in recent years, a large body of literature has been devoted to habitat preferences (review in Kunz and Parsons 2009), including some studies especially focused on morphologically similar or phylogenetically closely related species, i.e. sibling species (see Arlettaz 1999; Nicholls and Racey 2006; Davidson-Watts et al. 2006; Murphy et al. 2012).

One species complex that is widespread in the whole Palearctic is that of the long-eared bats (genus *Plecotus* spp., Swift and Racey 1983; Spitzenberger et al. 2006). In addition to two sympatric *Plecotus* species (*Plecotus auritus* and *P. austriacus*), molecular markers have identified a third "cryptic species", i.e. a "distinct species erroneously classified under one species name" (Bickford et al. 2007), namely, *P. macrobullaris* in the alpine area of Central Europe (Kiefer and Veith 2001; Kiefer et al. 2002; Spitzenberger et al. 2003; Ashrafi et al. 2010; Preatoni et al. 2011). These cryptic species overlap in most morphometric characters (Ashrafi et al. 2010) and are therefore expected to show very similar flight characteristics, notably in terms of speed and manoeuvrability. In addition, the echolocation signals of these cryptic bat species are very similar, as all show traits typical of the group of narrow-space gleaning foragers (Schnitzler and Kalko 2001;

Dietrich et al. 2006). Thus, species with highly similar morphology and comparable echolocation signals are expected to exploit their foraging habitat in a similar way.

We used the three cryptic and partly sympatric species of long-eared bats in Switzerland (Ashrafi et al. 2010) as a model to investigate the resource partitioning among sibling species. To our knowledge, no such study regarding resource partitioning of long-eared bats in Europe has been published so far.

Structurally complex habitats may well provide more niches and different ways of exploiting the environmental resources than those with simpler structures (Bazzaz 1975). In addition, positive relationships between habitat heterogeneity and animal species diversity are well documented on both local and regional scales (Davidowitz and Rosenzweig 1998). We therefore expected habitat heterogeneity to have a positive effect on the habitat selection of *Plecotus* bats in their foraging areas. Based on previous investigations of the trophic niche of these bats (Ashrafi et al. 2011; Alberdi et al. 2012) and models of predicted distribution (Rutishauser et al. 2012), we expected that *P. auritus* would show most heterogeneous foraging habitats as it has been identified as a food generalist (Ashrafi et al. 2011), compared to other *Plecotus* bat species, which are more specialised. Additionally, we hypothesised that *P. austriacus* and *P. macrobullaris* (the two more specialised species) would commute further to reach suitable foraging sites, and would consequently have larger home ranges than *P. auritus*.

We used radiotracking to investigate the habitat selection and niche partitioning pattern of all three *Plecotus* bat species in Switzerland. We explored the consequences of foraging habitat segregation for the conservation of these sibling species.

Materials and methods

Study sites and colonies

This study was conducted at six *Plecotus* colonies, two for each species, in North and South Switzerland (Table 1), during the summers of 2008 and 2009. The bat colonies were located in church attics in three bioregions of Switzerland: the Jura Mountains, the Central Plateau and the Western Central Alps (Gonseth et al. 2001). The sites were known for having relatively large maternity colonies (20–40 individuals) from a previous study (Ashrafi et al. 2010), that had genetically identified species based on several individuals per roost.

Radio-locations and random points

Eight female bats of the three species (total $N = 24$ individuals) were captured between June and September 2008. Bats were caught using mist nets (Ecotone, Gdynia, Poland), typically placed at roost entrance before dusk emergence. In a few cases, we captured individuals in the roost using hand nets. All animals were sexed and weighted. To ensure proper species identification, we also relied on the identification criteria developed by Ashrafi et al. (2010). For radiotracking, we chose adult female bats in breeding stage (mostly lactating), when bats' energy requirements peak (Kurta et al. 1989). These bats consequently are constrained to use foraging habitats in the vicinity of their roosts and to return to the maternity colony on an almost daily basis. Two types of radio tags were used (Holohil Systems Ltd., Carp, ON, Canada, BD-2N, 0.44 g and Biotrack, Wareham, Dorset, England, Pip 31, 0.45 g). Transmitter weight did not exceed 6 % of bat body weight to minimise adverse effects on flight behaviour (Bontadina et al. 2002). To fix the radio

Table 1 Radiotracking of *Plecoptus* females carried out in summer 2008

Species	Individual	Reproductive status	Colony	Date of capture	Number of nights ^a	Number of locations ^b	Home range ^c (MCP, ha)	Max. distance from roost (km)
<i>P. auritus</i>	1	Pregnant	Kirchrued (AG)	17.06.2008	1	35	43.35	0.78
	2	Not pregnant	Kirchrued (AG)	17.06.2008	3	17	81.84	0.47
	3	Not lactating	Kirchrued (AG)	22.09.2008	4	56	103.25	2.3
	4	Not pregnant	Kirchrued (AG)	17.06.2008	2	84	33.65	1.16
	5	Lactating	Blitzingen (VS)	18.07.2008	3	44	33.15	1.34
	6	Not lactating	Blitzingen (VS)	21.07.2008	3	44	5.21	0.74
	7	Post lactating	Blitzingen (VS)	24.08.2008	3	57	29.63	1.37
	8	Lactating	Blitzingen (VS)	21.07.2008	2	31	84.32	1.6
<i>P. austriacus</i>	1	Lactating	Mandach (AG)	21.06.2008	9	36	12.9	0.63
	2	Lactating	Mandach (AG)	21.06.2008	4	45	623.94	4.36
	3	Not lactating	Mandach (AG)	07.09.2208	3	45	148.93	4.7
	4	Lactating	Mandach (AG)	21.06.2008	3	37	113.49	3.9
	5	Lactating	Mönthal (AG)	03.07.2008	3	27	803.96	4.2
	6	Lactating	Mönthal (AG)	27.06.2208	5	35	63.89	1.55
	7	Post lactating	Mönthal (AG)	10.08.2008	3	48	470.18	2.56
	8	Post lactating	Mönthal (AG)	15.09.2008	7	62	126.43	2.03
<i>P. macrobullaris</i>	1	Not lactating	Obergesteln (VS)	16.07.2008	5	62	75.64	1.42
	2	Not lactating	Obergesteln (VS)	16.07.2008	5	30	64.08	1.08
	3	Not lactating	Obergesteln (VS)	16.07.2008	4	32	72.5	1.19
	4	Not lactating	Obergesteln (VS)	27.08.2008	2	53	87.46	1.5
	5	Lactating	Sembrancher (VS)	09.07.2008	4	34	797.02	4.65

