The effect of landscape structure and habitat composition on the presence of the threatened parasitic sand-living beetle *Apalus bimaculatus* (Coleoptera: Meloidae)

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Abstract—*Apalus bimaculatus* (Linnaeus) (Coleoptera: Meloidae) is a beetle currently managed for conservation in Sweden. The species inhabits at-risk ephemeral and patchily distributed sandy habitats. However, little is known about its ecology and the factors important for its distribution. We censused 158 discrete sand patches within 31 potential sites for *A. bimaculatus* and examined which environmental variables predicted the probability of finding the beetle. *Apalus bimaculatus* was found at 17 sites, its presence at sand-patch scale was positively correlated with sand-patch area, sand temperature, and medium-sized sand grains. Although the beetle is assumed to be a parasite on the solitary bee, *Colletes cunicularius* (Linnaeus) (Hymenoptera: Colletidae), presence of the bee was a very weak predictor for *A. bimaculatus*, while other sand-living Hymenoptera were a strong predictor. At site-level scale, the beetle was positively correlated with total amount of sandy habitat and presence of sand-living Hymenoptera. Our study suggests that management strategies for this species should not consider sandy habitats equally. Rather, management efforts should focus on maintaining sites with larger total sandy areas, creating larger sand patches with medium-grained sand and a high degree of sun exposure. We also highlight that biotic interactions between the beetle and sand-living Hymenoptera are still poorly understood but potentially important for successful *A. bimaculatus* management.

Résumé—*Apalus bimaculatus* (Linnaeus) (Coleoptera: Meloidae) est un coléoptère de Suède qui fait actuellement l'objet d'une gestion spéciale pour assurer sa conservation. L'espèce habite des milieux sablonneux éphémères qui sont à risque et sont répartis en taches. On connaît cependant peu son écologie et les facteurs déterminants de sa répartition. Nous avons inventorié 158 taches sablonneuses discrètes réparties dans 31 sites potentiels à la recherche d'*A. bimaculatus* et déterminé quelles variables environnementales permettaient de prédire la probabilité de la présence du coléoptère. *Apalus bimaculatus* a été retrouvé dans 17 sites et sa présence à l'échelle de la tache sablonneuse est en corrélation avec la surface de la tache sablonneuse, la température du sable et la présence de grains de sable de taille moyenne. Bien qu'on présume que le coléoptère est un parasite de l'abeille solitaire *Colletes cunicularius* (Linnaeus) (Hymenoptera: Colletidae), la présence de l'abeille est une faible variable prédictive de la présence d'*A. bimaculatus*, alors que la présence d'autres hyménoptères arénicoles est une forte variable prédictive. À l'échelle des sites, la présence du coléoptère est en forte corrélation avec la quantité totale d'habitats sablonneux et la présence d'hyménoptères arénicoles. Notre étude laisse croire que les stratégies de gestion de cette espèce ne doivent pas tenir compte de tous les habitats sablonneux de manière égale. Au contraire, les efforts de gestion devraient être concentrés sur le maintien des sites avec les plus grandes surfaces de zones sablonneuses et la création de taches sablonneuses plus grandes avec du sable de granulométrie moyenne et une forte exposition au soleil. Nous soulignons aussi que les interactions biotiques entre le coléoptère et les hyménoptères arénicoles restent encore mal comprises, bien qu'elles soient potentiellement importantes pour une gestion réussie d'*A. bimaculata*.

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Introduction

Degradation of natural landscapes has led to habitat loss and fragmentation that can negatively affect the species that inhabit these areas (Fahrig 1997, 2001; Marzluff and Ewing 2001; Baker and Harris 2007). Life history traits such as high specialisation, poor dispersal, patchy distributions, and/or an aggregated and seasonal appearance are linked to increased extinction risk when landscapes are degraded (McKinney 1997; Reinhardt *et al*. 2005). Thus, the ecology and distribution of a species form the foundation of its threat assessments – one example being the International Union for Conservation of Nature red list (International Union for Conservation of Nature 2012). In Sweden, 804 insect species are currently classified as threatened (vulnerable, endangered, or critically endangered) on the national red list, with the most common criteria for a taxon being included is that the distribution is small, largely fragmented, or only exist in few localities (Gärdenfors 2010). The species that specialise in ephemeral habitats, prone to change because of natural successional processes, are vulnerable to local extinctions; especially if these species are poor dispersers (Warren 1991; Ranius 2000).

One such species is the European beetle *Apalus bimaculatus* (Linnaeus) (Coleoptera: Meloidae) (Lundberg 1995; Fauna Europaea 2011). *Apalus bimaculatus* inhabits open sandy areas (Lönnell and Edelsjö 2004), a habitat that has declined in Northern Europe following changes in land use where a reduction in grazing and forest fires has promoted re-vegetation of these areas (Emanuelsson 2009). Unless active vegetation removal is carried out, this habitat usually becomes over-grown and unsuitable for sand-living beetles within a decade (Lönnell and Edelsjö 2004; Lönnberg and Jonsell 2012). Thus, the habitat specialisation of *A. bimaculatus* has resulted in this species having a highly fragmented distribution in central and southwest Sweden (Cederberg 2003, Lönnell and Edelsjö 2004; Lönnell 2005). Because of this, its current "near threatened" status on the Swedish red list is expected to be upgraded to vulnerable if the current habitat of $<2000\,\mathrm{km}^2$ continues to degrade through succession (Gärdenfors 2010). It is currently extinct in Finland (Lönnell 2010) and Estonia (eBiodiversity 2012).

