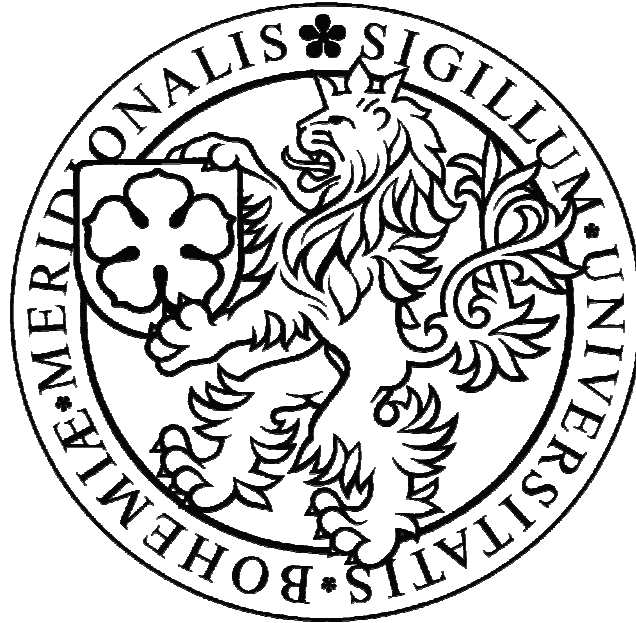


JIHOČESKÁ UNIVERZITA V ČESKÝCH BUDĚJOVICÍCH  
Přírodovědecká fakulta



## **DIPLOMOVÁ PRÁCE**

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**Demography and dispersal ability of the Alpine  
Longhorn *Rosalia alpina* (Coleoptera:  
Cerambycidae)**

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(Entomologický ústav AV ČR)

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### **Annotation**

This Master Thesis brings results of study on endangered species Alpine Longhorn *Rosalia alpina* in beech forest of National Nature Reserve Maly and Velky Bezdez and Slatinne Hills. We used mark-recapture method to study the population size, longevity and dispersal ability of this species. We also assessed the distribution pattern of the species on another 15 habitat patches in the Ralska Upland.

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## **Vyjádření spoluautorů**

Student, Lukáš Drag, se na vzniku publikace podílel sběrem dat v terénu v průběhu celé sezóny 2009, s pomocí Kamila Zimmermanna zajistil zpracování a vyhodnocení dat z obou sezón 2008 a 2009 a je též autorem většiny textu uvedeného v této práci (úpravy formulací anglického textu zajistil školitel Lukáš Čížek).

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## **Poděkování**

Především bych rád poděkovat svému školiteli, Lukáši Čížkovi, za pomoc při sestavování textu – za množství užitečných rad, nápadů a připomínek, stejně tak jako za spoustu času, který mi při psaní věnoval. Dále bych chtěl poděkovat Pavlu Pokludovi, Davidu Hauckovi, Štěpánu Vodkovi a Vladanu Riedlovi za pomoc při sběru dat, Kamilu Zimmermannovi a Zdeňku Fricovi za pomoc při statistických analýzách a panu hajnému Vaníčkovi, vedení státního podniku Vojenské lesy a statky ČR, Mimoň a správě CHKO Kokořínsko bez jejichž spolupráce by tento výzkumu neproběhl. Ze všeho nejvíce bych ale chtěl poděkovat rodičům a Kláře za toleranci a všeobecnou podporu v mém studiu. Práce byla podořena Ministerstvem školství, Ministerstvem životního prostředí a Agenturou ochrany přírody a krajiny ČR.

**CONTENTS**

1. INTRODUCTION..... 1

2. MATERIALS AND METHODS..... 3

    2.1 Study species..... 3

    2.2 Study sites..... 3

    2.3 Sampling design..... 4

    2.4 Data analysis..... 5

3. RESULTS..... 7

    3.1 Demography..... 7

    3.2 Dispersion and distribution..... 9

4. DISCUSSION..... 10

    4.1 Demography..... 10

    4.2 Mobility..... 11

    4.3 Distribution pattern..... 12

    4.4 Factors affecting local survival..... 12

5. REFERENCES..... 14

6. APPENDICES..... 22

# 1. INTRODUCTION

Organisms depending on dead wood are among the most rapidly declining elements of European biodiversity, and thus attain a prominent position in most national red-lists of European countries (e.g. Geiser, 1998; Farkač *et al.*, 2005; Komonen *et al.*, 2008). Low volume of dead wood (Økland *et al.*, 1996; Dudley and Vallauri, 2004; Müller *et al.*, 2006), and insufficient numbers of old and/or sun exposed trees (Ranius and Jansson, 2000; Lindhe *et al.*, 2005; Vodka *et al.*, 2009) brought by modern forestry practices and by abandonment of traditional management are considered among major causes of decline of numerous saproxylic (= dead wood dependent) organisms. Habitat fragmentation also contributes to decline of many species (Debinski and Hold, 2000; Ewers and Didham, 2006, Brückmann *et al.*, 2010). However, some guilds are particularly vulnerable to the fragmentation, such as species with poor dispersal abilities (Thomas, 2000, Ewers and Didham, 2006). Their small and isolated populations are prone to extinction as a result of environmental, demographic and genetic stochasticity (Shaffer, 1983; Frankham, 1995; Saccheri *et al.*, 1998). The ability to disperse between sites is therefore crucial and studying animal movement and understanding the factors affecting it have become important issues in conservation biology and landscape management (Clobert *et al.*, 2001).