Table 1 continued

Species	Individual	Reproductive status	Colony	Date of capture	Number of nights ^a	Number of locations ^b	Home range ^c (MCP, ha)	Max. distance from roost (km)
	6	Not lactating	Sembrancher (VS)	29.07.2008	7	35	581.91	4.61
	7	Post lactating	Sembrancher (VS)	29.07.2008	6	14	113.92	1.87
	8	Post lactating	Sembrancher (VS)	01.09.2008	2	52	123.48	4.41
Total	24				93	1015		

^a Night with successful radio-monitoring

^b Bearings with medium and high accuracy

^c Foraging home range (activity range)

transmitters, the fur between the scapulae was trimmed and the transmitters were attached using Torbot liquid bonding cement (Cranston, RI, USA).

The bats were tracked with Australis (26k Scanning Receiver, Titley Electronics, Australia) and Wildlife receivers (TRX-1000S, Wildlife Materials, USA). We used hand-held Yagi-antennae (Titley Electronics, Australia) to locate the bats, applying the triangulation technique (White and Garrott 1990; Bontadina et al. 2002). Bats first were tracked from a car to locate their foraging places, which were up to 4.7 km in aerial distance from the roost. Then radiotracking of an individual bat was performed on foot by a team of two (focal animal method, White and Garrott 1990), notably due to the complex alpine terrain. An observer team coordinated their work using walkie-talkies and timer watches to record simultaneously location data at 5 min intervals. At every interval, the time, observers positions, bearings of the bat signal and the estimated accuracies of the bat location were recorded on a dictaphone. We attributed each bat location to one of three categories of accuracy. The accuracy classes high, medium and low were attributed if the radius of the error range was estimated to be smaller than 50, 100 or 250 m, respectively (Bontadina and Naef-Daenzer 1996). Most of the observations (>90 %) had high to medium accuracy, and only these were retained for further analysis. This meant that the error polygon was mostly not larger than one hectare. In order to account for location errors, we buffered locations for the analysis with a radius of 50 m.

Home ranges were estimated as the 100 % Minimum Convex Polygon, MCP (White and Garrott 1990), in a geographic information system (GIS), encompassing all (50 m buffered) radio-locations during foraging of a given bat. For each bat the same number of random locations as that of those actually visited were generated within the buffered MCP to estimate habitat availability. Random locations were distributed within the home range. All spatial calculations were done in ArcView GIS 3.3 using the Animal Movement Extension (Hooge and Eichenlaub 1997). Moreover, to compare the bats' activity areas according to MCPs and maximum flight distances from roosts, we applied multiple Kruskal–Wallis tests using *pgirmess* package in R 2.10.0 (R Development Core Team 2009).

Habitat variables

In summer 2009, the habitat variables were mapped at the visited and random points within a buffer of 50 m. We grouped the variables into two main categories: habitat cover and heterogeneity (for details, see online Appendix S1). The percentage cover of each habitat type was estimated visually in the field in categories of 5 % steps. The category of heterogeneity included variables that describe habitat complexity in horizontal and vertical dimensions. As an indicator of horizontal heterogeneity, we used Simpson's index of diversity (Krebs 1999) with the percentage cover of each habitat type at the buffered location. The vertical structure and heterogeneity (variable VH) were estimated using digital terrain and surface models interpolated from airborne scanning LIDAR data (first and last pulse from Light Detection And Ranging; DTM-AV DOM-AV © 2009 swisstopo, #5704'000'000) (Artuso et al. 2003). These data describe the elevation of the terrain and vertical structures above the ground. The models are available in cell sizes of 2.5×2.5 m, and have a vertical accuracy of ± 0.5 m in open terrain and ± 1.5 m in forested terrain (digital surface model). The height of the vegetation layer was calculated as a continuous variable by contrasting the digital surface model with the terrain model. We then transformed the continuous height variable into a categorical layer of five different height classes (from ground to top, see online Appendix S1). From these, we extracted two types

of summary variables indicative of the vertical structure of the buffered locations: First we calculated the cover percentage of each height class (%HC1 to %HC5) and the number of unique pixels for each height class occurring within a buffer. Both kinds of variables describe the vertical structure in a non-spatial way. To take into account their spatial variation, we computed the total occurrence of each height class (HC1agg to HC5agg) within a close neighborhood of 9 LIDAR pixels (56.25 m²) by applying moving window techniques. We then used the mean (m.HC1agg to m.HC5agg) and standard deviation (sd.HC1agg to sd.HC5agg) of these aggregation measures to reflect the buffer conditions. The outcomes were 16 variables describing the vertical heterogeneity (see online Appendix S1 for details). The spatial averages of the buffers were improved by using weighted averages (quartic kernels, see Wing and Tynon 2006). Overall, our initial data set contained 30 predictors (online Appendix S1).