Apalus bimaculatus resides in the subterranean nests of its host species from the larval to the adult stage, where it feeds on food collected by the host (Notini 1942). It is believed that *A. bimaculatus* in Sweden is dependent on the solitary bee species *Colletes cunicularius* (Linnaeus) (Hymenoptera: Colletidae) for its persistence (Cederberg 2003). This bee also uses sandy habitats for its breeding chambers (Larsson and Tengö 1989), which are aggregated in sub-populations and located several cm below the surface (Lönnell and Edelsjö 2004); however, it is not clear if the beetle also uses other sand-living bee species as hosts (Notini 1942; Frycklund 2006).

Because the adult beetle is a poor flyer (Notini 1942; Lönnell and Edelsjö 2004), it has been suggested that *A. bimaculatus*, as with other species belonging to the family Meloidae, use phoresy – *i.e.*, where one organism "hitches a ride" on another for the purpose of dispersal (Bologna and Pinto 2001; Saul-Gershenz and Millar 2006; Bologna *et al.* 2008). Support for this comes from Notini (1942), who showed that *A. bimaculatus* behaviourally orient to substances secreted from *C. cunicularius*. The dispersal of *A. bimaculatus* may therefore be closely linked to the dispersal of *C. cunicularius*, further increasing the vulnerability of this species to the presence of a healthy host population. Thus, the distribution and dispersal ability of *A. bimaculatus* are likely to be linked to the distribution and dispersal behaviour of its host, suggesting that landscape variables influencing the distribution of *C. cunicularius* (or other sand-living bee species) are important for predicting the presence of *A. bimaculatus*.

To combat threats to *A. bimaculatus* populations in Sweden, the Swedish Environmental Protection Agency has established a species conservation management program (Lönnell 2010). Since 2004, management has focused on habitat restoration by removing vegetation from sandy habitats in the distribution area of the beetle. The aim is to expose the sandy substrate and to reduce the shading to increase the available warm habitat that encourages establishment or persistence of the beetle. These actions are based on national expert knowledge, but little is actually known about the species ecology and behaviour, its dispersal and habitat requirements, as very few studies have been carried out in Northern Europe (but see Notini 1942; Lönnell 2010). The current management of the species therefore relies on a limited amount of information of the species requirements.

Thus, the objective of this study is to examine which landscape and habitat factors influence the distribution of *A. bimaculatus* in the core distribution area in Sweden. Environmental data were measured at two different scales to investigate both landscape/habitat and microhabitat variables. We used environmental variables that current management work is based on to evaluate the correlation of these variables to the presence of *A. bimaculatus*. Additionally, we gathered data on the presumed host bee *C. cunicularius*, related sand-living Hymenoptera and environmental variables potentially important for the bees. This was to investigate possible correlations with environmental variables important for the host and the presence of *A. bimaculatus.*

Methods

Species and environmental censuses

We gathered environmental and species presence data from surveys of 31 sites that had previously been surveyed for *A. bimaculatus* (in 2004, 2005, and 2006; Fig. 1A). All sites had areas of sand substrate that consisted of several discrete sand patches of potentially suitable habitat (Fig. 1B). Because the census work was labour-intensive and involved careful ground searching, we could not survey all sand patches when a site contained >15 sand patches. Thus, we selected between 5 and 15 (number in proportion to available patches) of the sand patches from within those available at each site. The selection of patches was done to maximise the variation of the environmental variables measured. This resulted in a total of 158 sand patches censused. The species census work was carried out at a constant time per unit area rate of ~1 minute/m^2, during which each selected sand patch was visually screened for beetle and bee individuals present at the sand surface or in the air. Sand patches covered by snow or water at the time of the census were not censused.

Apalus bimaculatus adult activity occurs mostly between early March and mid-April (Lönnell and Edelsjö 2004), and *C. cunicularius* is one of the first bees to emerge during the Swedish spring (Peakall and Schiestl 2004) and is active mainly between March and May (Notini 1942). In addition to *C. cunicularius*, there are at least 10 other Hymenoptera families (including members from all families within Apoidea and some taxa within Vespoidea, Chrysidoidea, and Specoidea) that are commonly encountered in the sand habitats during this period. All censuses for *A. bimaculatus*, *C. cunicularius*, and other sand-living Hymenoptera were carried out between 1 April and 30 April 2009 (Notini 1942; Lönnell and Edelsjö, 2004). All census dates were noted and used in the analyses to help account for temporal relationship with species emergence. In all patches, the number, sex, and status (alive or dead) of all *A. bimaculatus* were noted. For *C. cunicularius*, we noted the number present in the patch. Other sand-living Hymenoptera were recorded only at the site scale, where we noted their presence or absence. All censuses were done between 0900 and 1800 hours. The study sites located furthest to the south (at slightly warmer latitudes) were censused first, to increase the likelihood of finding emerging beetles. To reduce the likelihood of false absences, we did not census during days with cold (<12 °C) or rainy weather, as the mobility of the beetles and bees are reduced at lower temperatures (Esch 1988; Jian *et al.* 2003).