Large, conspicuous beetles are among the most attractive representatives of saproxylic guild to the wide public, often targeted by insect collectors and researchers. Amount of knowledge on their distribution and life history is thus relatively large; charismatic species, including the *Osmoderma s.l. eremita* (Scopoli, 1763), *Lucanus cervus* (Linnaeus, 1758) or *Cerambyx cerdo* (Linnaeus, 1758) serve as umbrella species in biodiversity conservation (Ranius, 2002), environmental indicators and model species (Buse *et al.*, 2007; Thomaes *et al.*, 2008), and may even act as ecosystem engineers (Buse *et al.*, 2008). As the above saproxylic beetles, so the alpine longhorn (*Rosalia alpina*) (Linnaeus, 1758) is a widely known, attractive species; it serves as the umbrella species for the habitat of beech forests. *R. alpina* is highly endangered and strictly protected throughout its range, listed in the EU Habitats Directive as priority species of community interest (Council of the European Communities, 1992). Unlike the three above species whose distribution is highly fragmented in most of Europe (Korbel, 1992; Sláma, 1998; Szwajko, 2004; Ranius *et al.*, 2005; Jurc *et al.*, 2008), *R. alpina* distribution shows a different pattern. It disappeared from large part of its range; a single population survives north of the Alps and west of the Carpathians. In the both

mountain systems, its occurrence is rather continuous despite marked retreat during the last century (Sláma, 1998; Gepp, 2002; Duelli and Wermelinger, 2005; Reißmann, 2010). In the south of Europe, the species is widely distributed (Russo *et al.*, in press), and found also in lowlands (Sláma, 1998; Simandl, 2002), whereas in the Central Europe it inhabits mainly beech forests of middle and higher altitudes (Dominik and Starzyk, 1989; Heyrovský, 1992; Sláma, 1998 *but see* Jendek and Jendek, 2006). *R. alpina* develops in wood of broad-leaf trees, including beech, maples, elms and other genera (Kovács, 1998; Ciach *et al.*, 2007; Cizek *et al.*, 2009); it prefers old, sun-exposed trees in semi-open woodlands with minimum undergrowth (Russo *et al.*, in press).

Although *R. alpina* is endangered and strictly protected throughout its range, detailed knowledge on ecology and biology of the beetle is still missing. Recently, its habitat preferences have been investigated (Russo *et al.*, in press), but data describing demography, phenology and dispersal activity are still lacking. We thus performed a mark-recapture study of *R. alpina* population in Ralska Upland, Czech Republic, in 2008 and 2009 where we estimated the size of the population, adult longevity, and dispersal ability. To assess reliability of *R. alpina* mobility estimates, we studied distribution pattern of the species on another 15 habitat patches in the Ralska Upland.

## 2. MATERIALS AND METHODS

### 2.1 Study species

*Rosalia alpina* is one of the most popular beetles of the European fauna, especially due to its large size (males: 15 – 38 mm; Heyrovský, 1992) and attractive black and blue coloration. Adults exhibit sexual dimorphism; male antennae length exceeds body length (up to twofold) and their mandibles are larger (Heyrovský, 1992). The life cycle of *R. alpina* takes at least three years (Dominik and Starzyk, 1989; Sláma, 1998). Larvae develop in dead wood and pupate in the spring, adult beetles then make elliptic holes about 6 – 7 mm wide to exit the wood (Dominik and Starzyk, 1989). Their activity period starts at the end of June and last until September (Heyrovský 1992, Sláma 1998). Females oviposit into the crevices and cracks of wood.

Some other aspects of *R. alpina* biology might be inferred from information available on closely related species. Adults of *R. coelestis* (Semenov-Tjan-Shanski, 1911) do not feed, breed immediately after exiting the wood, females lay ~100 eggs (Tcherepanov, 1981). Males of *R. funebris* (Motschulsky, 1845) produce aggregation pheromone (Ray, 2009).

### 2.2 Study sites

The study was carried out in the Ralska Upland (50 km north of Prague) in northern Bohemia, Czech Republic. The area is formed by sand and marlite bedrock with steep phonolite hills (Mackovčín *et al.*, 2002). It is covered mainly by pine plantations with fragments of old beech forest remaining on several hill-tops.

Three hills inhabited by *R. alpina* were selected to carry out the mark-recapture survey, including Maly Bezdez (50°32'23.1"N, 14°42'48.4"E; 400 – 577 m a. s. l.; old beech forest 18 ha), Velky Bezdez (50°32'20.7"N, 14°43'11.6"E; 400 – 604 m a. s. l.; old beech forest 20 ha) and Slatinne Hills (50°33'13.8"N, 14°42'24.1"E; 350 – 430 m a. s. l.; old beech forest 12 ha). The beech forests on Maly Bezdez and Velky Bezdez are connected forming a single National Nature Reserve (28.2 ha) and Site of Community Importance (70.3 ha), with *R. alpina* as one of its target species. Hill-tops and steeper slopes are mostly covered by low, semi-open forests with no or sparse undergrowth; even old trees are small and crooked (average DBH of study area is 44 cm and average height is 16 m) due to dry and shallow-soil conditions, and probably also former management. The Slatinne Hills were also declared as Site of Community Importance (138.5 ha, *R. alpina* as target species); the beech growth there



is mainly high forest (average DBH of study area is 57 cm and average height is 27 m) on deeper soils.

Using aerial photos, other sites with old beech forests were selected within the Ralska Upland (Figure 1). Current and historical cover of old beech forest were determined for each site using the version 10 of the ArcGIS software (ESRI, Redlands, CA, USA) and aerial photomaps from 1953 and 2007 (CENIA, 2010). Each site was inspected by experienced coleopterologists for presence of *R. alpina* adults and exit holes for two to six person days, depending on its area. Search for the exit holes is an effective way of locating the *R. alpina* populations and inhabited trees (cf. Russo *et al.*, in press); it took place in 2008, 2009 and 2010, always between 7<sup>th</sup> and 25<sup>th</sup> July, from 10 a.m. to 5 p.m., and under suitable weather conditions (*see below*). Sites were subsequently divided into three categories according to the estimated volume of available dead wood (low, medium, high) and according to status of *R. alpina* local population: (i) large population - adults and exit holes commonly found, (ii) small population – rare presence of exit holes and/or adults, (iii) no evidence sites – neither exit holes nor beetles observed.