Data preparation

We first excluded the habitat descriptors that occurred marginally, or at very low densities (<1 % on average), for a given species, and then removed the infrastructure variables, settlements and roads, which occurred at low densities and were not the main focus of this study. Second, we assessed the correlation between continuous predictors using a Spearman rank correlation test. To avoid collinearity among the first main group predictors (habitat cover), we excluded one variable of a pair if their correlation coefficient was >|0.7| (Hosmer and Lemeshow 1989). We then re-grouped the variables of the main habitat cover category into two subcategories: I) farmland and grassland comprising steppe, arable, vineyard, extensive grassland, intensive grassland, traditional orchard and fruit tree plantation; II) forest and hedges, composed of deciduous forest, coniferous forest, mixed forest and hedgerow. We used the term “extensive grassland” for grassland managed at low intensity (≤2 cuts/year), and “intensive grassland” as that managed at high intensity (>2 cuts/year). We excluded the variable “vineyard” for all species and “steppe” for *P. auritus* and *P. austriacus* because of their marginal utilisation density.

In the second main group, heterogeneity, where Spearman’s correlation tests indicated high correlations among all variables apart from horizontal heterogeneity, we applied principal component analysis (PCA) to decrease the number of variables. The first and second principal components of vertical heterogeneity (VH1 and VH2), which described 77 % of the total variance, were then used in the modelling procedure. These two components describe the variance of habitat complexity along the vertical dimension within the buffered location circle.

All the continuous variables retained were centred and rescaled using a Z-standardisation procedure to achieve a set of unit-free predictors that are directly comparable and allow easier interpretation:

$$Z = \frac{X - M}{SD}$$

where Z is the standardised value of the variable X, M the mean of X and SD the standard deviation of X. Z values have, by definition, a mean of zero and a SD of 1.

Modelling procedure

We modelled the use of habitat characteristics for the three *Plecotus* species separately using generalized linear mixed models (GLMM) with binomial distribution, including

random effects. Mixed effects models enabled the analysis of all radiotracked bats, with the individuals treated as a random effect, to account for the variability among the individuals (Johnson et al. 2005). Additionally, to control for large-scale variation across the sites, “site” was implemented as a fixed effect in all models according to Whittingham et al. (2005). We applied a priori defined sets of candidate models to avoid difficulties in the stepwise regression (Whittingham et al., 2006). After excluding the infrastructure variables, we had three sets of variables: I) farmland and grassland, II) forest and hedges and III) heterogeneity (Fig. 1). Models were built by combining different covariates with all variables of each set combined with single variables of the other sets, and vice versa (Fig. 1). This resulted in 180, 180 and 276 a priori defined models for *P. auritus*, *P. austriacus* and *P. macrobullaris*, respectively. Different numbers of models were used because there were differences in the number of relevant and used variables for each species.

Logistic Mixed Effects Regressions (lmer) in the Lme4 package of the software R 2.10.0 were used to model the habitat use of *Plecotus* bat species, i.e. to compare visited versus random locations within the observed home range. Adapted models were ordered according to their best fit to the data using the Akaike Information Criterion (AIC) and Akaike weight. We used the top set of candidate models contributing $\geq 90\%$ of the AIC weights (relative importance) to get more robust estimates (Burnham and Anderson 2002).

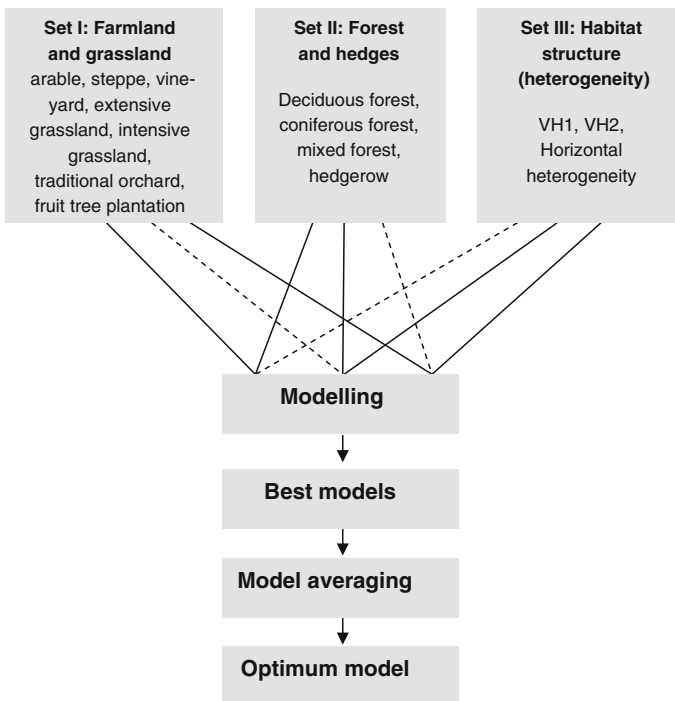


Fig. 1 Design of model selection approach. Sub-categories contained variables from farmland and grassland (*set I*), forest and hedges (*set II*) and habitat heterogeneity (*set III*). All predictors of each set are listed in the *boxes* (variables are described in detail in online Appendix S1). Models were constructed according to all variables of each set, indicated with *dashed lines*, combined with single variables from the other sets (*solid lines*)

With these we applied model averaging, which resulted in a weighted coefficient estimate for each variable. Finally, we ranked the explanatory variables based on their relative importance, using the coefficients of estimated standardised variables. All variables had already been standardised: Therefore, the coefficients indicate the change from complete absence of one habitat to its maximal presence within the observed home range.

Results

Altogether 24 females, eight per species, each species originating from two different study sites, were successfully radiotracked (Table 1). In total, we mapped 368 radio locations for *P. auritus*, on average (\pm SD) 46 ± 2.0 locations per bat, 355 locations for *P. austriacus*, on average 41 ± 1.3 per bat, and 312 locations for *P. macrobullaris*, on average 39 ± 1.9 per bat. The average areas of the home ranges (\pm SD) were: 51.8 ± 33.8 ha (range: 5.2–103.2 ha) for *P. auritus*, 295.5 ± 296 ha (range: 12.9–804.0 ha) for *P. austriacus* and 239.5 ± 284 ha (range: 64.0–797.0 ha) for *P. macrobullaris* (Table 1). Two separate Multiple Kruskal–Wallis tests indicated that the home ranges of *P. auritus* were smaller and their flight distances shorter than those of the other two species (Table 1, $p < 0.05$), but no significant difference was found between *P. austriacus* and *P. macrobullaris* ($p > 0.05$). Moreover, the variable “site” was a non significant factor in all three species.

