



**Habitat preference and dispersal of a sand
associated beetle, *Apalus bimaculatus***

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Abstract

Species that have a high degree of specialization and poor dispersal ability can be more prone to extinction than more generalist species and good dispersers. How these species traits affect the viability of populations is dependent on landscape factors, such as isolation and connectivity. Additionally, interactions between species (e.g. symbiosis), and how these interactions vary spatially and temporally can have a large impact on populations. When the range and habitat areas of a species continuously decrease, management strategies are often needed if the species shall be able to survive. Management strategies have been formulated for the beetle *Apalus bimaculatus* (L.). The species is classified as Near Threatened (NT) due to a continued degradation of the quality and area of the species' habitat. The beetle has a complex life-history which includes parasitism on a solitary bee species, *Colletes cunicularius* (L.). Both species are dependent on disturbance requiring bare sand habitats, which vary both in time and space. The dispersal ecology of *A. bimaculatus* is poorly known. An increased understanding would be very beneficial to help explain the species abundance pattern and the effect of landscape factors. A number of 31 study sites were selected from a set of locations that had previously been surveyed for *A. bimaculatus* (2004, 2005 and 2006). The study sites were censused for *A. bimaculatus*, *C. cunicularius*, and other sand associated hymenopterans. Habitat quality of the sites were estimated using a number of abiotic (e.g. temperature, habitat area) and biotic (presence of food resources) measures. I found *A. bimaculatus* in 17 study sites. In less than a third (9) of the study sites *C. cunicularius* were present, while in more than half of the sites (18) other sand associated hymenopterans were seen. *A. bimaculatus* were more often found in sites with few shadowing trees and where sub-patches were large with fine- or medium-grained sand as dominating fractions. In sites where the species was found, the habitat area was often much larger than in the sites where it was not detected. This study suggests that management strategies for this species should consider: 1) that cutting down trees can be good for sites with low solar insolation, 2) to make sure that at least some sub-patches are dominated by fine to medium grained sand, 3) that when searching for areas which would be suitable to restore or translocate *A. bimaculatus* to, it can be successful to use several species of sand associated hymenopterans as indicators.

Keywords: *Apalus bimaculatus*, management, habitat quality, metapopulation, phoresy, dispersal, *Colletes cunicularius*

Sammanfattning

Arter som är starkt specialiserade och har dålig spridningsförmåga löper en högre risk att bli utrotade. Många arter påverkas av landskapsfaktorer såsom isolering och konnektivitet. Om två arter lever i symbios beror deras rumsliga och tidsmässiga fördelning även på den andra artens val av habitat. Då en arts utbredning och förekomstareal minskar allt mer, behövs ofta åtgärdsstrategier för att arten ska kunna fortleva. Åtgärdsstrategier har utarbetats för bibaggen (*Apalus bimaculatus*) som är en skalbagge klassad som missgynnad (NT) i den svenska Rödlistan. Anledningen till klassningen är en kontinuerligt minskande kvalitet och yta av artens habitat. Bibaggen har en komplicerad levnadshistoria och parasiterar på vårsidenbiet (*Colletes cunicularius*), som är ett sandlevande solitärbi. Båda arterna är beroende av områden med bar sand. Det är ett habitat som förekommer naturligt fragmenterat i tid och rum, på grund av att en viss störningsgrad krävs för att sanden ska förbli bar. *A. bimaculatus* spridningsekologi är oklar och ökad kunskap om denna vore önskvärt eftersom det kan vara en låg spridningskapacitet som är orsak till artens ringa förekomst i Sverige. Utifrån ett antal lokaler som hade inventerats för *A. bimaculatus* under åren 2004-2006 valde jag ut 31 studieområden för denna studie. De utvalda lokalerna inventerades för *A. bimaculatus*, *C. cunicularius* och andra sandbundna stekelarter (Hymenoptera). För att kunna bedöma kvalitén av habitatet inom varje studieområde mättes ett antal abiotiska (t.ex. temperatur och area habitat) och biotiska (t.ex. förekomst av födoresurser) variabler. Jag hittade *A. bimaculatus* i 17 av studieområdena, *C. cunicularius* fanns i knappt en tredjedel (9) av områdena och andra sandbundna steklar fanns på fler än hälften (18) av lokalerna. Förekomsten av *A. bimaculatus* var högre på lokaler med låg skuggningsgrad från skogen runtomkring och inom delområden som var stora, med i första hand fin- och mellankornig sand. Även storleken på habitatet påverkar; för lokaler där arten hittades var arean av habitatet mycket högre än arean för de lokaler där bibaggen inte hittades. Resultat från denna studie indikerar att åtgärdsplaner för bibaggen bör ta hänsyn till: 1) att det kan vara bra att hugga ner vissa träd inom lokaler där solinstrålningen är låg, 2) att några delområden inom varje lokal borde bestå av till större delen fin- till mellankorning sand, 3) att ett sätt för att finna lämpliga områden för restaurering eller translokering av *A. bimaculatus* kan vara att utnyttja sandbundna arter inom familjen Hymenoptera som indikatorer.

Nyckelord: bibagge, *Apalus bimaculatus*, åtgärdsprogram, habitatskvalité, metapopulation, foresi, spridning, vårsidenbi, *Colletes cunicularius*

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Introduction

It is well known that the degradation of natural landscapes in footsteps of human developments has lead to habitat loss and fragmentation for many species (see e.g. Marzluff & Ewing, 2001). This change of the landscape has lead to both population declines and extinctions of many species (Fahrig, 1997; Fahrig, 2001; Baker & Harris, 2007). Species that have certain traits or abundance patterns may be more susceptible to extinction than others (McKinney, 1997). Such traits are high specialization and poor dispersal ability, as well as spatially patchy abundance and aggregated seasonal appearance. Classical metapopulation theory (Hanski, 1989), is one suitable framework to understand how species are affected by the landscape, and is especially appropriate for species living in highly fragmented landscapes (Schneider *et al.*, 2003; Hanski, 2004). To be regarded as a metapopulation the local populations should be isolated from each other but some degree of migration of individuals should exist between sub-populations (Hanski, 1998). Populations that can not be regarded as belonging to a metapopulation may still be much affected by landscape factors, such as isolation and connectivity (Burkey, 1989; Warren, 1991; Karlsson *et al.*, 2007).

When the suitable habitat of a species is highly fragmented in the landscape, each patch has a lower probability of becoming colonized (With & Crist, 1995; Hanski, 1999) and the gene flow between patches is diminished (Dixo *et al.*, 2009). Smaller patches can hold smaller populations and have therefore a higher probability of going extinct (Burkey, 1989). Patches more isolated from other populations have a lower chance of becoming re-colonized if the population would go extinct (Warren, 1987). If the connectivity between patches is high it helps the whole network of patches to hold vital populations (Hanski, 1998). The connectivity depends on how the species responds to the spatial arrangement and quality of the landscape as well as the dispersal ability of the species (Tischendorf & Fahrig, 2000). The qualities of the existing patches also have a profound effect on the survival of the populations (Warren, 1991; Gyllenberg & Hanski, 1997; Moilanen, 2004). Species specialized in ephemeral habitat patches, which naturally disappears as succession continues, are especially prone to extinction if the species are not able to easily disperse between the patches (Warren, 1991; Ranius, 2000). If two species are symbiotic, their spatial and temporal distributions are also much dependent on the habitat utilisation and dispersal ability of the other species (Morris, 2003).