Habitat and landscape variables

We collected data on environmental variables that are considered important for the study species on two different scales, the sand patch and the site scale. In addition to amount and distribution of habitat, we measured other habitat features. It is believed that the beetle's activity is positively correlated to sand temperature, so factors that shade the ground (*e.g.*, tree density around a habitat) may affect the habitat suitability for the species (Lönnell and Edelsjö 2004) and were therefore measured. As adult bees collect pollen and nectar primarily from *Salix* Linnaeus (Salicaceae) species within 350 m of their nest chamber (Wesserling 1996, cited in Gathmann and Tscharntke 2002), with *Salix caprea* Linnaeus suggested being the most important food resource for Swedish populations of *C. cunicularius* (Cederberg 2003), information on this was gathered.

Fig. 1. Layout of the study areas: with (A) a map of Sweden and a closer map of the studied area showing the 31 study sites, and (B) a landscape view showing the distribution of the sand habitats and a close-up of one of the sites consisting of several patches of sand. Lines connecting the circles symbolise the measured distance between the study site and the nearest known *Apalus bimaculatus* population. The circles around the site (grey line representing 350 m radius) show the area used for measuring the amount of sand habitat and number of *Salix caprea* (black dots) outside the habitat.

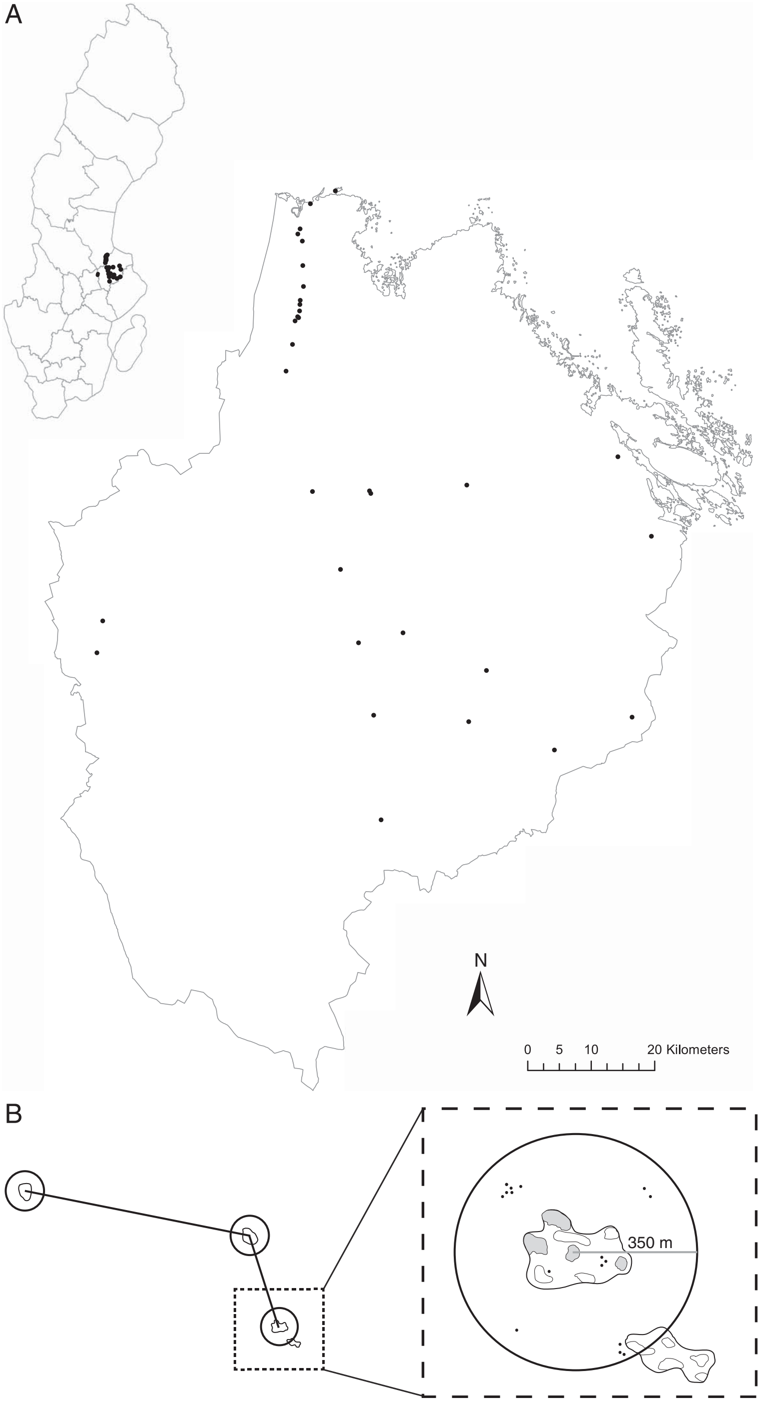


Table 1. Descriptive statistics for independent environmental variables used in analyses of site and sand-patch features affecting the presence of the beetle *Apalus bimaculatus.*