Habitat selection

Plecotus auritus

Averaging the seven best models explained 91 % of the AIC weights (online Appendix S2, Table A). The ranking of the coefficients of the eight variables in the final models suggested by the model averaging was: $-(\text{intensive grassland}) > \text{traditional orchard} > \text{horizontal heterogeneity} > -(\text{extensive grassland}) > -(\text{VH2}) > -(\text{arable}) > \text{VH1} > -(\text{fruit tree plantation})$ (negative relations are indicated by a minus sign, while positive relations with no sign; Table 2A).

The optimum model, i.e. the average of the top ranked models, showed that the occurrence probability of *P. auritus* in traditional orchards is high. Horizontal heterogeneity had a positive impact on the probability of occurrence (Fig. 2a, b). The occurrence of these bats was negatively affected by “arable” and grasslands i.e. by “extensive” and “intensive grassland” (Fig. 2c). “Fruit tree plantation” slightly and negatively influenced the occurrence of this species. Finally, vertical heterogeneity, indicated by VH1 and VH2, only had slight and opposed effects on the occurrence probability. The optimum model revealed very small coefficients and relatively high uncertainty for these two variables, as well as for “fruit tree plantation”.

Plecotus austriacus

Averaging the nine best models explained 90 % of AIC weights (online Appendix S2, Table B). The ranking of the coefficients of the nine variables in the model suggested by the model averaging was: $-(\text{deciduous forest}) > -(\text{arable}) > -(\text{intensive grassland}) > -(\text{mixed forest}) > -(\text{extensive grassland}) > \text{fruit tree plantation} > \text{hedgerow} > -(\text{traditional orchard}) > \text{coniferous forest}$ (Table 2B).

Table 2 Estimated coefficients and standard errors for the variables of the optimum model for (A) *P. auritus*, (B) *P. austriacus* and (C) *P. macrobullaris*

Variable	Estimate	Standard error
(A) <i>P. auritus</i>		
Intensive grassland	-0.822	0.158
Traditional orchard	0.632	0.119
Horizontal heterogeneity	0.468	0.107
Extensive grassland	-0.346	0.125
VH2	-0.087	0.094
Arable	-0.056	0.090
VH1	0.018	0.108
Fruit tree plantation	-0.013	0.050
(B) <i>P. austriacus</i>		
Deciduous forest	-0.879	0.218
Arable	-0.611	0.200
Intensive grassland	-0.566	0.174
Mixed forest	-0.531	0.166
Extensive grassland	-0.441	0.188
Fruit tree plantation	0.274	0.188
Hedgerow	0.114	0.107
Traditional orchard	-0.027	0.080
Coniferous forest	0.013	0.098
(C) <i>P. macrobullaris</i>		
Steppe	-0.438	0.154
Deciduous forest	0.288	0.101
VH2	0.276	0.159
Intensive grassland	0.230	0.111
Coniferous forest	-0.203	0.191
Mixed forest	0.135	0.146
Extensive grassland	0.080	0.134
Horizontal heterogeneity	0.064	0.093
Arable	0.055	0.091
Hedgerow	0.036	0.086
VH1	0.036	0.079
Fruit tree plantation	0.032	0.058
Traditional orchard	0.011	0.027

Absolute values of coefficients are given in decreasing order of importance

The optimum model showed that the occurrence probability of *P. austriacus* is positively influenced by the presence of “fruit tree plantation” and “hedgerow”. These bats appeared to avoid “deciduous forest”, “arable land”, “mixed forest” and grasslands, i.e. “extensive” and “intensive grassland” (Fig. 3).

Plecotus macrobullaris

Averaging the nine best models explained 90 % of AIC weights (online Appendix S2, Table C). The ranking of the coefficients of the variables in the model suggested by the

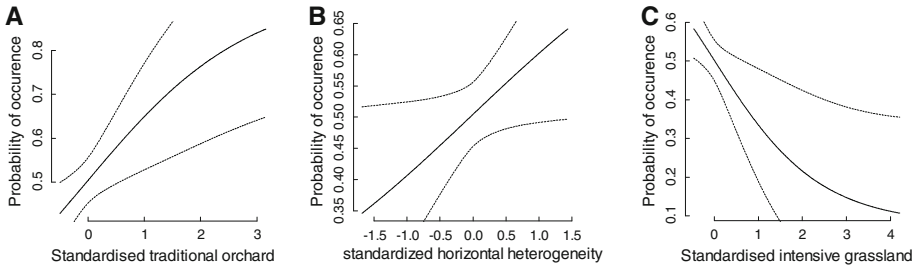


Fig. 2 *P. auritus* parameter estimates of habitat variables included in the averaging model, derived from a Generalised Linear Mixed Model (GLMM) procedure: Estimate of occurrence probability in relation to **a** traditional orchard; **b** horizontal heterogeneity; **c** intensive grassland. Broken lines show 95 % confidence intervals

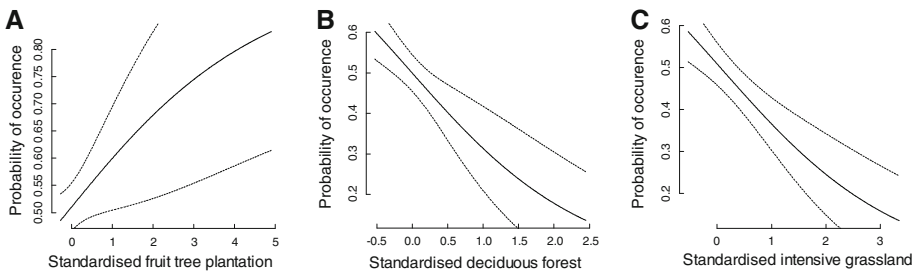


Fig. 3 *P. austriacus* parameter estimates of habitat variables included in the averaging model: Estimate of occurrence probability in relation to **a** fruit tree plantation; **b** deciduous forest; **c** intensive grassland. Broken lines show 95 % confidence intervals

model averaging was: $-(\text{steppe}) > \text{deciduous forest} > \text{VH2} > \text{intensive grassland} > -(\text{coniferous forest}) > \text{mixed forest} > \text{extensive grassland} > \text{horizontal heterogeneity} > \text{arable} > \text{hedgerow} > \text{VH1} > \text{fruit tree plantation} > \text{traditional orchard}$ (Table 2C).