When working with conservation management of a species it is important to have good knowledge of the species and to understand how it interacts with its environment. Many studies have shown the importance of considering the spatial (Huxel & Hastings, 1999; Steffan-Dewenter *et al.*, 2002; Morris, 2003) and temporal (Warren, 1991; Mc Nally, 2008) dynamics in ecosystems for conservation planning. A prioritised work when managing a threatened species would therefore be to acquire knowledge of the species' life history traits (Warren, 1991), and especially its dispersal ecology (Bowler & Benton, 2005). National and international red-listings are well established methods for classifying organisms into threat categories and are much used in conservation work. In the 2005 Red List of Swedish Species there are more than 3700 taxa included and categorised as red-listed (Data Deficient, Near Threatened, Vulnerable, Endangered, Critically Endangered or Regionally Extinct), of which 1683 are insects (Gärdenfors, 2005). The most common criteria (category B)

for a taxon being included in this list is if its distribution areas are small, largely fragmented or composed of few local areas (Gärdenfors, 2005). When the range and habitat areas of a species continue to diminish, management strategies are often needed for the species to persist (Warren, 1991). This is often even more urgent if the focal habitat is of an early-successional stage and need disturbance to persist (Urban *et al.*, 1987).

The Swedish Environmental Protection Agency (EPA, Naturvårdsverket) has established a number of conservation management programs. One of these programs considers the beetle *Apalus bimaculatus* (L.) (Lönnell, in press), with a highly fragmented distribution (Cederberg, 2003) of populations in central and southwest Sweden (Lönnell & Edelsjö, 2004; Lönnell, 2005). The species was earlier considered vulnerable (VU) (Gärdenfors, 2000), because of an observed decrease in population sizes (category A1a), a small distribution range and small habitat areas (category B1+2). In a later red-list it has been classified as Near Threatened (NT) (Gärdefors, 2005). One reason probably being that several new local populations have been reported (Lönnell & Edelsjö, 2004). Still the species is close to being categorised as VU, due to the continued degradation of the quality and area of the species habitat and the fact that it only occupies < 2000 km² within the country (Gärdenfors, 2005). Since 2004, conservation management activities for the species have included habitat restorations of locations that were known to previously been habitat suitable for *A. bimaculatus*, but that were becoming less suitable due to replanting of spruce and pine, as well as natural succession (Lönnell & Edelsjö, 2004). The main restoration aim for the work performed was to alter the sites to a state believed to be better suited for *A. bimaculatus*. Before the restorations were done, the distribution of the beetle was censused during three seasons between 2004-2006 (Frycklund, 2006; the county administration board in Uppsala, unpublished data).

The first aim of this study is to increase the knowledge of how habitat and landscape factors affect the distribution of *A. bimaculatus*. This is carried out by examining how habitat isolation and habitat quality correlate with the presence of the species. Gathering data at several scales made it possible to investigate the effect of both landscape and local variables on *A. bimaculatus*. The importance of not only using a single scale in landscape studies has been addressed several times (Kotliar & Wiens, 1990; Winfree *et al.*, 2007). A second aim of the study is to examine how the habitat restorations have affected the presence of the species. This was done by censusing the presence of *A. bimaculatus* in a number of habitats during the spring of 2009, and comparing this new data with previous distribution information and data on restorations. The species has a complex life-history and is a parasite on a solitary bee species *Colletes cunicularius* (L.) (Notini, 1942); this was considered in the analyses.

Study species

Apalus bimaculatus belongs to the family of blister beetles (Coleoptera: Meloidae). The meloids are a large family (Pinto, 1977) that has attained plenty research attention; however the taxonomy is still not completely detangled (Bologna & Pinto, 2001; Bologna *et al.*, 2008). *A. bimaculatus* is an easily recognizable 1 cm black beetle with brightly yellow-orange elytra (the hardened front wings) and a single black dot located at the hind part of each elytron (Notini, 1942). The female abdomen is swollen with several of the segments having a yellowish colour (Lönnell & Edelsjö, 2004). The species inhabit sandy habitats and in Sweden it emerges as soon as the snow melts in spring, the adult activity period normally takes place from early March to the middle of April (Lönnell & Edelsjö, 2004). The species develops in the nests of the bee *Colletes cunicularius*, which has a somewhat later activity period predominantly in March to May (Notini, 1942). *A. bimaculatus* needs a dense population of *C. cunicularius* for successful reproduction (Cederberg, 2003). The first instar larva of the beetle, called triangulin (Bologna & Pinto, 2001), goes down the bee nests and feed of the bee's provision and the bee larva (Notini, 1942). There are no estimations on populations sizes available, but a record of 300 individuals within a restricted area has been published (Notini, 1942). It is suggested that *A. bimaculatus* is sensitive to the amount of trees in the habitat area (Lönnell & Edelsjö, 2004), as denser tree stands in the surroundings result in less solar insolation and a colder microclimate. The species' high specialization, dependence on a successional habitat (Lönnell & Edelsjö, 2004) and its fragmented presence in time and space are all features that make it sensitive to extinction.

There are different theories on the dispersal ecology of *A. bimaculatus*. It is suggested that the beetle is a poor flyer (Notini, 1942; Lönnell & Edelsjö, 2004) and that it is predominantly the first instar larva that is mobile (Notini, 1942). Several studies have shown that many blister beetles use phoresy (the act of one organism attaching to another for the purpose of dispersal) to locate their food source (e.g. Saul-Gershenz & Millar, 2006; see also Bologna & Pinto, 2001 for a phylogenetic review). This tactic can also enable the species to disperse further than it would be able unaided (Houck & O'Connor, 1991). There are no studies showing that the larva of *A. bimaculatus* uses their bee hosts to disperse, but the presence of this strategy in several related species (Bologna & Pinto, 2001) make it plausible that this also occurs in *A. bimaculatus* (Bologna *et al.*, 2008). Additionally, Notini (1942) showed that a behavioural response exists in *A. bimaculatus* on secret from *C. cunicularius*. This indicates that the triangulins are adapted to localize adult bees, which is the first step in using them for phoresy. The dispersal of *A. bimaculatus* may therefore be closely linked to the dispersal of *C. cunicularius*.