### **2.3 Sampling design**

Mark–recapture study of *R. alpina* was conducted between 12<sup>th</sup> July and 10<sup>th</sup> August 2008 at the three sites and between 5<sup>th</sup> July and 16<sup>th</sup> August 2009 on Slatinne Hills. At each site, trees suitable for *R. alpina* (old, dead or with dead parts), coarse woody debris, and other trees (live, rotten, stumps etc.) were selected to cover as large portion of the *R. alpina* habitat as possible. In Slatinne Hills, the whole area of old beech forest was covered; accessible sites with suitable trees and dead wood were selected on Maly Bezdez and Velky Bezdez. In 2008, 59 trees were selected on Maly Bezdez, 36 on Velky Bezdez and 62 on Slatinne Hills, making total of 157 trees. In 2009, 155 trees were selected on Slatinne Hills (Figure 1b, 1c). The selected trees and dead wood parts were searched for adult beetles in suitable weather (>15°C, no rain) between 10 a.m. and 6 p.m. All trees were numbered and visited on regular basis; order of trees inspected was irregular.

Individuals were marked on elytra using black permanent marker, and tip of elytra was cut. During each handling, the beetles were photographed; their body-length, sex and exact position were recorded. The individually unique color pattern on elytra allowed confirming each individual identity even if the marker was washed or unreadable. Marked beetles were immediately released to their original positions. Individuals observed on the same tree more

than once a day were counted only for the first time. We observed no increased flight activity as a result of handling, and no flight problems due to missing tip of elytra.

## 2.4 Data analysis

The mark-recapture data were analyzed in order to investigate demography and dispersal of the studied *R. alpina* population.

For demography analyses, we used the constrained linear models (CLM), applying the methodology of generalized linear models to mark-recapture data (Lebreton *et al.*, 1992). In MARK package (White and Burnham, 1999), the Jolly-Seber method (POPAN parameterization - suitable for open populations with births, deaths, emigration and immigration) was applied to estimate three primary parameters:  $\phi_i$  - daily residence rate (combining mortality and emigration in open populations),  $p_i$  - catchability, and  $pent_i$  - the probability of entering the population (combining natality and immigration). Obtained parameters are daily births ( $B_i$ ), daily population size ( $N_i$ ) and total population size ( $N_{tot}$ ). The primary parameters can be independent on sex and marking day – i.e., (.) in MARK notations, can differ between sexes (g), or can respond to time in a factorial (t), linear (T) or polynomial ( $T^2$ ) manners. Sex-time interactions can be either additive – e.g., (g+t), or multiplicative – e.g., (g\*T<sup>2</sup>). From sets of models differing in parameterization, MARK selects model(s) having high explanatory power with minimum redundant parameters, using the information theory approach (quasi-Akaike information criterion, cAIC), herein referred as best models. We selected best models for all localities in both years. Average value of residence  $\phi'$  was obtained in MARK by defining the best-fitting models with the respective parameters not dependent on time. Comparing models where these parameters differ and not differ between sexes, i.e.  $\phi$  (g) vs.  $\phi$  (.), allowed direct comparison of sexes. Average residence was converted to residence time (“longevity”), using the formula  $-(\ln \phi')^{-1}$  (Cook *et al.*, 1967). Moreover, observed lifespan was calculated as the number of days between the first and last capture of given individual. In order to allow comparison with results of other studies, the population sizes of males and females were also estimated for both years using Craig’s model (1953).

For dispersal analyses, straight distances between capture trees were summed to obtain lifetime movements for each beetle recaptured at least once. Based on these distances, we computed for each sex the inverse power function (IPF), expressing the probability density  $I$  of movements to distances  $D$

$$I = C \cdot D^{-n}$$

The function is fitted by plotting the logarithm of cumulative fractions of individuals moving specific or greater distances ( $\ln I$ ) against linearized expressions of the distances, i.e.,  $\ln I = \ln C - n(\ln D)$  (Hill *et al.*, 1996; Fric and Konvicka, 2007). We compared slopes and intercepts of the resulting linear regressions using t-tests (Zar, 1996). Parameter  $n$ , the slope of the linearized function, expresses relative dispersal propensity so that the shallower the slope, the higher probability of long-distance dispersal (Baguette *et al.*, 2000; Baguette, 2003). We carried out these tests to compare male and female movements, and to obtain predictions of movements to long distances (100, 500, 1000 and 3000 m) within Maly Bezdez, Velky Bezdez and Slatinne Hills. Probabilities of long-distance movements, based on the IPF regressions, were estimated for males and females, separately for years 2008 and 2009. In 2008, the maximum distance flight was excluded, in order to illustrate its impact on the estimates. Due to a high number of zeroes in the data on individual movements, the nonparametric Mann-Whitney U tests were used in comparisons of individual lifetime movements between sexes.

### 3. RESULTS

The total number of marked individuals was 595 in 2008 (Maly Bezdez - 157, Velky Bezdez - 240, Slatinne Hills - 198) and 375 in 2009 (Slatinne Hills only). The recapture rate was 26 % in 2008 and 33 % in 2009 (Table 1). Males were recaptured more frequently than females in both years ( $\chi^2 = 21.8$ ,  $df = 1$ ,  $p < 0.001$  and  $\chi^2 = 6.8$ ,  $df = 1$ ,  $p = 0.009$ ).

In 2008, the first beetle was captured on 12<sup>th</sup> July and the last one on 10<sup>th</sup> August. In 2009, the first beetle was captured on 5<sup>th</sup> July and the last one on 16<sup>th</sup> August. Despite search, no individuals were found before and after these periods. The length of the season was equal for both sexes. Under sunny and warm weather conditions, adult activity started in late morning (10 - 11 a.m.) and ceased in the late afternoon (4 - 6 p.m), peaking at ~12 a.m. and then again at ~2 p.m.

#### 3.1 Demography

Based on the Jolly-Seber method, the estimated population sizes were 875 individuals (49 individuals/ha) for Maly Bezdez, 839 individuals (41 individuals/ha) for Velky Bezdez and 674 beetles (56 individuals/ha) for Slatinne Hills in 2008. The estimation for Slatinne Hills in 2009 was higher (1014 beetles, 84 individuals/ha). The results based on combined data from three sites in 2008 gave lower estimates in both sexes but corresponding with the standard error. In both years, the resulting sex-ratio neared to 1:1 (Table 2).