The optimum model showed that the occurrence probability of *P. macrobullaris* is high in “deciduous forest” and “intensive grassland” (Fig. 4a, b). These bats seemed to avoid “steppe” and “coniferous forest”. Finally, vertical heterogeneity, indicated by VH2, was positively associated with the occurrence probability (Fig. 4c). This principal component was mostly correlated with variables expressing occurrence of higher vegetation (height classes 2, 3 and 5, see online Appendix S1). In addition, horizontal heterogeneity was slightly positively related to the occurrence probability of *P. macrobullaris*.

Discussion

In this paper we have explored the habitat segregation in three cryptic *Plecotus* bat species. We found that these species differed not only in their foraging range, but undoubtedly also in their habitat selection, as could be predicted from niche theory for very similar species. There seemed to be a correlation between species and habitat types. “Traditional orchard” was especially favoured by *P. auritus* (online Appendix S3), “fruit tree plantation” and “hedgerow” by *P. austriacus*, and “deciduous forest” and “mixed forest” and grassland by *P. macrobullaris*. Habitat heterogeneity was favoured by the former and latter species.

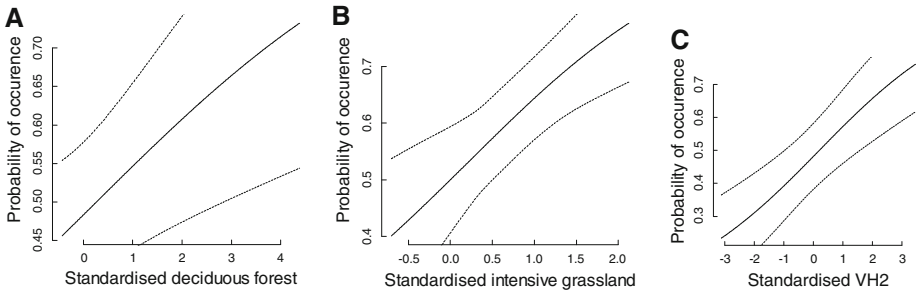


Fig. 4 *P. macrobullaris* parameter estimates of microhabitat variables included in the averaging model: Estimate of occurrence probability in relation to **a** deciduous forest; **b** intensive grassland; **c** VH2. *Broken lines* show 95 % confidence intervals

Foraging behaviour

The mean foraging distance (\pm SD) from the roost of *P. austriacus* and *P. macrobullaris* was more than twice that of *P. auritus* (2.9 ± 1.5 , 2.5 ± 1.6 and 1.2 ± 0.6 km, respectively), which is still longer than that determined for *P. macrobullaris* in the Southern Alps (1.1 ± 1.5 km, Preatoni et al. 2011). Suitable foraging sites for these bats were typically isolated and dispersed in the landscape. This suggests that they might use hedges and other linear structures, like forest edges, as commuting routes to reach their preferred foraging sites. *P. austriacus* showed a preference for fruit tree plantations, hedges and, in contrast to *P. macrobullaris* largely avoided farmland and grassland as well as deciduous forest. During field work we observed that *P. austriacus* could rapidly commute far from the roost (up to 4.7 km) to reach patches of fruit tree plantations. There they captured arthropods in flight during foraging bouts lasting several hours, taking them from under the hail protection nets covering the plantations (online Appendix S4). Similarly, radiotracked individuals of *P. macrobullaris* were found in patches of deciduous and mixed forests 4.6 km away from their roosts. We observed individuals of *P. macrobullaris* crossing open meadows in fast and low flight over the ground to reach their foraging areas of semi-open woodlands (online Appendix S5).

Our comparison of the mean activity areas (MCPs) reflects the differences in foraging ranges of the three species. The larger polygons in *P. austriacus* and *P. macrobullaris* result from the fact that their commuting flights to reach suitable foraging sites are longer. In a previous study, Ashrafi et al. (2011) showed that *P. austriacus* and *P. macrobullaris* have a narrower trophic niche than *P. auritus*. We suggest that a higher specialisation (higher selectivity of specific habitats) results in the bats having to fly further to reach their suitable foraging sites. In contrast, *P. auritus*, which are more generalist in dietary patterns, seem to find a wider range of potential foraging sites in the vicinity of their roosts.

Resource partitioning by cryptic *Plecotus* species

Our study is the first to attempt to test habitat selection simultaneously in three cryptic *Plecotus* bat species in the Alps. We focused on female bats during pregnancy and lactation as this is a time when they are energetically stressed and restrict their foraging habitats to the vicinity of their maternity roosts. Although these cryptic *Plecotus* species are so similar that they overlap in all morphometric characteristics (Ashrafi et al. 2010) as

well as in their echolocation calls (Dietrich et al. 2006), our study reveals that they select different foraging habitats.