Colletes cunicularius (Hymenoptera: Colletidae) is a solitary bee, slightly more than 1 cm in length (Peakall & Schiestl, 2004), that utilise sand habitats for their nests (Larsson & Tengö, 1989). These nests are positioned a few centimetres down in fine sand (Lönnell & Edelsjö, 2004), and are aggregated in clearly separated sub-populations (Larsson & Tengö, 1989). *C. cunicularius* is one of the earliest appearing bees in spring (Peakall & Schiestl, 2004) with males developing and emerging before females (Larsson & Tengö, 1989). It has been shown that even though the area

covered with nests can be large, each male only patrol a limited space ($\sim 10 \text{ m}^2$) in the search for mature females and often clusters of males fighting for emerging females are formed (Larsson & Tengö, 1989; Peakall & Schiestl, 2004). *C. cunicularius* collect pollen and nectar from primarily *Salix* species, with *S. caprea* (the willow tree) stated as the most important species for the Swedish populations (Cederberg, 2003; Lönnell, in press). Spring flowering plant species from families such as Asteraceae, Aceraceae and Fabaceae, can also contribute to the bee's diet (Müller & Kuhlmann, 2008). The brood cells are lined with a cellophane-like surface and the adult bee provision them with a liquid mixture of pollen and nectar (Almeida, 2008).

The population size can be up to several thousand adults during the peak of the active period (Peakall & Schiestl, 2004) with a density of 15 to 21 individuals per m^2 (Larsson & Tengö, 1989). In Sweden the peak usually occurs in April and early May (Notini, 1942; Lönnell & Edelsjö, 2004). Generally, solitary bees have a fairly small foraging range (Gathmann & Tscharntke, 2002; Steffan-Dewenter *et al.*, 2002), for *C. cunicularius* the only estimated value I found states that the maximum foraging range is about 350 meters (Wesslerling, 1996 in Gathmann & Tscharntke, 2002). Experiments with solitary bees have shown that the body size of a species is the best estimation of its foraging range (Gathmann & Tscharntke, 2002), using bee species with body length varying from 5 mm to 25 mm and maximum foraging ranges of 100-1200 m. For the medium bodied *C. cunicularius* (measured as 13.5 mm in that study) a range of 350 m is therefore probable. However, a distance of 2 km between sand habitats has previously been shown not to constitute a barrier for wild bees (Wesslerling & Tscharntke, 1995) but the sizes of the species included in that study are not known.

Materials and methods

Study sites

A number of 31 study sites were selected from a set of locations that had been surveyed for *A. bimaculatus* in 2004, 2005 and 2006 (see Fig. 1). From the previous surveys; habitat coordinates, a short description of the biotope and the presences of *A. bimaculatus* and *C. cunicularius* were available for all sites. In the set, all sites that had been restored (9 sites) by the county administrative board of Uppsala were included. In addition, 22 patches with suitable *A. bimaculatus* habitats were also included. Out of these 22 sites, 13 were sites with previous findings of *A. bimaculatus* and 9 were sites where *A. bimaculatus* had not been found during previous surveys.

The 22 additional sites were selected using several different criteria: the sites should 1) resemble the restored sites with regard to size and habitat, 2) represent different geographic areas of the county of Uppsala, 3) include suitable habitat for *A. bimaculatus*, and 4) the gathered data should represent a variety of the landscape. The data used for the selection was gathered from previous censuses, digital maps, orthophotos and ground truthing. The habitat was considered suitable for the beetle if an area $> 50 \text{ m}^2$ was covered predominantly with bare sand. If two potential habitats were within 100 meter from each other, only one of the sites was selected to avoid pseudo replication of the landscape data.

I divided each habitat in several sub-patches (Fig. 2). Some parts have more vegetation and others have larger grain size, only the sub-patches consisting entirely of bare sand were considered. When coming across sub-patches still covered by snow or water, these were considered unsuitable regardless of the quality of the sand.

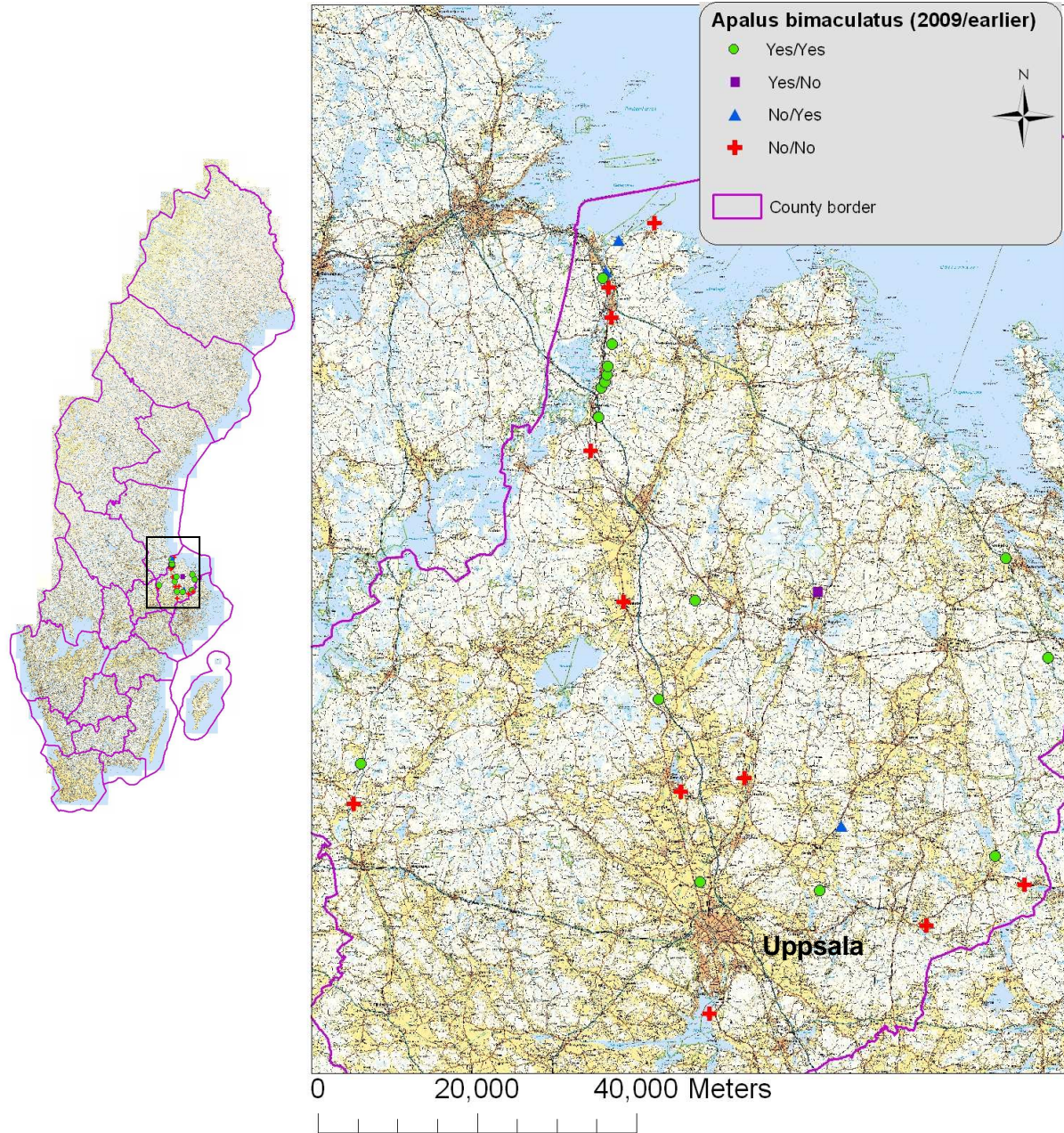


Figure 1. Map of Sweden to the left with the study area framed, the county of Uppsala enlarged to the right with the city of Uppsala indicated and showing the 31 study sites. Presence and absence of *A. bimaculatus* during the census of 2009 and previous census years are indicated, with signs explained in the legend (background map from Kartdatabasen, 2008).