The best-fitting MARK model (Table 2) revealed that residence ( $\phi$ ) was constant in time and sex-dependent (Maly Bezdez, Slatinne Hills both years) or equal in sexes (Velky Bezdez). The catchability ( $p$ ) was always time-dependent and equal between sexes on Maly Bezdez and Slatinne Hills in both years, and time- and sex-dependent on Velky Bezdez and for data pooled over the three sites sampled in 2008. The recruitment ( $pent$ ) showed polynomial ( $T^2$ ) response (Slatinne Hills 2009, Velky Bezdez) and linear ( $T$ ) response (Slatinne Hills 2008). It was constant in time and sex-dependent on Maly Bezdez.

The estimates of *R. alpina* population size at the three sites in 2008 differed between Jolly-Seber method and Craig's model just about 10 % (2026 individuals estimated by Jolly-Seber method compared to 2221 individuals estimated by Craig's model); the estimates of population size for Slatinne Hills in 2009 were almost equal (1014 individuals compared to 1055).

The daily estimates of population size were lower for females than for males; the activity patterns were synchronous for both sexes (Figure 2a). The daily estimates of recruitment (*pent*) were identical for both sexes indicating the highest rate of entering the population in the middle of July, or ca. a week after recording the first individual (Figure 2b).

The oldest observed male was still alive 24 days after capture; the oldest female lived for minimum of 15 days (Figure 3). The mean residence time and its 95 % C.I. based on the residence ( $\varphi$ ; 95 % C.I.), was estimated at 4.2; 3.0-6.1 days ( $\varphi = 0.79$ ; 0.72-0.85) for females and 4.7; 3.8-5.9 days ( $\varphi = 0.81$ ; 0.77-0.84) for males pooled over the three sites sampled in 2008. On Slatinne Hills in 2009, the mean residence time was 4.1; 3.1-5.3 days ( $\varphi = 0.78$ ; 0.73-0.83) for females and 7.0; 5.7-8.6 days ( $\varphi = 0.87$ ; 0.84-0.89) for males. The difference between sexes was significant only in 2009.

### 3.2 Dispersion and distribution

In 2008, we recorded 93 movements of males (73.8 % of recaptured beetles) and 20 movements of females (69 %) between at least 2 sites. In 2009 we registered 70 movements of males (80.5 %) and 29 movements of females (80.6 %). In both years, no difference in the total dispersal distance was found between sexes (2008: Mann-Whitney U-test,  $p = 0.515$ , males: mean/median: 57/21 m, range: 0 – 634 m, females: mean/median: 116/25 m, range: 0 – 1628 m; 2009: Mann-Whitney U-test,  $p = 0.776$ , males: mean/median: 111/50 m, range: 0 – 658 m, females: mean/median: 86/55 m, range: 0 – 309 m). The longest movement was recorded in 2008, when a female marked on Maly Bezdez was 11 days later found on Slatinne hills, i.e. 1628 m from its original marking site. The longest male movement was recorded between Maly Bezdez and Velky Bezdez (634 m) (Figure 4).

Probabilities of long-distance flights, based on the IPF regressions, were estimated for 100, 500, 1000 and 3000 m for males and females, separately for years 2008 and 2009. In 2008, the maximum distance flight was excluded, in order to illustrate its impact on the estimates (Table 3). The fitted IPF regressions differed among the sexes neither in 2008 (slope:  $t = 1.330$ ,  $df = 31$ ,  $p = 0.097$ ; elevation:  $t = -1.317$ ,  $df = 31$ ,  $p = 0.099$ ) nor in 2009 (slope:  $t = 1.05$ ,  $df = 46$ ,  $p = 0.151$ ; elevation:  $t = 1.121$ ,  $df = 46$ ,  $p = 0.134$ ).

Using aerial photos, 15 additional sites in the Ralska Upland were selected as possibly suitable for *R. alpina*; total of 18 sites with potentially suitable habitat was thus found in the region (Figure 1). Mature-beech forests covered ca. 730 ha in 2008 and ca. 916 ha in 1953; aerial photos revealed that most of the habitat loss occurred due to felling within the last 20

years, i.e. following cease of the military activities. Individuals of *R. alpina* were found only on three sites (same places where mark-recapture study was conducted). Single or a few exit holes were found at six further sites indicating presence of a small population and no evidence of *R. alpina* presence was discovered on the rest nine sites (Table 4).

## 4. DISCUSSION

The studied the population of *Rosalia alpina* inhabiting old beech forests on hill tops of the Ralska Upland. Our results demonstrate capability of the species to disperse among individual hills. The system is thus interconnected and contained more than 2000 adults in 2008.

### 4.1 Demography

Since the total population at the three studied sites (Maly Bezdez, Velky Bezdez and Slatinne Hills) consists of ~ 2000 individuals a year, and the life-cycle of *R. alpina* lasts for minimum of three years (Sláma, 1998); the total number of adults that emerge during three years may reach ~6000 individuals. The between-year fluctuations in population size are probably high as the population estimates for Slatinne Hills in 2009 were by 50 % higher than in 2008. *R. alpina* is able to reach high population densities; the adult density at the sites ranged between 41-84 adults a year per hectare of old, open, beech forest. It is necessary to note, however, that the distribution of individuals is not even within a habitat patch (cf. Russo *et al.*, in press) and during the activity period (*see below*). The observed high density is probably rather exceptional in comparison to other localities of the species in the Czech Republic and elsewhere in Europe (Bořucký, 2007; Russo *et al.*, in press). It might be attributed to suitable conditions at the remnants of beech forest, including large proportion of old trees, no undergrowth and open-canopy structure (Russo *et al.*, in press).

The mean residence time is ~4 days for females and ~5-7 days for males. It is short, compared to maximum observed lifespan, but similar results were obtained for *Cerambyx welensii* (Küster, 1846) (López-Pantoja, 2008). Although partly attributable to reasons other than mortality (e.g. emigration), the short residence time is probably real. It might be explained by the beetle biology. Numerous species of subfamily Cerambycinae require no food as adults (see Edwards, 1961). This applies also to the closely related *Rosalia coelestis* (Tcherepanov, 1981) and very likely also to *R. alpina*, as no feeding was recorded during the > 1500 adult capture events in this study (*pers. obs.*). Although *R. alpina* adults are active and mobile (*see below*) they do not feed and their energy resources are probably very limited. This may explain for the short residence time of both sexes. The shorter female residence time might be attributed to the high costs of egg production. In comparison to males, female investment into eggs leaves less energy available to other activities. The short mean residence time, though, does not necessarily mean that many females die before laying eggs. In females

of many Cerambycinae genera, gametogenesis is compressed into a short period in the pupal stage and imaginal gonads are senescent (Edwards 1961). Females of such genera including *Rosalia* (Tcherepanov 1981) are able to copulate and oviposit nearly immediately after emerging.