Plecotus auritus and *P. macrobullaris*, which occupy roosts next to each other or even share a common roost, might theoretically exhibit spatial competition (Ashrafi et al. 2010). However, our results suggest that these two species select different habitats. *P. auritus* prefers traditional orchards over all other habitat types, whereas *P. macrobullaris* selects mainly deciduous forest and intensive grassland. Both species had horizontal heterogeneity playing a role in habitat selection (Tables 2A, C). *P. auritus* tends to prefer heterogeneous habitat types as its foraging niche breadth is wider than that of the other two species (Ashrafi et al. 2011). Apparently, heterogeneous habitat types provide more diverse food resources because they boost the species richness and diversity (Tews et al. 2004). Previous studies (Swift and Racey 1983; Entwistle et al. 1996) have found that *P. auritus* mainly selected forest, but our data indicate forest habitat is not among the preferred habitat types. These habitats did not appear in the best models, although in the raw data, the average frequency with which *P. auritus* visited forest types is slightly larger compared to the frequency of the random points (e.g. in 5 of 8 individuals, online Appendix S6). However, habitat selection strongly depends on the scale at which it is measured (Whittingham et al. 2005, Razgour et al. 2011). Our result do not indicate that *P. auritus* has any preference for forest habitat types on a local scale (foraging sites within its home range). However, the results obtained with distribution models on a landscape scale with a km² resolution (Rutishauser et al. 2012) provided evidence for a selection of forest edges.

Plecotus macrobullaris tends to select its foraging habitat according to the heterogeneity of vertical vegetation structures. This indicates that it probably exploits the vertical structures themselves and that its foraging is not restricted to the ground level.

Plecotus auritus and *P. austriacus* avoided arable habitats for foraging. This corresponds with findings from previous studies (Wickramasinghe et al. 2004) and is in accordance with our earlier findings (Ashrafi et al. 2011), which indicate that arthropods are less diverse in intensified farmlands.

Implications for conservation

Several authors have highlighted the need for special considerations to be given to cryptic species when planning conservation measures (e.g. Schonrogge et al. 2002, Bickford et al. 2007). Our results demonstrate that habitat segregation is a major mechanism for resource partitioning among the complex of *Plecotus* bat species.

The distinct foraging habitat niches of each of the *Plecotus* species demonstrate the need to have targeted strategies for effective conservation management. Because *P. austriacus* and *P. macrobullaris* search for suitable foraging patches scattered in their home ranges, it is important to preserve not only these key habitat patches, but also linear structures to connect suitable foraging sites. Suitable commuting structures could be hedges, tree lines, groves and woodland corridors (Russo et al. 2002; Nicholls and Racey 2006; Obrist et al. 2011; Boughey et al. 2011). Increasingly intensified agriculture across Europe has amplified the problems for species conservation arising from the associated landscape and habitat fragmentation (Frey-Ehrenbold et al. 2013). Therefore, ensuring these bats have access to suitable foraging sites and have sufficient arthropod prey supplies is essential for the preservation of bat populations. Long-eared bats that select for heterogeneous habitats may be particularly badly affected by habitat simplification and intensified use of farmland. Our results indicate that *P. auritus* notably is at risk, but also

that the other two *Plecotus* species are affected because of their selection for patchy foraging grounds.

The occurrence of *P. austriacus* and their roosts at the landscape scale appears to be clearly associated with lower and warmer areas (Ashrafi et al. 2010; Rutishauser et al. 2012). Therefore, we suggest targeting conservation action towards managing mainly sites below 500 m a.s.l. Additionally, maintaining the structural connectivity of foraging areas and roosts appears to be essential if the remaining populations of this endangered species are to be preserved.

More generally, our observations of species-specific habitat preferences in three cryptic species highlight the possible need of distinct conservation measures even for species that are morphologically almost indistinguishable.

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Appendix S1. Variables recorded at visited (radiotracking) and random locations.

Main category	Sub-category	Variable	Definition
Habitat cover	I.	Steppe	% cover
		Arable	% cover
		Vineyard	% cover
		Extensive grassland	% cover
		Intensive grassland	% cover
		Traditional orchard	% cover
		Fruit tree plantation	% cover
	II.	Deciduous forest	% cover
		Coniferous forest	% cover
		Mixed forest	% cover
		Hedgerow	% cover of hedges and tree lines
		Settlement	% cover
		Road	% cover
		Heterogeneity	III.
veg1wp	% of HC1 (0-1.5 m)		
veg2wp	% of HC2 (1.5-3 m)		
veg3wp	% of HC3 (3-10 m)		
veg4wp	% of HC4 (10-20 m)		
veg5wp	% of HC5 (>20 m)		
cp1wp	% aggregation HC1		
cp2wp	% aggregation HC2		
cp3wp	% aggregation HC3		
cp4wp	% aggregation HC4		
cp5wp	% aggregation HC5		
cp1wsd	SD aggregation HC1		
cp2wsd	SD aggregation HC2		
cp3wsd	SD aggregation HC3		

cp4wsd

SD aggregation HC4

cp5wsd

SD aggregation HC5

Vertical structure
richness

weighted mean number of unique
vegetation height classes (in the 50
m buffer)

Appendix S2. The top best GLMM models explaining the occurrence of *P. auritus* (A), *P. austriacus* (B) and *P. macrobullaris* (C) based on Akaike's Information Criterion (AIC). For each model, the number of estimated parameters (K), the difference in the AIC between that model and the best model (Δ AIC), and the Akaike weight are shown.