Censuses in the study sites

The study sites were censused for *A. bimaculatus* between the 1st of April and the 30th of April 2009 when the beetle emerged for the breeding season. All censuses were done between 0900 and 1800. To increase the possibility to visit all sites during the peak of the species activity period, only the sub-patch variables were collected at the same time as the census for all sites. Missing variables were measured at later visits. Within a site, the sandy habitat was censused by walking, covering all parts. When a sub-patch of the preferred habitat of dry and not too coarse-grained sand (< 2 mm) was detected, I stopped for five minutes and censused the area carefully for both *A. bimaculatus* and *C. cunicularius*. For any found individuals, the numbers, sex and status (if found alive or dead) of the beetles were noted. The numbers of *C. cunicularius* were also noted and if other sand-living hymenopterans were seen their presence were recorded as well. Other sand associated hymenopterans can constitute a competition for either *C. cunicularius* or *A. bimaculatus*. They are also of interest as they could possibly function as key-species for determining if the habitat is suitable for the study species. If an *A. bimaculatus* were detected at a later visit this was recorded and added to the data set. The study sites located furthest to the south were censused first, to increase the likelihood of finding emerging beetles. Censuses were not carried out in days with cold or rainy weather, as this may influence the detection probabilities from beetles reducing their movements.

If the number of sub-patches within a site was high (> 15 or more than five per 10 m²) a subset of the areas were used (Fig. 2B), as the census would otherwise be too time consuming. In the selection I aimed for a variation in the sub-patches regarding cardinal direction of the sandy habitat, patch area and temperature of the sand. Sub-patches with medium or fine sand grains (grain size < 0.6 mm) were prioritized before patches with larger grains, and sub-patches including other soil fractions than sand were avoided.

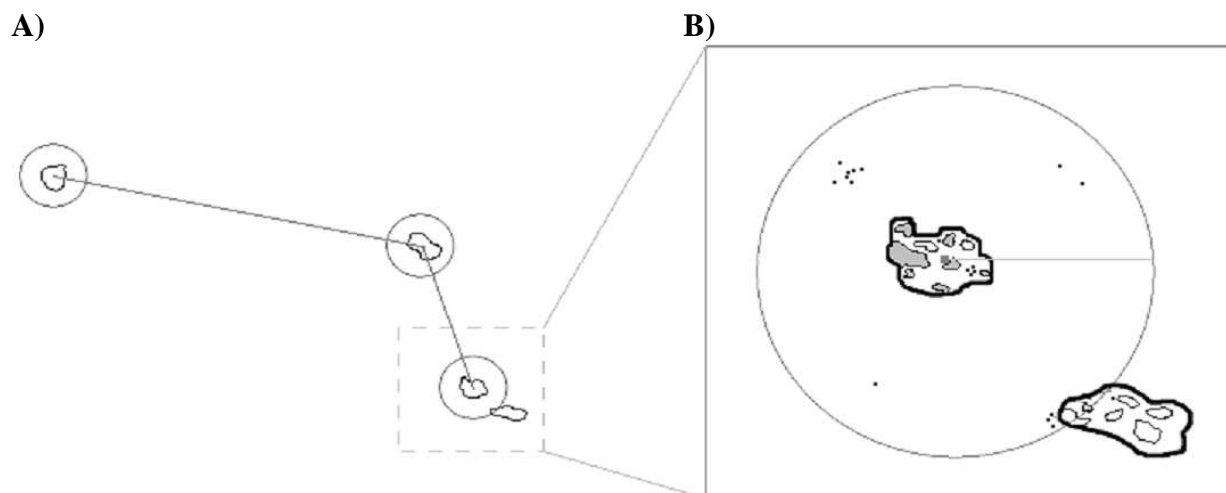


Figure 2. Lay-out of the study areas, with A) a *landscape* view and B) a close-up of one of the study sites. Lines connecting the circles symbolize the measured distance between populations. The circles represent the *study sites*, each covering an area with a 350 meter radius, with the site coordinate shown as a dot in the centre. The *habitat* is outlined in bold and includes several *sub-patches*, the ones selected for the study are here shown as grey while unselected are white. The small black dots represent sallow trees (*S. caprea*).

Measurements in the study sites

To get an estimation of the quality of the habitat within each site, a number of variables were measured (see Appendix 1 for the field protocol). In all sub-patches, four different types of habitat data were gathered, which were then also used to get mode (the most common) or mean values for the whole habitat.

As *A. bimaculatus* becomes active as soon as the temperature of the ground is high enough (Lönnell & Edelsjö, 2004); the temperature of 350 m the ground is probably important for the detection of the beetles. Sand temperature was measured with a digital thermometer (resolution of 0.1° C) at two different depth levels. Surface temperature was measured by placing the thermometer close to the surface of the sand without being exposed to direct sun. Temperature was also measured at a depth of 11.5 cm, since below ground temperature is of interest for ground dwelling poikilotherms (Larsson & Tengö, 1989).

It has been stated that *A. bimaculatus* need fine-grained sand (Cederberg, 2003; Lönnell & Edelsjö, 2004), but this has never been studied in detail and the exact grain fractions that is suitable for the species is not known (Lönnell, in press). Thus, it was interesting to examine if there was a correlation between grain size and presence of the species. The sizes of the sand particles in the sub-patches were estimated using the SGF fraction scale (Swedish: SGF's korngruppskala) as reference, giving three size categories of sand grain. Fine-grained sand (> 0.06 mm) was categorized as 1, medium-grained (> 0.2 mm) as 2 and coarse-grained sand (> 0.6 mm) was categorized as 3. At each sub-patch, the sand category was determined from sand samples and visual inspection. If the sand had approximately equal ratios of two grain fractions, their mean value was used. When no fraction was more common than the others, the sub-patch was categorized as 0. As a measure for the quality of the sand within the whole habitat, the sand grain size that was most common (by means of the mode value and not the mean value, since I am using categories) among the sub-patches within that habitat was used.