Variable	Mean	SE	*n*
Site level			
Area sand within 350 m (m^2)	19 000	4170	30
Shadowing trees (m^2/ha)	4.5	1.14	31
Distance to closest *A. bimaculatus* population (m)	4472	784	30
Salix caprea within 350 m (number)	60.5	8.16	31
Sand-patch level			
Sand patch size (size category 1–4)	2.16	0.053	158
Sand grain size (mm)	1.98	0.054	132
Sand temp nest depth (°C)	9.92	0.342	157
Sand surface temp (°C)	20.17	0.623	157

In the sand patches we collected the following data: (1) sand-patch size: we placed each patch into four categories based on visual estimates of the sand patch – *i.e.*, small ($<1\,m^2$), medium ($1–10\,m^2$), large ($10–100\,m^2$), or very large ($>100\,m^2$); (2) sand grain size: the average size of surface sand particles in the surveyed sand patch was categorised using the Atterberg grain size scale (Wiklander 1976) as reference: fine-grained (0.06–0.20 mm), medium-grained (0.2–0.6 mm), and coarse-grained (0.6–2.0 mm) sand; (3) sand temperature: sand temperature was measured at two depths with a digital thermometer ($\pm 0.1\,°C$) at the centre of each sand patch: (a) surface temperature (at bee and beetle emerging level), by placing the thermometer close to the surface of the sand without exposure to direct sun, and (b) breeding chamber level temperature, at a depth of 11.5 cm; and (4) the presence of the beetle, and the bee *C. cunicularius.*

On the site-level scale we used five environmental variables: (1) area of bare sand (available habitat) within 350 m of the habitat center (estimated from orthophotos); (2) tree shade, to estimate tree shade of the habitat we used an angle gauge counting all trees within sight from a center point (Eid 2001); this gives the basal area factor, which is an estimate of the local tree density; (3) Distance to nearest sandy habitat with known *A. bimaculatus* population. We calculated the amount of sandy habitat and the distances on the site scale using digital maps and orthophotos (with ArcGIS 9.2). One of the sites could not be detected on the orthophotos and this resulted in a reduced sample size of 30 for these variables; (4) *Salix* abundance: we counted the number of mature *S. caprea* (one of the major food resources for *C. cunicularius*) within the 350 m foraging distance of the centre of the surveyed sand patches between the 1 and 15 May, a period when the trees are easy to recognise; and (5) the presence of the beetle, *C. cunicularius* and other sand-living Hymenoptera. All variables and their measurements are in Table 1.

Statistical analyses

We used generalised linear mixed models (binomial GLMMs with logit link in R using the “lme4” package; R Core Development Team 2011) to evaluate the strength of support for the environmental variables on predicting the presence of *A. bimaculatus* at the sand-patch level ($n = 158$) and the site level ($n = 31$). Because of the large number of potential environmental predictors on beetle presence, and hence the very large number of potential combinations of these predictors, we used an information theoretic model-averaging approach to account for model uncertainty in model selection and parameter estimation (Burnham and Anderson 2002). Because of the possibility that sand temperature and grain size might have an optimal value in the middle of measured extremes, we tested for nonlinear relationships between presence of the beetle and these variables by included quadratic terms in the model selection procedure. None of the predictor variables, included in the final models, were strongly correlated when tested using pairwise correlations, with the exception of the temperature measures in the sand-patch level analyses; thus, we only included the temperature data from the nest chamber after initial examination showed it was the better predictor of the two measures.

For model prediction at sand-patch level the site identity was included as a random factor, with fixed factors being combinations of (1) date of census, a Julian date starting on 1 April; (2) sand temperature in °C at a depth of 11.5 cm (approximate chamber depth where the beetles live); (3) presence of the host bee; (4) sand patch size (range 1–4, small–very large); and (5) sand grain size (range 1–5, fine-grained–coarse-grained). Both sand patch size and sand grain size were treated as continuous variables in the analysis. To consider interactions between environmental variables, we also included all two-way interactions between sand grain size, temperature and patch size. For model predictions at the site level, the following explanatory variables were examined: (1) presence of host bees, (2) area of bare sand (in m^2) within 350 m radius of the center of the site, (3) presence of other sand-living Hymenoptera, (4) density of shadowing trees (m^2/ha), (5) number of *S. caprea* trees within 350 m of the centre of the site, (6) distance (m) to the nearest known population of *A. bimaculatus*, and (7) the date of the census. To consider interactions between environmental variables, we also included interactions between the distance to nearest *A. bimaculatus* population and number of *S. caprea*, density of shadowing trees and area of bare sand. For both sets of analyses, we created a balanced candidate model set and ranked the models using Akaike's information criteria corrected for sample size (AIC_C), and used AIC differences (ΔAIC_C) and AIC_C weights (w_i) to determine the strength of support for each model (Burnham and Anderson 2002) using the R package "MuMIn" (Barton 2012). In addition, we assessed the strength of support for explanatory variables by calculating their relative variable importance weights; for this the sum of AIC weights for each model that contains a particular variable was calculated, with one being the maximum value and indicating strong support. All models within ΔAIC_C 10 of the best model were used for generating model-averaged parameter estimates (using the zero method) and relative importance weights of variables (Burnham and Anderson 2002). Means are presented with standard errors.