#### 4.2 Mobility

Both males and females frequently move among dead trees and other coarse woody debris within a habitat patch. Such movements were recorded in 77 % of recaptured males and 75 % of females; 42 % of recaptured males and 45 % of females moved for more than 50 m. Adults of both sexes are also able to cross distance of at least several km, as dispersion of beetles among sampling sites was observed (max. 1.6 km); predictions of long distance flight probabilities of *R. alpina* were also relatively high (>1 % of individuals cover the distance of 1 km) even after exclusion of the longest flight.

Dispersal-ability estimates for other saproxylic beetles range from ~200 m to ~170 km, depending on the beetle species, sampling method and spatial scale (Franzén and Nilsson, 2007). Direct comparisons of dispersal rates among studies and species are thus difficult. Using mark-recapture, the longest dispersal observed for a large species inhabiting tree hollows, the Hermit beetle *Osmoderma eremita*, did not exceed 190 m (Ranius and Hedin, 2001) and telemetry corroborated the result (Hedin *et al.*, 2008). In France, however, telemetry of the same species showed considerably longer movements of 700 m (Dubois and Vignon, 2008). Movements observed for the Stag beetle *Lucanus cervus* using mark-recapture (maximum distance ~150 m; Fremlin, 2009) were ca 10 % of telemetry results (~2000 m; Rink and Sinsch, 2006). For tenebrionid beetle *Bolithophagus reticulatus*, mark-recapture study suggested limited dispersal ability (Nilsson, 1997 in Jonsell *et al.*, 2003), whereas flight-mill studies demonstrated its capability to fly for several kilometers (Jonsson, 2003) and genetic studies proposed dispersal even for tens of kilometers (Jonsson *et al.*, 2003). The largest movements observed in *Ips typhographus* reached tens to hundreds of kilometers but often above the forest canopy using passive dispersal (Bottweg, 1982; Nilssen, 1984; Forsse and Solbreck, 1985).

The mark-recapture gives low estimates due to underestimation of long-distance movements (Koenig *et al.*, 1996; Jonsell *et al.*, 2003). Our results thus likely underestimated the species mobility. We may infer, though, that *R. alpina* is rather mobile species in comparison to other large and endangered saproxylic beetles. For better understanding of the species dispersal ability, telemetric and genetic studies are needed.



### **4.3 Distribution pattern**

In addition to the three “main” sites where mark-recapture was performed, signs of *R. alpina* presence were found at six more sites. All of them were within ~5 km distance from the “main” sites, except for the largest and the most conspicuous Ralsko hill. Occasional observations of adults and larvae by other researchers suggested the same distribution pattern (Hrdlička, 1964; Honců, 2002; Honců and Roztočil, 2006).

During July 2008 and 2009, *R. alpina* was of the most frequently encountered saproxylic beetles on hill-tops of Maly Bezdez, Velky Bezdez and Slatinne Hills. At these “main” sites, populations consisted of hundreds of individuals a year, and presence of the species was apparent even outside the adult activity period. Typical exit holes (c.f. Dominik and Starzyk, 1989) were commonly found on available dead-wood, including standing or fallen logs, broken or fallen thicker branches (>15 cm) and even relatively small logging residues on the ground. On the “minor” sites, on the other hand, exit holes were extremely rare, localized to usually single trees and most of the suitable dead wood was unexploited. The populations at the “minor” sites are thus likely much smaller than those on “main” sites, probably consisting maximum of tens individuals a year. Such small populations would be prone to extinction, and presence of the species on the “minor” sites is unlikely to be continuous, but it is rather a history of extinctions and re-colonization. Large *R. alpina* population inhabits Slatinne Hills despite small area of the habitat (12 ha) and intensive dead-wood removal. At some of the “minor” sites, though, the conditions are at least parallel to Slatinne Hills, including terrain, volume of potentially suitable dead-wood, and extent of habitat. In comparison to Slatinne Hills, area of old-beech forest is much larger on Pecopala and Ralsko; the dead-wood volume is larger on Mlynsky, Ralsko, and Velka Bukova hills; and finally, nearly no dead wood removal occurs on Mlynsky and Ralsko hills owing to their conservation status.

Despite the high mobility of the species and several habitat patches within its reach, the *R. alpina* population is concentrated on the “main” sites, i.e. three nearby hill-tops of Maly Bezdez, Velky Bezdez and Slatinne Hills. Distance from the “main” sites thus seems to be the main factor affecting the distribution of *R. alpina* in the Ralska Upland.

### **4.4 Factors affecting local survival**

The studied population is probably the last *R. alpina* population surviving in Central Europe north of the Alps and west of the Carpathians. It is isolated from other known populations by

hundreds of kilometers, probably for decades (Bense, 2002; Sama, 2002; Starzyk, 2004; Cizek *et al.*, 2009).

The transformation of beech forests into conifer plantations is often given as a major cause of *R. alpina* decline (Sláma, 1998; Duelli and Wermelinger, 2005). The mature beech forests cover only a negligible portion (1.1 %) of the study area (see Figure 1 and Table 4) otherwise mostly covered by conifer plantations. The extent and structure of mature-beech forests is, on the other hand, relatively stable. The study area is a former army-training ground where forestry activities were minimized between 1950s and 1990s. Extent of mature beech forests is thus rather stable. Only about 20 % of the beech forest was felled since 1953, most during the last two decades. Owing to slow succession on shallow soils of rocky slopes and hill-tops, the forest structure is also relatively stable as the abandonment of traditional managements has not yet resulted in full canopy closure and/or expansion of undergrowth at the study sites. Further, the old beech forests remained mainly on hill-tops dominating horizon. This possibly facilitates for effective visual location of even small habitat patches by migrating adults as it is known from other Coleoptera species (Nalepa *et al.*, 2005). We consider the stability in habitat structure and the distribution pattern of habitat patches as vital factors allowing the survival of the studied *R. alpina* population despite low extent of the habitat.