As there might be a threshold in connected habitat area needed for *C. cunicularius* to build large enough colony-aggregations for *A. bimaculatus* to survive (Cederberg, 2003), the size of the sub-patches were interesting. The sub-patches were categorized into one of four sizes; small (1) (approx. < 1 m²), medium (2) (1 - 10 m²), large (3) (10 - 100 m²) or very large (4) (> 100 m²). The most common value (the mode value) was used as a measure for the whole habitat. The area of the entire habitat within one study site was also measured, using digital maps (see below, under "measuring landscape variables").

Some values that could be important for *A. bimaculatus* were collected for each site as a whole instead of for each sub-patch. Two of these measurements, describing the quality of the habitat, were gathered in field. A measurement of the tree coverage around the habitat was taken at one representative area within the site, with a Relascope. This is an instrument used in forestry to estimate the basal area as a description of the productivity of a forest stand (Eid, 2001). Here the basal area was

used to measure how much the forest around a habitat shadows the sand in that area. One measurement of basal area was taken from each site.

To get an estimation of available food resources for *C. cunicularius* within the site, both digital maps and ground surveys were carried out. From a point selected at the centre of the site, a circular area with a radius of 350 meters (maximum foraging range for *C. cunicularius*) was used. The number of *Salix caprea* was counted within this area. The sallow census was carried out between the 1st of Mars until 15th of May. Sallow trees are easily recognizable during this entire period.

Measuring landscape variables

To be able to test the effect of landscape variables on *A. bimaculatus* presence, several types of landscape data were estimated. Data on the area of bare sand habitat within each study site and between the sites was calculated using digital maps, ArcGIS 9.2 (ESRI, 2007) and orthophotos. The isolation and connectivity of the sites were estimated using digital maps and ArcGIS 9.2. This gave me measures of distance between all study sites and the closest previously known location of *A. bimaculatus*. The values of sand area within each site are also used as a measure of the habitat size, as this was not measured in field.

Analyses and statistics

Data were tested for normality using a Shapiro-Wilks W test. If the data was not normally distributed it was transformed to normality. A Spearman Rank Correlation test was used to see if any of the variables measured were highly correlated or if they correlated with the date or time taken. The test was also used to detect variables that correlated with the abundance of *A. bimaculatus* and *C. cunicularius*. A t-test was performed to investigate the relationship between the different landscape and habitat variables on the presence of *A. bimaculatus*. The correlations between species' presence and correlations between species' absence were tested using a Chi Square-test. I used a Linear Regression to analyse the effect of distance and area of habitat (between sites) on the presence of *A. bimaculatus*, the interaction effect of these variables were also included in the analysis. The restoration actions made by the county administrative board of Uppsala could not be statistically analyzed due to the small sample size of the different activities. The data gathered from the different sites are evaluated and discussed with respect to the other findings. For the Chi Square-test and the Linear Regression the software JMP was used (SAS Institute, 2007) All other above mentioned analyses were performed using STATISTICA (StatSoft, 2008). Mean values are presented with standard error and the significance of tests as exact P-values.

Results

Of the 31 locations included in the study, *A. bimaculatus* were found in 17 sites, while *C. cunicularius* were found in 9 sites. In sites where *A. bimaculatus* existed, the mean number of individuals was 2.7 ± 0.54 per site with a maximum of 9 individuals. The mean number of *C. cunicularius* for all sites was 1.2 ± 0.54 , with a maximum of 15 individuals.

Censused species

There was a trend to a correlation between the presence of *A. bimaculatus* and presence of its host species ($\chi^2 = 2.49$, $P = 0.114$) (Table 1.). The presence of *A. bimaculatus* were often linked to the presence of other sand associated hymenopterans ($\chi^2 = 11.08$, $P < 0.001$). The presence of *C. cunicularius* were also linked to the presence of other hymenopterans ($\chi^2 = 3.91$, $P = 0.048$). If other hymenopterans were seen at a location, in 83 % of these cases *A. bimaculatus* was also seen. While the species only could be detected at 15 % of the sites where no other hymenopterans (than *C. cunicularius*) were noted.

Table 1. The ratio of presence of *A. bimaculatus* and *C. cunicularius* in the study sites grouped by presence or absence of the different species censused. This shows to what degree the groups could be seen to coexist at the sites and if they were likely to exist at sites without the other groups. (*C. cun* = *Colletes cunicularius*, Hym. = other hymenopterans)

| Species | Hym. present | Hym. absent | <i>C. cun</i> present | <i>C. cun</i> absent |
|---|-----------------|----------------|--------------------------|-------------------------|
| <i>A. bimaculatus</i> Present (ratio) | 0.83 | 0.15 | 0.78 | 0.45 |
| <i>C. cunicularius</i> Present (ratio) | 0.44 | 0.08 | | |

Variables from study sites

At the surface of the sand, the temperature was between 5.3° C and 40.3° C with a mean of $20.3^\circ \pm 0.63^\circ$ C, no effect on the presence of *A. bimaculatus* could be detected ($t = -0.23$, $P = 0.82$, $df = 150$). The temperature of the sand at 11.5 cm depth was between 1.7° C and 20.9° C with a mean of $10.1^\circ \pm 0.34^\circ$ C. Sub-patches with *A. bimaculatus* were at this depth warmer than sub-patches without *A. bimaculatus* ($t = 2.92$, $P = 0.004$, $df = 150$).

The size of the sand grains in each sub-patch was not significantly correlated to the presence of *A. bimaculatus* in that sub-patch ($t = -0.59$, $P = 0.554$, $df = 151$). When looking at the habitat scale by using the mode value from all sub-patches within each site, a correlation between grain size and beetle presence was detected (Fig. 3). Smaller grain sizes were more common on locations where *A. bimaculatus* had been seen ($t = -4.07$, $P < 0.001$, $df = 28$). Beetles were never present at locations where the majority of patches had sand grains > 0.6 mm (coarse-grained, cat. 3).