Results

Of the 31 sites surveyed, we found *A. bimaculatus* in 17, *C. cunicularius* in nine, and other sand-living Hymenoptera in 18 sites. The mean number of *A. bimaculatus* individuals found per site was 2.8 ± 0.53 (range 1–9), and for *C. cunicularius*, 4.2 ± 1.48 (range 1–15).

At the sand-patch scale, there was evidence that the presence of *A. bimaculatus* was correlated with higher sand temperature at the depth of the bee nests and also linked to areas with an intermediate size of sand grain (with some support for these relationships being quadratic rather than linear). Also, larger sand patches and the presence of sand-living Hymenoptera other than *C. cunicularius* were strong predictors for the presence of the beetle (Figs. 2, 3; Tables 2, 3). The negative interaction between sand grain size and patch size (Table 2; Fig. 2) strongly suggests that large grain sizes are poor habitat for the beetle regardless of patch size; while any aversion the beetle has to the smallest grain size is overcome in larger patches. Beetles were not found on any of the sand patches that belonged to the smallest size category ($<1\ m^2$). We found no support for a positive correlation between the presence of *C. cunicularius* and *A. bimaculatus* (Tables 2, 3).

At the site scale, there was evidence that the presence of the beetle was positively related to the amount of sandy habitat within a 350 m radius, and the presence of other sand-living Hymenoptera (Fig. 4; Tables 2, 4). *Apalus bimaculatus* was present in 83% of the 18 locations containing sand-living Hymenoptera other than *C. cunicularius*. As with the sand-patch scale analysis, we did not find any strong evidence for a link between the presence of the host bee and the presence of the beetle. *Apalus bimaculatus* was never detected at the sites where only *C. cunicularius* and no other Hymenoptera were noted, and was detected at 17% of the sites where no Hymenoptera at all were observed (in total 12 sites). At the site scale, tree cover, local *S. caprea* availability

Fig. 2. Estimated probability of finding *Apalus bimaculatus* within a sand patch (quadratic function from the highest ranked model prediction, Table 3) within the five categories of grain size (1 = finest to 3 = coarsest). Each line represent a simulation with the sand patch size set to 1 (minimum), 2.16 (average), or 4 (maximum), the three levels are included to show the dependence of sand patch area when considering effect of grain size. Observed data are presented as mean probability of occurrence (number of occurrences divided by total number of observations) ± SE for each sand grain size category.

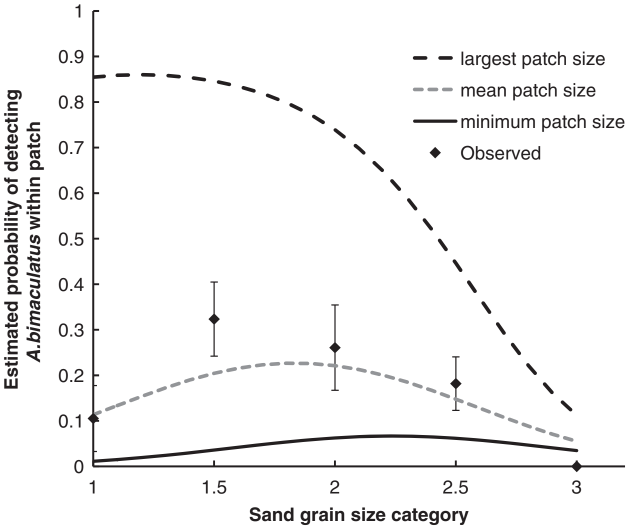


Fig. 3. Estimated probability of finding *Apalus bimaculatus* within a sand patch (quadratic function from the highest ranked sand-patch model prediction, Table 3) within the sand temperature range of the study (1.5–21.0 °C). Grain size category has been set constant to the most common value of 2.5. Sand patch size category is set to 1 (minimum value), 2.16 (mean value), or 4 (maximum value). Observed data is presented as mean probability of occurrence (number of occurrences divided by total number of observations) ± SE for categories of 15 consecutive temperature observations, except for the last category containing only the seven remaining highest temperature observations.