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## 6. APPENDICES

**Table 1.** Summary of mark-recapture data obtained during a study of population of *Rosalia alpina* beetle.

Locality	Year	Marking period	Marking days	Marked beetles (♂/♀)	Recaptured beetles* (♂/♀)	Capture events (♂/♀)
Maly Bezdez	2008	12.7.-7.8.	17	96/61	45/9	173/74
Velky Bezdez	2008	16.7.-10.8.	19	158/82	46/7	244/95
Slatinne Hills	2008	26.7.-8.8	10	122/76	35/13	219/94
Slatinne Hills	2009	5.7.-16.8.	39	222/153	87/36	407/209

\* number of individuals caught next day at the earliest

**Table 2.** Summary of best-supported Jolly-Seber model (POPAN parametrization) used to estimate demography parameters and population sizes of *Rosalia alpina* in studied hills.

Locality	Year	Best models	cAIC	Par.	♂♂ (±S.E.)	♀♀ (±S.E.)	Total
Maly Bezdez	2008	$\phi(g) p(t) \text{Pent}(g) N(g)$	624.9	23	366 (±115)	509 (±137)	875
Velky Bezdez	2008	$\phi(.) p(g+t) \text{Pent}(T^2) N(g)$	712.1	27	447 (±57)	392 (±76)	839
Slatinne hills	2008	$\phi(g) p(t) \text{Pent}(t+lin) N(g)$	490.1	16	388 (±64)	286 (±60)	674
Total*	2008	$\phi(g) p(g+t) \text{Pent}(g+T^2) N(g)$	1731.3	33	1096 (±107)	930 (±126)	2026
Slatinne Hills	2009	$\phi(g) p(t) \text{Pent}(T^2) N(g)$	1909.2	47	519 (±46)	495 (±62)	1014

\* Maly Bezdez + Velky Bezdez + Slatinne Hills 2008

**Table 3.** Results of fitting the inverse power function (IPF) to movements of *Rosalia alpina* and predicted probability of movements to 100 m, 500 m, 1000 m and 3000 m.

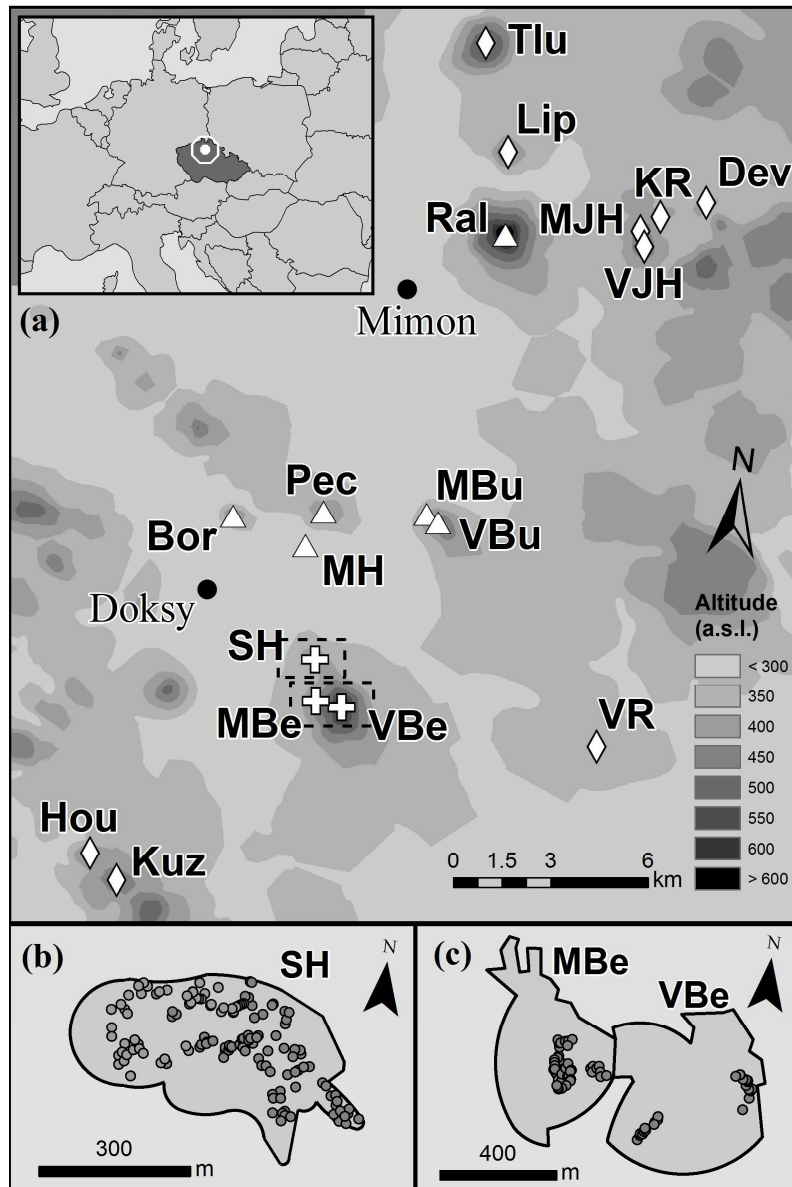
Year	Sex	IPF: $\ln I = \ln C(\pm S.E.) - a(\pm S.E.) * \ln D$	R <sup>2</sup>	F	df	100 (m)	500 (m)	1000 (m)	3000 (m)	Max. distance (m)
2008	M	$\ln I = -1.15(\pm 0.073) - 4.55(\pm 0.175) * \ln D$	0.92	248.99*	1,21	0.149	0.023	0.011	0.003	634
	F	$\ln I = -0.71(\pm 0.071) - 3.06(\pm 0.199) * \ln D$	0.91	99.68*	1,10	0.238	0.077	0.047	0.0218	1628
	F <sup>a</sup>	$\ln I = -0.86(\pm 0.151) - 3.61(\pm 0.443) * \ln D$	0.78	32.32**	1,9	0.195	0.049	0.027	0.0105	223
2009	M	$\ln I = -0.94(\pm 0.091) - 3.41(\pm 0.198) * \ln D$	0.79	107.12*	1,29	0.292	0.064	0.033	0.0117	658
	F	$\ln I = -0.85(\pm 0.109) - 3.25(\pm 0.276) * \ln D$	0.78	59.94*	1,17	0.272	0.07	0.039	0.0154	309