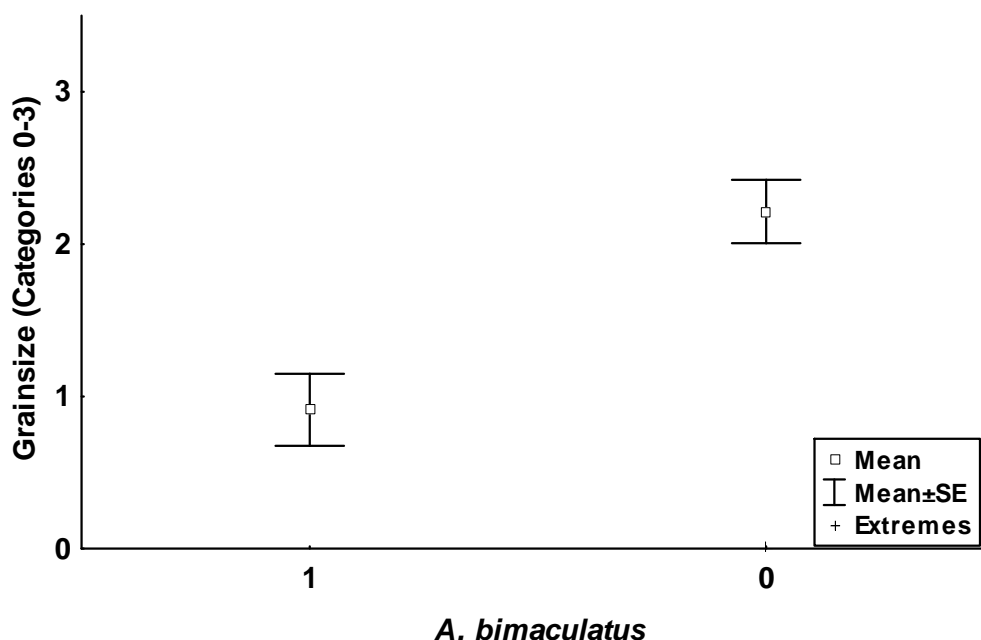


Figure 3. The localities are grouped after presence (1) or absence (0) of *A. bimaculatus* and categorized according to the sand grain size of the majority of patches (1 = fine-grained, 2 = medium-grained, 3 = coarse-grained, 0 = mixture of all fractions; when two fractions were included the value in between them are used, such as 2.5 for medium & coarse-grained).

The presence of *A. bimaculatus* differed between sites depending on the mean size of the habitat, on both sub-patch and sites scale. The sub-patches where *A. bimaculatus* was present were larger than the sub-patches where no beetles were found ($t = 3.54$, $P < 0.001$, $df = 151$) (Fig. 4). No beetles were found on any of the sub-patches that belonged to the smallest category (< 1 m²). At the scale of sites, the size of the habitat area was positively correlated with occurrence of *A. bimaculatus* ($t = 2.39$, $P = 0.024$, $df = 27$) (Fig. 5). The value of the basal area varied between 0 and 23.5 m²/ha, with a mean of 4.5 ± 1.1 m²/ha. Sites where *A. bimaculatus* were present had a lower mean basal area, indicating a less shadowed habitat, than the sites where the beetle was not observed ($t = -2.12$, $P = 0.04$, $df = 29$) (Fig. 6). The number of *Salix caprea* within the areas varied between 2 and 211, with a mean number of 60.5 ± 8.16 . There was no correlation between the number of *S. caprea* around the habitat and the presence of *A. bimaculatus* ($t = 0.80$, $P = 0.428$, $df = 29$), and there was only a weak correlation between the date of the survey and the numbers of *S. caprea* seen (Spearman Rank Order Correlation, $r = 0.175$, $P \geq 0.05$).

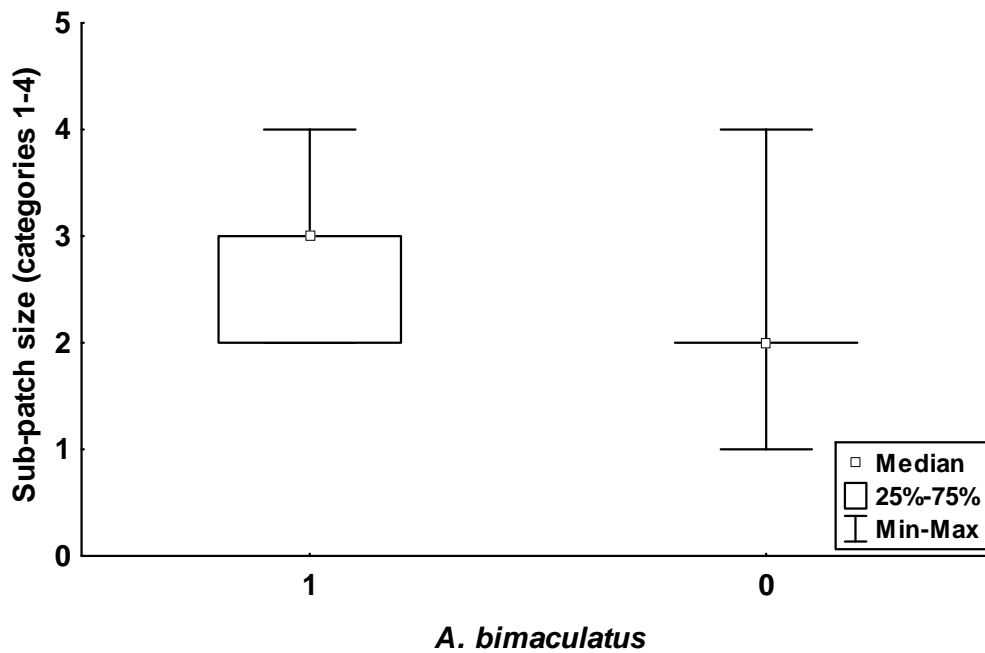


Figure 4. Size of the sub-patches with (1) and without (0) *A. bimaculatus*. The sizes were categorized as small (1), medium (2), large (3) or very large (4). Median value, 1st- and 3rd-quartile as well as minimum and maximum values are shown.

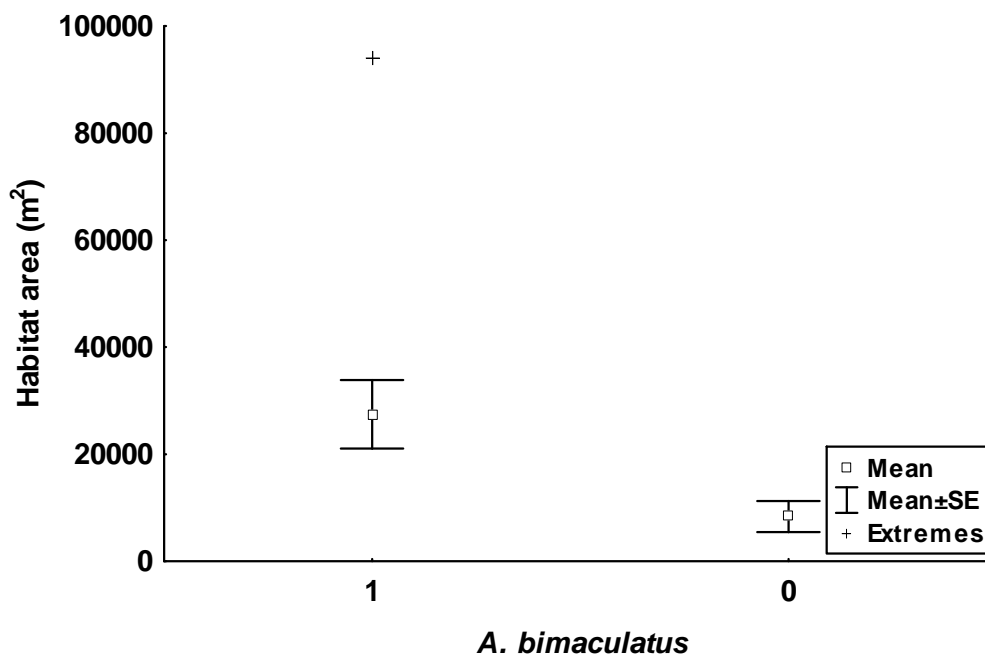


Figure 5. Area covered by sand within a location in a Box-and-Whisker plot, grouped by presence (1) or absence (0) of *A. bimaculatus*.