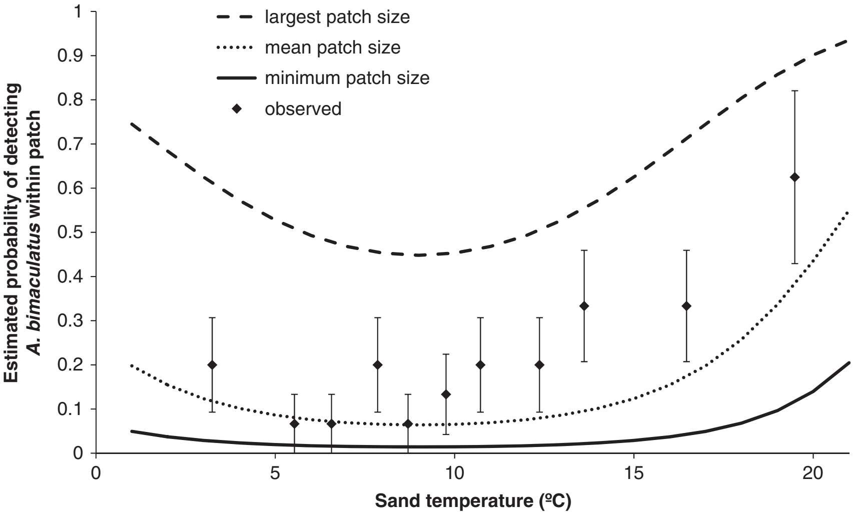


Table 2. AIC-weighted relative variable importance weights for predictor variables and model-averaged parameter estimates included in models (Tables 3, 4) when estimating the probability of finding *Apalus bimaculatus* at the site or sand-patch level.

Model parameters	Relative variable importance	Model-averaged estimate
Site level		
Main effects		
Intercept	na	−3.12 (1.72)
Presence of sand-living bees	1.0	3.6 (1.3)
Area of sand habitat within 350 m	0.85	0.0003 (0.0002)
Distance to nearest *Apalus* population	0.24	<−0.00001 (0.0001)
Census date	0.21	−0.0001 (0.005)
Area of shadowing trees	0.21	−0.01 (0.08)
Presence of *Colletes cunicularius*	0.19	0.03 (0.30)
Salix caprea abundance within 350 m	0.19	−0.0003 (0.005)
Interaction terms		
Distance × Area sand	0.04	<0.00001 (0.0001)
Distance × *S. caprea*	0.01	<−0.00001 (0.0001)
Distance × area trees	0.01	<0.00001 (0.0001)
Sand-patch level		
Main effects		
Intercept	na	−11.73 (6.18)
Patch size	1.0	2.91 (2.03)
Sand grain size	0.95	6.16 (4.12)
Sand temperature	0.78	−0.12 (0.21)
Census date	0.52	0.026 (0.017)
Presence of *C. cunicularius*	0.49	0.53 (0.32)
Interaction terms		
Sand grain size^2	0.65	−1.19 (0.68)
Patch size × sand grain size	0.57	−0.83 (0.50)
Sand temperature^2	0.51	0.01 (0.006)
Sand grain size × sand temperature	0.22	−0.02 (0.03)
Patch size × sand temperature	0.17	0.001 (0.01)

Variable relative importance weights of main effects terms of >0.9 suggest strong support for the parameter, 0.5–0.9 moderate support and <0.5 weak or no support. Because interactions and quadratic terms are contained in fewer models than main effects terms, the relative importance strengths are lower and should only be compared with other interactions and not with main effects.

AIC, Akaike's information criteria.

and distance to the nearest *A. bimaculatus* population had very little support as predictors of *A. bimaculatus* (Tables 2, 4).

Discussion

Several studies have emphasised the importance of considering spatial (Huxel and Hastings 1999; Steffan-Dewenter *et al.* 2002; Morris 2003) and temporal (Warren 1991; Mac Nally 2008) dynamics in ecosystems for conservation planning. For species living in patchily distributed habitats, also the quality of existing patches are important (Warren 1991; Gyllenberg and Hanski 1997). The current management activities for *A. bimaculatus* are aimed at modifying the vegetation in the habitat of this species to an early successional stage with plenty of bare sand (Lönnell 2010). While our results support the current management practice of increasing the area of sand habitats, they also indicate that particular factors should be considered when undertaking this practice; namely grain size and the temperature of the sand. Our results suggest that the importance of environmental factors should be weighed depending on the scale at which habitat restoration is viewed (Tables 2–4).

Table 3. AIC-ranked set of candidate models ($\Delta\text{AIC}_c < 2$) for predicting *Apalus bimaculatus* presence at the local sand-patch level.