\* p < 0.0001; \*\* p = 0.0003

<sup>a</sup> excluded max. flight (1628 m)

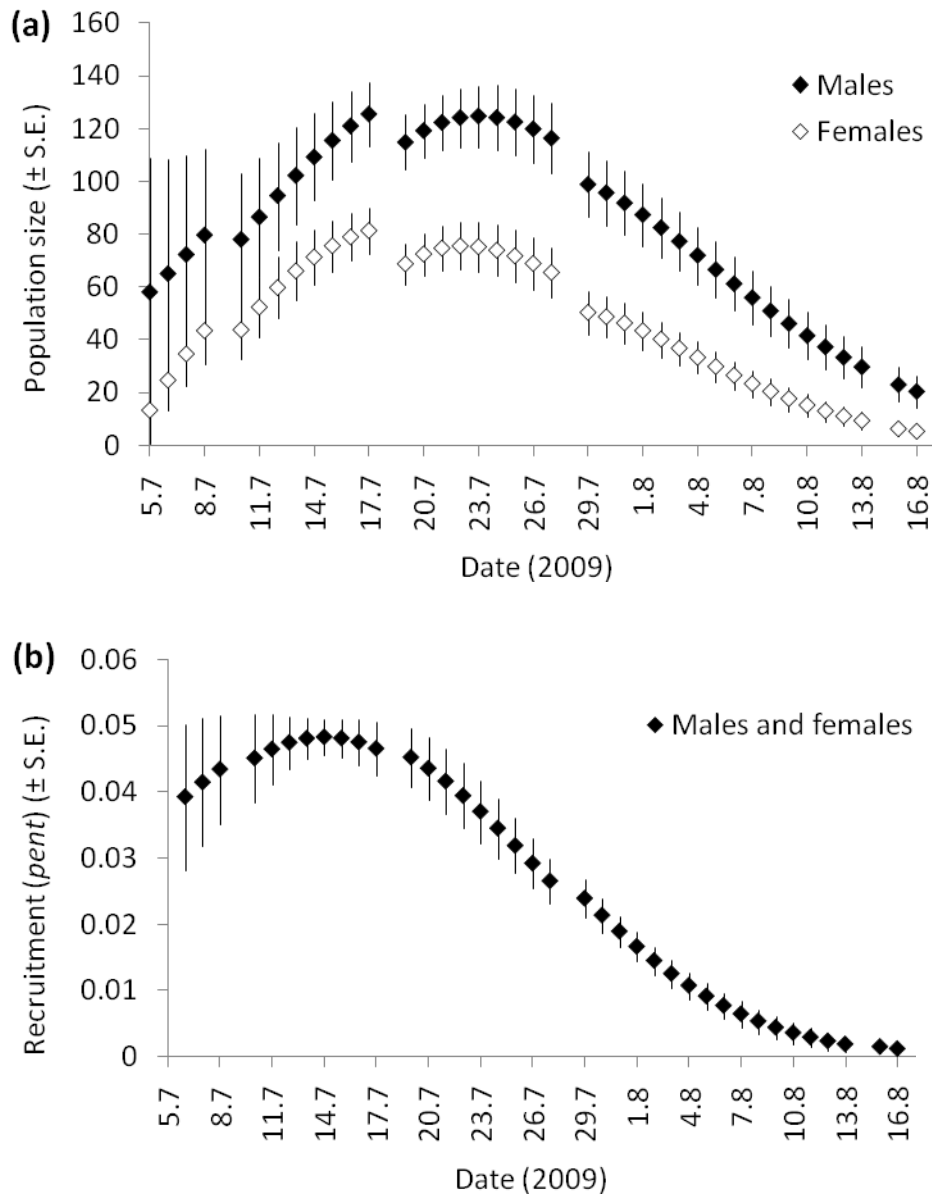
**Table 4.** Old beech forest patches found in the Ralska Upland, status of *Rosalia alpina* population, dead wood volume, current and historical area, altitude and GPS location.

Site	<i>R. alpina</i> population	Dead wood volume	Area (ha) 2007(1953)	Altitude (m a.s.l.)	North 50°	East 14°
Maly Bezdez	large	high	17.9 (28.8)	604	32'25"	42'49"
Velky Bezdez	large	high	20.3 (22.7)	577	32'21"	43'12"
Slatinne Hills	large	medium	12.1 (15.4)	430	33'13"	42'15"
Mlynsky Hill	small	high	11.2 (11.2)	389	34'58"	41'55"
Pecopala	small	high	202.8 (265.7)	451	35'36"	42'9"
Borny	small	medium	11.6 (19.2)	446	35'22"	39'46"
Velka Bukova	small	high	29.4 (65.2)	474	35'32"	45'20"
Mala Bukova	small	medium	14.1 (27.1)	431	35'44"	44'47"
Ralsko	small	high	217.6 (247.3)	696	40'26"	46'0"
Lipka	no-evidence	low	37.9 (40.1)	473	41'42"	45'46"
Tlustec	no-evidence	low	66.2 (78.7)	591	43'33"	44'39"
Devin	no-evidence	medium	8.3 (8.3)	452	41'34"	51'16"
Kozi Ridge	no-evidence	low	10.1 (10.1)	422	41'11"	50'8"
Maly Jeleni Hill	no-evidence	medium	3.2 (3.2)	474	40'52"	49'32"
Velky Jeleni Hill	no-evidence	low	19.5 (19.5)	513	40'36"	49'36"
Velky Radechov	no-evidence	low	23.8 (28.5)	392	32'18"	50'7"
Houska	no-evidence	medium	16.3 (16.3)	440	29'26"	37'23"
Kuzelik	no-evidence	low	8.3 (8.3)	480	29'3"	38'7"