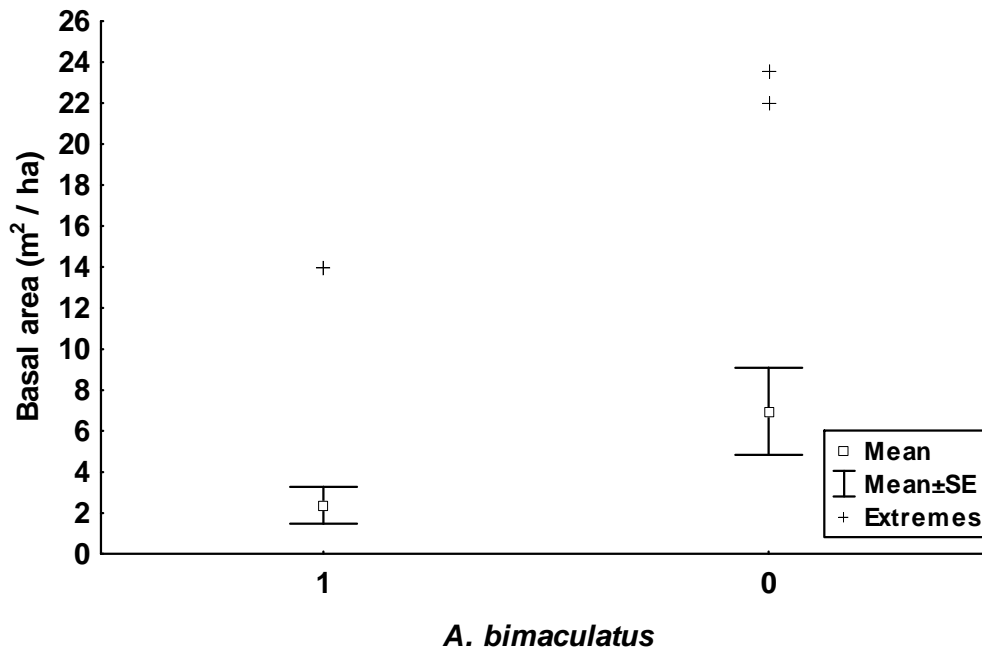


Figure 6. Box-and-Whisker plot showing the difference in basal area (density of trees around habitat) between the locations with (1) *A. bimaculatus* and locations without (0) the beetle.

Landscape variables

None of the variables measured on the landscape level showed a significant linear relationship with the presence of *A. bimaculatus* (see Table 2 for statistics). The distance to the closest known population of *A. bimaculatus* was not correlated with the presence of the beetle in 2009. Neither was the amount of sand habitat between a known population and a study site correlated with the presence of *A. bimaculatus* in the study site. There was no significant interaction effect between the two variables on the presence of the beetle (Table 2).

Table 2. Result from a logistical regression testing the effect of distance between sites, amount of suitable habitat and the interaction effect of these on the presence of *A. bimaculatus*. Model statistics: $\chi^2 = 1.33$, $P = 0.72$, $df = 3$.

| Parameter | Estimate | Chi-Square | P |
|------------------------|---------------|------------|-------|
| Distance | $-5.28e^{-6}$ | 0.00 | 0.965 |
| Habitat area | $-5.67e^{-6}$ | 0.35 | 0.553 |
| Distance* Habitat area | $-2.02e^{-9}$ | 0.66 | 0.418 |

Discussion

There are no known data on population sizes of *A. bimaculatus*, which makes it hard to evaluate the conservation status of populations. There have, however, been reports of several hundreds of individuals seen at some locations (Notini, 1942; Lönnell & Edelsjö, 2004). The numbers of *A. bimaculatus* found in this study were low, never exceeding 10 individuals in any one location. We know from previous reports that from single visits to a location it is hard to estimate population sizes (Lönnell & Edelsjö, 2004). The year previous to the study year (2008) had an early warm period during the spring followed by an unusually cold period. The individuals that had already become active during the warm days probably died from the cold weather without being able to reproduce that year (Lönnell, pers. com.; Lönnell & Edelsjö, 2004). This could be one explanation to why low numbers of adult beetles was seen during this study year. The population sizes of *A. bimaculatus* are hard to determine and the timing of the survey largely affects how many *A. bimaculatus* that are seen (Lönnell & Edelsjö, 2004). Therefore, the number of individuals detected cannot be taken as absolute measures of population size. The analyses performed in this study were carried out using only the presence or absence of *A. bimaculatus*. This method gives a rougher but probably more accurate measure of the quality of any patch.

Previous studies on *C. cunicularius* in Sweden have shown populations sizes of 1500-2000 individuals in an area of 100 m² (Larsson & Tengö, 1989). The number of *C. cunicularius* seen during this study period (≤ 15 individuals/study site) was much lower. The available time for this study was not enough to do census at all sites during the peak of both species activity periods. Since the bee has a slightly later activity period than *A. bimaculatus* it is possible that some *C. cunicularius* colonies were missed, leading to false absences of the bee species in the data set. The majority of the censuses were carried out in late April when the habitat had dried up and when the bees should have emerged from their burrows (Notini, 1942). Another sand nesting bee species (probably *Andrena vaga*) with similar ecological constraints (Lönnell,

pers. com.), was observed in large numbers during the surveys. These facts suggest that the census period should have included the activity period of *C. cunicularius* and therefore give a good estimate of the species presence in the study sites. Further studies of this system should however consider to census *C. cunicularius* during their activity peak during another year than the census of *A. bimaculatus*, to increase the possibility to detect both species. The population size of *A. bimaculatus* depends mostly on its host's population size the previous year, why it is advisable to census *C. cunicularius* first.

Since the beetle needs a dense population of *C. cunicularius* for a successful reproduction (Cederberg, 2003) it is likely that larger areas of connected and suitable sand habitat would be preferred for both species. My data support this assumption as the presence of the beetle was correlated with sub-patch size and as no sub-patch categorized as small had any presence of *A. bimaculatus*. In the sites where *A. bimaculatus* were found, the area of sand cover was almost three times higher than in the areas where the beetle was absent. As survey-time per area was the same for all sites, this did not have an effect on the result. Even if the beetle does not exist in metapopulations, larger habitats may have a higher probability of becoming colonized by individuals and for established populations to survive (Hanski, 1998). For a species with the relatively low dispersal ability (Notini, 1942; Cederberg, 2003) and high habitat specificity (Lönnell & Edelsjö, 2004) of *A. bimaculatus*, the size of the habitat may be even more vital than for other species.