Rank	Model	K	AIC$_c$	ΔAIC$_c$	w_i
1	patch + grain^2 + temp^2 + date + patch*grain	8	116.82	0.0	0.03
2	patch + grain^2 + date + bee + patch*grain	7	117.26	0.43	0.03
3	patch + grain^2 + bee + patch*grain	10	117.67	0.84	0.02
4	patch + grain^2 + date + patch*grain	9	118.08	1.26	0.02
5	patch + grain^2 + temp^2 + date	9	118.22	1.40	0.02
6	patch + grain^2 + bee	10	118.22	1.40	0.02
7	patch + grain^2 + temp^2 + patch*grain	7	118.34	1.52	0.02
8	patch + grain^2 + date + bee	5	118.44	1.62	0.02
9	patch + grain^2 + temp^2 + bee + patch*grain	7	118.57	1.74	0.01
10	patch + grain^2 + temp^2 + date + bee + patch*grain	9	118.62	1.79	0.01
11	patch + grain^2 + temp^2	8	118.71	1.88	0.01
12	intercept only	2	137.9	21.2	0.0

Variables included: sand temperature (temp), sand-patch size (patch), sand-grain size (grain), census date (date), presence of *Colletes cunicularius* within the sand patch (bee).

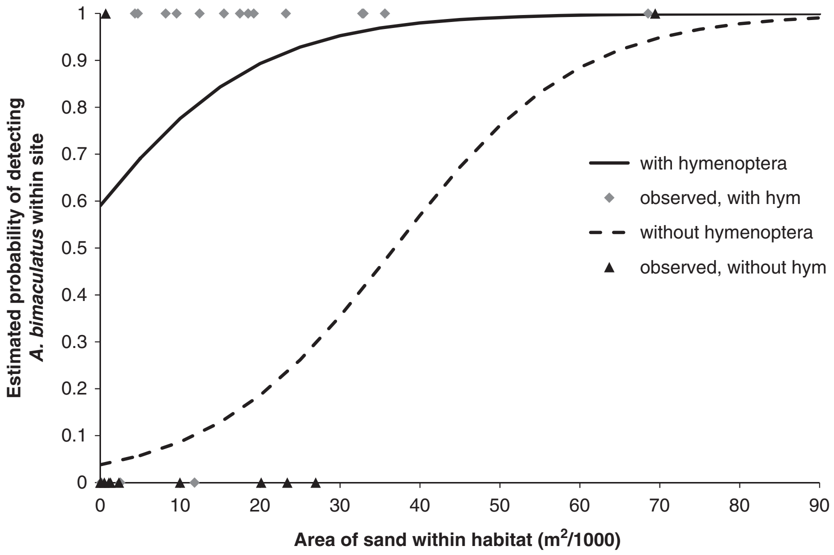
(+) indicates additive effects and (*) interactions.

Where quadratic terms are shown, the model includes the corresponding linear term (*e.g.*, temp^2 = temp + temp^2).

Site identity was included as a random factor in all models.

K, number of parameters; AIC$_c$, Akaike's information criterion with sample size correction; ΔAIC$_c$, difference in AIC$_c$ relative to the highest-ranked model; w_i, Akaike weight (note that the sum of w_i does not equal 1 because not all models are shown).

Fig. 4. Estimated probability of finding the beetle *Apalus bimaculatus* at a site (quadratic function derived from the highest ranked model prediction, Table 4) with different sand area (0–90 000 m^2) within the habitats. The lines represent simulations either with (—) or without (- - -) sand-living Hymenoptera present in the habitat. The raw data are included as habitats with (grey diamonds) or without (black triangles) sand-living Hymenoptera.



Landscape factors correlated with species presence

The number of *A. bimaculatus* that we found in this study was low and never exceeded nine individuals in any sand patch and the number of *C. cunicularius*, ≤15 individuals/habitat, which responds to ~0.08 individuals/100 m^2, was lower than has been found in other studies

Table 4. AIC-ranked set of candidate models ($\Delta AIC_c < 5$) for predicting *Apalus bimaculatus* presence at the site level.

Rank	Model	K	AIC_c	ΔAIC_c	w_i
1	hym + sand	3	27.44	0.0	0.25
2	hym + sand + tree	4	29.91	2.46	0.07
3	hym + sand + date	4	30.09	2.65	0.07
4	hym + sand + salix	4	30.10	2.66	0.07
5	hym + sand + bee	4	30.11	2.67	0.07
6	hym + sand + dist	4	30.12	2.68	0.07
7	hym	2	31.48	4.03	0.03
8	hym + sand + dist + sand*dist	5	32.32	4.88	0.02
9	hym + date	3	32.36	4.91	0.02
50	intercept only	1	37.04	9.59	0.0

Variables included: presence of sand-living Hymenoptera other than *Colletes cunicularius* (hym), presence of *C. cunicularius* (bee), estimation of shadowing trees (tree), sand area within 350 m (sand), *Salix caprea* within 350 m (salix), distance to nearest known population of *A. bimaculatus* (dist), and Julian census date (date). Also included were interactions for salix, tree, and sand with dist.

(+) show additive effects and (*) show interactions.

K, number of estimated parameters; AIC_c, Akaike's information criterion with sample size correction; ΔAIC_c, difference in AIC_c relative to the highest-ranked model; w_i, Akaike weight (note that the sum of w_i does not equal 1 because not all models are shown).

(Larsson and Tengö 1989, although this was within an extremely favourable habitat).