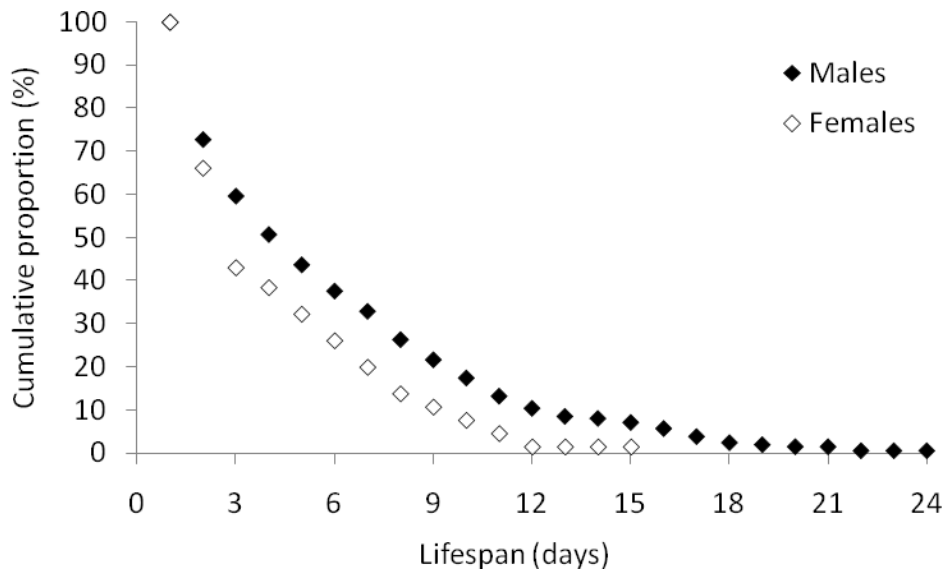


**Figure 1.** Distribution of *Rosalia alpina* in Ralska Upland (a), and distribution of trees and dead-wood on (b) Slatinne Hills (SH), (c) Maly Bezdez (MBe) and Velky Bezdez (VBe) where mark-recapture study took place. Eighteen sites with mature beech forest were found within the depicted area. Search for individuals and exit holes of *R. alpina* revealed that three sites host large populations (>500 adults a year, adults regularly found and abundant) (crosses), six sites host very small populations (>10 exit-holes found, adults occasionally reported) (triangles), while no evidence of the beetle presence was found on the remaining nine sites (diamonds). Within the area depicted (69 100 ha), forests cover 55.5 % (38 338 ha of mostly conifer plantations), mature-beech forests covered 1.1% (730.6 ha) in 2008 and 1.3 % (915.6 ha) in 1953.

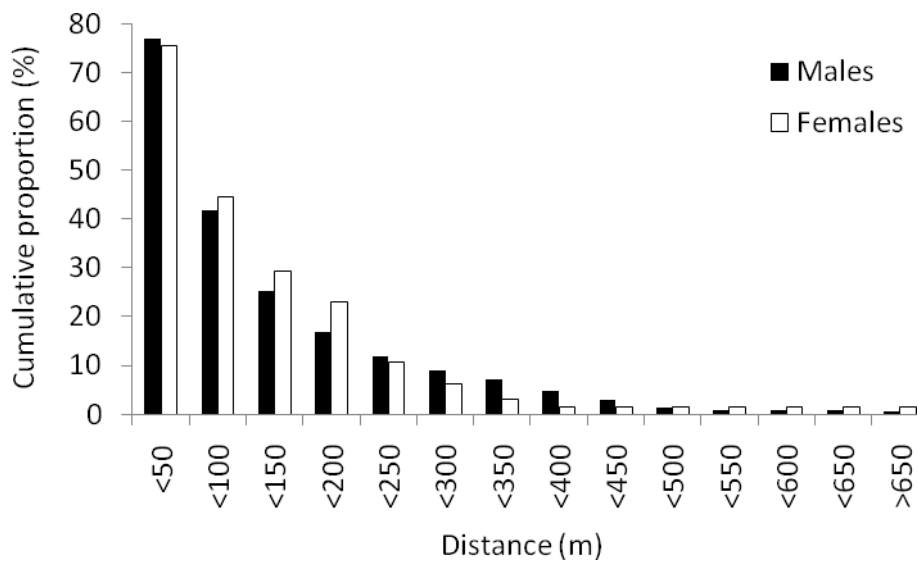
*Abbreviations:* Bor: Borny, Dev: Devin, Hou: Houska, KR: Kozi Ridge, Kuz: Kuzelik, Lip: Lipka, MBu: Mala Bukova, MBe: Maly Bezdez, MJH: Maly Jeleni Hill, MH: Mlynsky Hill, Pec: Pecopala, Ral: Ralsko, SH: Slatinne Hills, Tlu: Tlustec, VBu: Velka Bukova, VBe: Velky Bezdez, VJH: Velky Jeleni Hill, VR: Velky Radechov.



**Figure 2.** Daily estimates of population size (a) and recruitment (b) of *Rosalia alpina* in Slatinne Hills 2009. The estimates are derived from the mark-recapture data and modeled using the POPAN method in the program MARK. Used model:  $(\varphi(g) p(t) Pent(T^2) N(g))$ .



**Figure 3** Cumulative proportion of recaptures of *Rosalia alpina* in dependence on observed lifespan (number of days between the first and last capture of given individual). Data from the mark-recapture study were combined from years 2008 and 2009. ( $N_{males} = 213$ ,  $N_{females} = 65$ ).



**Figure 4** Cumulative proportion of beetles of *Rosalia alpina* in dependence on their lifetime movements. Data from the mark-recapture study were combined from years 2008 and 2009. Distances of 0 m (recaptures caught at the same place) were excluded, the rest were divided in 50 m classes ( $N_{males} = 164$ ,  $N_{females} = 49$ ).