A <i>P. auritus</i>				
Model No.	Variables	K	Δ AIC	Akaike weight
151	Horizontal heterogeneity+VH1+ VH2+Intensive grassland + Extensive grassland +Traditional orchard	8	0.000	0.256
49	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation +Traditional orchard + Horizontal heterogeneity	8	0.787	0.173
56	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation +Traditional orchard + Horizontal heterogeneity + VH2	9	1.282	0.135
155	Horizontal heterogeneity+ VH1+ VH2+Arable+Intensive grassland + Extensive grassland + Traditional orchard	9	1.391	0.128
158	Horizontal heterogeneity+ VH1+ VH2+Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard	9	1.888	0.100
55	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation	9	2.706	0.066

59	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard + Horizontal heterogeneity + VH1 + VH2	10	3.273	0.050
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B *P. austriacus*

Model	Variables	K	Δ AIC	Akaike weight
115	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Arable + Intensive grassland + Extensive grassland + Fruit tree plantation	10	0.000	0.256
40	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard + Deciduous forest + Mixed forest + Hedgerow	10	0.038	0.173
22	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard + Deciduous forest + Mixed forest	9	0.542	0.135
44	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard + Deciduous forest + Coniferous forest + Mixed forest + Hedgerow	11	1.982	0.128
100	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Arable + Intensive grassland + Extensive grassland	9	2.095	0.100
37	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard + Deciduous forest + Coniferous forest + Mixed forest	10	2.420	0.066

116	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Arable + Intensive grassland + Extensive grassland + Traditional orchard	10	2.808	0.050
101	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Arable + Intensive grassland + Fruit tree plantation	9	3.636	0.050
117	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Arable + Intensive grassland + Fruit tree plantation + Traditional orchard	10	4.586	0.050

C <i>P. macrobullaris</i>				
Model	Variables	K	Δ AIC	Akaike weight
189	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Horizontal heterogeneity + Steppe+ Horizontal heterogeneity + VH2	10	0.000	0.25
187	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Steppe+ VH2	8	0.230	0.223
191	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Horizontal heterogeneity + Steppe + VH1 + VH2	10	1.334	0.128
190	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Steppe + VH1+ VH2	9	1.634	0.11
22	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard + Steppe + Deciduous forest + Mixed forest	10	2.818	0.061

178	Deciduous forest + Coniferous forest + Mixed forest + Hedgerow + Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Steppe	11	3.558	0.042
37	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard + Steppe + Deciduous forest + Coniferous forest + Mixed forest	11	3.755	0.038
40	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard + Steppe + Deciduous forest + Mixed forest + Hedgerow	11	4.521	0.026
44	Arable + Intensive grassland + Extensive grassland + Fruit tree plantation + Traditional orchard + Steppe + Deciduous forest + Coniferous forest + Mixed forest + Hedgerow	12	4.719	0.024



Appendix S3. Preferred foraging habitats selected by *P. auritus*: traditional orchard



Appendix S4. Preferred foraging habitats selected by *P. austriacus*: (A) fruit tree plantation, (B) hedgerows



Appendix S5. Preferred foraging habitats selected by *P. macrobullaris*: deciduous and mixed forest

Appendix S6. Observed frequency of habitat variables for each individual bat from all three *Plecotus* bat species. Radiotracking points are indicated by visited vs. the random points within the MCP.

Species, ID	Point type	Steppe	Arable	Vineyard	Extensive grassland	Intensive grassland	Traditional orchard	Fruit tree plantation	Deciduous forest	Coniferous forest	Mixed forest	Hedgerow	Infrastructure
<i>P. auritus</i> , 1	visited	0.0	0.3	0.0	25.9	0.7	0.0	0.0	1.7	42.9	17.3	1.2	9.9
<i>P. auritus</i> , 2	visited	0.0	5.9	0.0	36.6	5.6	1.6	0.0	17.8	0.0	23.5	3.5	5.4
<i>P. auritus</i> , 3	visited	0.0	0.0	0.0	18.8	2.5	1.3	0.3	43.1	0.0	17.8	1.9	14.4
<i>P. auritus</i> , 4	visited	0.0	18.7	0.0	13.5	12.3	13.2	0.0	1.6	0.0	1.4	9.2	30.1
<i>P. auritus</i> , 5	visited	0.0	0.3	0.0	36.0	4.8	0.0	0.0	9.8	23.2	10.5	3.3	12.0
<i>P. auritus</i> , 6	visited	0.0	0.0	0.0	31.7	4.5	0.0	0.0	17.7	15.3	10.9	3.7	16.1
<i>P. auritus</i> , 7	visited	0.0	0.0	0.0	31.2	0.2	0.0	0.0	1.6	51.0	4.4	0.8	10.7
<i>P. auritus</i> , 8	visited	0.0	12.7	0.0	36.5	3.3	6.7	0.0	20.5	0.0	2.5	0.0	17.8
	average	0.0	4.8	0.0	28.8	4.2	2.8	0.0	14.2	16.5	11.1	3.0	14.5
<i>P. auritus</i> , 1	random	0.0	0.1	0.0	37.1	3.4	0.1	0.0	3.3	36.5	3.5	5.8	10.2
<i>P. auritus</i> , 2	random	0.0	6.5	0.0	24.0	18.5	0.6	0.1	22.1	0.0	17.4	1.8	9.1
<i>P. auritus</i> , 3	random	0.0	10.6	0.0	16.9	23.4	2.2	0.0	38.1	0.0	1.3	0.9	6.6
<i>P. auritus</i> , 4	random	0.0	7.4	0.0	32.7	25.2	2.1	0.0	4.9	0.0	23.9	1.2	2.5
<i>P. auritus</i> , 5	random	0.0	0.0	0.0	30.8	5.2	0.0	0.0	9.0	28.0	6.8	5.3	14.8
<i>P. auritus</i> , 6	random	0.0	0.0	0.0	38.7	12.2	0.0	0.0	5.2	24.5	7.9	4.3	7.3
<i>P. auritus</i> , 7	random	0.0	0.7	0.0	29.9	0.0	0.0	0.0	0.0	59.2	3.4	1.4	5.5
<i>P. auritus</i> , 8	random	0.0	19.9	0.0	26.2	22.6	3.5	0.0	12.8	0.0	6.0	1.0	8.0
	average	0.0	5.7	0.0	29.5	13.8	1.1	0.0	11.9	18.5	8.8	2.7	8.0
<i>P. austriacus</i> , 1	visited	0.0	28.5	0.0	15.4	27.9	1.5	0.0	11.0	6.2	0.0	1.9	7.7
<i>P. austriacus</i> , 2	visited	0.0	2.0	0.0	13.6	1.4	2.4	32.7	8.3	18.3	14.0	0.9	6.4
<i>P. austriacus</i> , 3	visited	0.0	24.4	0.0	22.7	0.6	1.4	0.0	29.1	0.0	11.1	0.4	10.1
<i>P. austriacus</i> , 4	visited	0.0	9.2	0.0	0.2	2.4	0.6	0.0	39.8	25.7	16.7	0.0	5.3
<i>P. austriacus</i> , 5	visited	0.0	36.3	0.0	27.3	6.8	5.1	0.1	4.7	0.0	0.0	5.2	14.6
<i>P. austriacus</i> , 6	visited	0.0	4.2	0.0	20.6	5.7	5.7	46.3	1.5	0.0	6.7	0.6	8.9
<i>P. austriacus</i> , 7	visited	0.0	13.6	0.0	31.4	32.6	7.3	0.1	0.2	0.0	0.0	1.6	13.2