The presence of *A. bimaculatus* is believed to be positively correlated to fine-grained sand (Cederberg 2003; Lönnell and Edelsjö 2004), but the exact grain fractions suitable for the species is not known (Lönnell 2010). We found that contrary to this belief, the sand patches with the finest-grained sand were not the ones most likely to contain the beetle, instead fine-medium, medium, and medium–large-grained sand had the highest probability of containing *A. bimaculatus* (Fig. 2). One reason for *A. bimaculatus* preferring sand patches with intermediate grain fractions could be that this sand composition is preferred by Hymenoptera for their brooding chambers (Lönnell and Edelsjö 2004). The effect of grain size on beetle presence seemed to be dependent on the size of the sand patch, with small patches only being moderately suitable if also the optimal grain size was present. The largest grain size category was not correlated with the presence of the beetle even if the patch was large, indicating that this substrate size is not suitable for nesting sites (Fig. 2).

The size of the sandy habitat area appears important for *A. bimaculatus* (Tables 2–4, Figs. 2, 3). At both scales, the area of sandy habitat shows a strong positive correlation with the presence of the beetle. At the sites where *A. bimaculatus* was found, the area of sand cover was more than three times higher than in areas where the beetle was absent (27 500 ± 6560 m^2 versus 7700 ± 2720 m^2). A larger patch will likely offer a higher number of nests for *A. bimaculatus* to parasitise and a possibility to sustain larger populations (Cederberg 2003). Larger areas of suitable sand habitat may be preferred by sand-living Hymenoptera, as large sand patches offer many nesting sites from the heterogeneity of the habitat (Larsson and Tengö 1989). Overall, the larger habitats probably have both a higher probability of becoming colonised by individual beetles and Hymenoptera (Matter 2009), and for established populations to survive (Hanski 1998). The reason that the effect of patch size is of a high importance for the existence of *A. bimaculatus* can be from the presence of a minimum habitat threshold, where a high-quality patch in terms of grain size composition cannot fully compensate for a too small area (but see Fleishman *et al*. 2002; Bauerfeind *et al*. 2009; Heisswolf *et al*. 2009). For a species such as *A. bimaculatus* with assumed low dispersal ability (Notini 1942; Cederberg 2003), and high habitat specificity (Lönnell and Edelsjö 2004), the size of the habitat may be even more vital than for other species, as large habitats may both be able to hold larger populations and have a higher buffering capacity when environmental changes occur (Verboom *et al*. 2010).

The probability of finding *A. bimaculatus* increased with the temperature of the sand at the depth of the bee nests (Fig. 3). The higher presence of the species in the warmer areas implies that nest temperature is an important variable for beetle populations and that patches may be of different quality in terms of temperature suitability (Sorvari *et al*. 2010). Ground temperature is highly dependent on sun exposure and the melting of snow cover early in the season and these factors are likely to vary between the patches depending on the direction and position of the slopes.

The support for a positive correlation between the presence of *A. bimaculatus* and other sand-living Hymenoptera was higher than that with *C. cunicularius*. This result could either be because we may not have timed the censuses equally well for the beetle and its host, or *A. bimaculatus* also uses other Hymenoptera as hosts.

The possibility for *A. bimaculatus* to use phoresy may mean that beetle populations are more connected by dispersal than they seem when the focus is solely on the beetle's active dispersal behaviour. If the beetle uses phoresy, the dispersal pattern of *A. bimaculatus* would be similar to the dispersal ability of their hosts (Schwarz and Koulianos 1998; Krishnan *et al*. 2010). Therefore, to fully understand the dispersal capacity of *A. bimaculatus* and their ability to reach and colonise new habitats, we need to understand more about both the interaction between the beetle and the species that it parasitises and the dispersal behaviour of the host.

Implications for conservation management

To decrease the threat to *A. bimaculatus* from a reduction of available habitat, we suggest the following should be considered in management of the species. When restoring sandy areas we recommend that the main aim should be to create a few sand patches, each with an area of at least $>10\,\mathrm{m}^2$ and ensure that they have intermediate grained sand with high sun exposure. In addition to fulfilling the habitat demands of the species short term, large patches are likely to hold larger populations and increase the long-term survival of populations (Berggren *et al*. 2001; Rosin *et al*. 2011). Our study shows that for a successful management of this threatened species, it is important to acknowledge that sandy habitats are not equal in quality and restoration work is best focused in areas where physical properties are suitable for the species both on a small and large scale.

Additionally, this study shows that other sand-living Hymenoptera other than the host *C. cunicularius* might be used as indicator species for habitat suitable for *A. bimaculatus*. In more than 80% of the sites, the occurrence of this group of insects correctly predicted the presence of *A. bimaculatus* in the habitats searched. This indicates that there may be additional and unknown hosts among sand-living Hymenoptera that may be important for the beetle's persistence and that new knowledge in this area would be very useful. Also our findings show that using sand-living Hymenoptera as an indicator group can make the habitat suitability surveys for the beetle easier, since the beetle itself can be hard to detect due to its short timespan as an active adult.

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