A. bimaculatus was present more often in sites where the sand was finer, while most sites without the beetle were dominated by medium- or large-grained sand. It has been stated before that they need fine-grained sand (see Cederberg, 2003; Lönnell & Edelsjö, 2004), but this is the first study showing this correlation. The presence of *A. bimaculatus* in fine-grained areas may be due to *C. cunicularius*' use of sand as substrate when building their brooding nests (Lönnell & Edelsjö, 2004). If this is the only factor tying the beetle to sandy habitats, the absence of *A. bimaculatus* from sites with *C. cunicularius* must be explained by other variables than grain size. Sand temperature was only relevant for the presence of *A. bimaculatus* when different sub-patches were compared. At the habitat level no such relationship could be detected. This suggests that the likelihood of missing the species at a study site, due to the ground being too cold, can be disregarded. The higher presence of the species in the warmer areas within a habitat implies that this is an important variable for their activation and that the habitat is not regarded as homogeneous. As the temperature of the sand varies with time and was measured during different days (but no correlation with date was detected), these findings cannot be taken as absolute proof of this link.

The number of *S. caprea* within the bees' foraging area did not affect the presence of *A. bimaculatus*. It is possible that *C. cunicularius* is not as heavily dependent on the surveyed sallow species as previously believed. The bee can also utilize a number of other *Salix* species as a food source, as well as other early-flowering genera (Müller & Kuhlmann, 2008). Therefore, the studied areas may have had enough pollen from other sources for the bee colonies to survive on. It is likely that the numbers of *S. caprea* are not a limiting factor as long as there are some additional pollen supplies. Another possibility for a lack of effect is that the 350 meters used as a limit for the bees foraging range is not a valid distance to investigate this relationship on. The lack

of strong correlation between date of the sawfly tree surveys and number of *S. caprea* found suggest that the prolonged survey period did not affect the result.

This study shows that it is more likely to find *A. bimaculatus* in locations with less dense tree cover, as suggested by previous authors (Lönnell & Edelsjö, 2004). At most sites where the species were present the basal area was below five m²/ha, indicating few large trees around the habitat. *A. bimaculatus* is dependent on warm weather conditions in the early spring, and too many trees close to the sand habitat lead to shadowed conditions and colder microclimate (Lönnell & Edelsjö, 2004). It is suggested that moderate numbers of trees help to create optimal conditions for *C. cunicularius* by giving stability to their nests via the root network (Lönnell & Edelsjö, 2004) or for *A. bimaculatus* by giving protection from the wind and thereby warmer microclimate (Frycklund, pers. com.). These theories could not, however, be evaluated by this study.

If *A. bimaculatus* populations function as sub-populations of a metapopulation it would be expected that the distance between suitable habitats should affect the presence (Schneider *et al.*, 2003; Moilanen, 2004). Since the beetle is thought to be a poor disperser (Notini, 1942; Cederberg, 2003) it is likely that dispersal limits which areas becomes colonised. Today we do not know much about the dispersal behaviour of this species. It is information that is much needed when determining the minimum number of sub-populations needed and the maximum distance between populations for the survival of the species. The quality of the landscape in between two sites might also have an effect on the colonization probability of the sites (Tischendorf & Fahrig, 2000). If the sand areas in between two sites would help improve the degree of connectivity between them, in theory, the negative effect of a long distance would be balanced by a large sand area. In this study no such effects could be detected. The data did not show a correlation between beetle presence and the distance between sites. The summarised area of habitat between a site and the nearest known population did not affect the occupancy probability. Neither was the interaction of distance and amount of habitat significantly correlated to the presence of the beetle. This lack of correlation does not mean that *A. bimaculatus* cannot be studied in a metapopulation context. It may be that the measured variables do not describe the species dispersal pattern in a correct way.

Solitary bee species has been studied in the context of metapopulation ecology earlier (Steffan-Dewenter *et al.*, 2002) and the spatial structure of their foraging and nesting sites showed to be important for their foraging pattern. If *C. cunicularius* function as living in metapopulations, it is probable that *A. bimaculatus* also has this dynamic. The possibility for *A. bimaculatus* to use phoresy for dispersal can result in that populations are more connected then they seem when focus is only on the beetle's active dispersal behaviour. If phoresy is in fact used, the dispersal pattern of *A. bimaculatus* would be close to the same as for *C. cunicularius*. And *C. cunicularius* are likely to be good dispersers. Presence of the beetle at islands and other areas hard to colonize for a species with limited flight ability could be one sign of this ability, interesting to investigate in the future. This type of dispersal behaviour could mean that the limited range of *A. bimaculatus* would be explained by other factors than the examined here. The possibility of both species living in metapopulations intervened in each others' is interesting and should be further investigated in the future. The

frequency with which *C. cunicularius* individuals move between sub-populations and to what degree the triangulins are carried between sub-patches are factors that are then important, to understand the dynamics of *A. bimaculatus* populations.

At most sites a high activity of sand associated hymenopterans could be seen. Only less than a third of the study sites had presence of *C. cunicularius*, in comparison with that more than half of the sites had other sand associated hymenopterans. The relationship between the presence of *A. bimaculatus* and sand associated hymenopterans should be further investigated. Several of these species can be parasitoids on *C. cunicularius* (Lönnell, in press) and thereby be competing with *A. bimaculatus* for brooding nests. Most other sand associated hymenopterans are competing with *C. cunicularius* for suitable sand habitat patches. Both groups might therefore affect *A. bimaculatus* negatively by reducing the size of their host population.

Management suggestions

Today most management activities for this species are aimed at restoring the habitat of the species to an early succession stage with plenty of bare sand (Lönnell, in press). This is done by digging holes in the ground, by creating slopes with fine-grained sand, and by cutting down trees. That cutting down trees is a good management activity is supported by this study, as *A. bimaculatus* primarily existed in habitats with surrounding forest of less than five m²/ha. Another important factor for the presence of the species is sand grain size. The habitat could be improved at sites if measures were taken so that sub-patches were dominated by fine- to medium-grained sand. This study shows that using sand living hymenopterans as indicator species' for habitat suitable for *A. bimaculatus* could be successful. For more than 80 % of the sites the occurrence of this guild correctly predicted the presence of *A. bimaculatus*. Using such an indicator guild can make the survey for suitable habitats easier, since the beetle itself can be hard to detect as its active time span is short.

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APPENDIX 1 – Field protocol

| | | |
|---------------|---------------|---------------|
| Locale name: | X-coordinate: | Y-coordinate: |
| Date: | Start time: | End time: |
| Date shallow: | | |

| | | |
|-------------|-------------|----------------------|
| No. sawlow: | Basal area: | Other hymenopterans: |
| Comments: | | |

[illegible]