Habitat selection in cryptic bats

<i>P. austriacus</i> , 8	visited	0.0	35.5	0.0	19.9	21.9	3.0	0.0	5.2	0.0	0.0	2.6	12.0
	average	0.0	19.2	0.0	18.9	12.4	3.4	9.9	12.5	6.3	6.1	1.6	9.8
<i>P. austriacus</i> , 1	random	0.0	14.4	0.0	17.3	18.5	2.3	0.0	39.8	0.0	3.8	0.4	3.5
<i>P. austriacus</i> , 2	random	0.0	16.3	0.0	13.1	17.9	2.9	2.9	26.1	6.9	9.6	0.4	4.0
<i>P. austriacus</i> , 3	random	0.0	31.1	0.0	9.1	10.3	1.0	0.0	34.7	0.0	6.6	0.4	6.7
<i>P. austriacus</i> , 4	random	0.0	18.7	5.8	12.6	10.6	5.5	0.0	26.8	7.7	5.7	0.9	5.8
<i>P. austriacus</i> , 5	random	0.0	33.2	0.0	21.9	10.7	1.5	0.2	23.6	0.0	2.9	2.4	3.8
<i>P. austriacus</i> , 6	random	0.0	3.3	0.0	17.8	12.6	5.1	9.0	8.1	3.1	30.0	0.8	10.1
<i>P. austriacus</i> , 7	random	0.0	33.4	1.5	14.9	38.5	2.6	0.0	2.2	0.0	0.0	0.9	6.0
<i>P. austriacus</i> , 8	random	0.0	16.1	0.4	18.6	6.2	0.4	0.0	33.2	0.0	20.9	0.7	3.6
	average	0.0	20.8	1.0	15.7	15.7	2.7	1.5	24.3	2.2	9.9	0.9	5.4
<i>P. macrobullaris</i> , 1	visited	0.0	2.6	0.0	10.8	29.8	0.0	0.0	11.6	32.1	0.0	2.3	10.8
<i>P. macrobullaris</i> , 2	visited	0.0	0.0	0.0	7.7	58.1	0.2	2.6	4.8	15.3	2.3	0.9	8.0
<i>P. macrobullaris</i> , 3	visited	0.0	25.5	0.0	30.5	28.5	0.5	0.0	1.8	0.0	0.0	2.3	11.1
<i>P. macrobullaris</i> , 4	visited	0.0	0.3	0.0	44.1	4.3	0.9	0.9	4.9	5.9	33.1	1.9	3.8
<i>P. macrobullaris</i> , 5	visited	0.7	0.3	0.0	29.7	29.8	0.0	0.0	6.3	10.3	9.7	1.2	12.0
<i>P. macrobullaris</i> , 6	visited	0.0	0.8	0.0	44.2	0.0	0.4	0.0	9.6	20.4	16.2	2.7	5.8
<i>P. macrobullaris</i> , 7	visited	0.0	13.3	0.0	10.4	29.2	0.1	0.0	35.2	0.0	4.7	2.8	4.2
<i>P. macrobullaris</i> , 8	visited	0.5	1.0	0.0	35.0	18.8	0.0	0.0	5.9	8.0	20.1	1.0	9.8
	average	0.1	5.5	0.0	26.5	24.8	0.2	0.4	10.0	11.5	10.8	1.9	8.2
<i>P. macrobullaris</i> , 1	random	0.0	3.4	0.0	10.8	38.7	0.0	0.0	5.5	28.2	0.0	1.6	11.8
<i>P. macrobullaris</i> , 2	random	0.9	0.0	0.0	18.3	36.4	0.0	0.0	10.3	21.4	5.3	1.2	6.1
<i>P. macrobullaris</i> , 3	random	0.0	30.9	0.0	34.4	19.8	0.0	0.0	3.6	0.0	0.0	3.3	7.9
<i>P. macrobullaris</i> , 4	random	0.0	0.4	0.0	22.9	6.5	0.6	0.0	2.9	37.1	16.2	1.8	11.6
<i>P. macrobullaris</i> , 5	random	2.2	0.2	0.0	22.2	37.3	0.0	0.0	5.8	5.8	12.7	1.3	12.5
<i>P. macrobullaris</i> , 6	random	0.0	0.4	0.0	47.3	3.5	1.5	0.0	9.2	13.1	11.5	3.8	9.6
<i>P. macrobullaris</i> , 7	random	0.0	0.8	0.0	17.5	4.5	0.1	0.0	6.5	30.0	15.0	0.6	25.0
<i>P. macrobullaris</i> , 8	random	4.2	0.9	0.0	36.2	11.2	0.0	1.3	10.0	13.3	14.8	1.3	7.0
	average	0.9	4.6	0.0	26.2	19.7	0.3	0.2	6.7	18.6	9.4	1.9	11.4