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Movement patterns, nesting preferences and population estimates of the digger wasp *Bembix rostrata*


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Table of content

1 Introduction and problem

In this master thesis, ecological characteristics of the coastal digger wasp *Bembix rostrata* and the implications for species conservation are investigated. The results of this study intent to contribute to a more extensive biodiversity conservation management in the threatened coastal dune area.

1.1 European coastal dunes

i. *Situation*

Coastal dunes are a unique biotope of high ecological importance. In Belgium, 30 to 50% of all Flemish plant and animal species can be found, although most of them not exclusively, in the dunes. In neighbouring countries, the number of typical dune species is even higher. The geographical isolation and the younger age of the Belgian dunes has restricted the number of species able to reach the dunes (Bonte and Provoost, 2004).

This valuable ecological community is structured by an aeolian dynamic that creates an ongoing disturbance through sand displacement. In some places, sand movement leads to erosion, while fresh sand is deposited elsewhere. This can cause a continuous movement of the dunes: shifting or 'walking' dunes (Bonte and Provoost, 2005).

The resulting dynamic landscape is responsible for a rich variety of habitat types. These are formed following a gradient of decreasing wind activity and increasing soil stabilization by vegetation (Provoost et al., 2004). According to this gradient, the dune landscape evolves from embryonic shifting dunes with scarce soil development to blond dunes with European Marram grass vegetation (*Ammophila arenaria*) over grey dunes and eventually to scrub and woodland vegetation (Houston, 2008). This heterogeneity in habitats makes that dune regions have a very high biodiversity. In the grey dunes (fixed coastal dunes with herbaceous vegetation), a highly unpredictable environment and a microclimate that can reach desert-like conditions are present. The surface temperature can be more than 60°C and the soil can dry out to a depth of 20 cm. This harsh situation only allows specially adapted species (habitat specialists) to persist in this unique biotope. Surface walking species, for example tiger beetles, developed special adaptation strategies to deal with the challenging conditions: decreased summer activity, a burrowing lifestyle, a larger body size, long hairy legs... These adaptations come with the cost of a slower development, which makes them extra sensitive for extinctions due to changing conditions (Bonte et al., 2006; Bonte and Provoost, 2005; Provoost et al., 2004).

Plant adaptations consist of very long roots and root networks to extract water from meters below the surface, leaf morphology suited to avoid desiccation, like succulent leafs, and resistance to sand burial, such as fast growth and darkness tolerance (Bonte et al., 2006; Bonte and Provoost, 2005; Provoost et al., 2004).

Next to the effects on biodiversity, the shifting of the sand keeps the soil calcareous. In this way, the soil counteracts acidification due to nitrogen deposition (Bonte and Provoost, 2005).

ii. *Human influence and deterioration*

Since its origin, the dune area has been strongly associated with humans, mainly for agricultural purposes. Livestock grazing and harvest of trees and shrubs were common practices, therefore grey dunes occupied a large portion of the coastal dunes. To protect their living grounds from becoming covered with sand, people tried to stabilize the sand masses through planting them. Despite this, humans formerly failed in entirely controlling the dunes, and often human settlements were completely buried by sand (Bonte and Provoost, 2005; Provoost et al., 2004).

Until the First World War, large dynamic dune areas still remained. However, in the last 100 to 150 years, increasing urbanisation, the growing tourism and the stabilisation of dunes by coastal defence works (groynes, bunkers) have led to a decrease in dune area (e.g. Bonte and Provoost, 2004, 2005). During the 20th century, the Belgian coastal dune area decreased from about 6000 to 3800 ha (Provoost and Bonte, 2004). The areal decrease has also led to a homogenisation of the remaining dune parts: in the small remaining patches, the wind dynamics are not able to support the constant sand disturbance present in the larger and unfragmented parts. The supply of fresh beach sand has stopped, and this will allow soil stabilisation by European Marram grass, moss or shrubs, leading to fixation of the dunes. The agricultural practices disappeared, and this change in land use additionally permitted a transition to a landscape of a later successional stage. The open dynamic system has been transformed to a closed, stabilised landscape (Bonte and Provoost, 2005; Maes et al., 2006; Provoost and Bonte, 2004; Provoost et al., 2011).

Additional causes of the deterioration of the dunes are the increased tourist and recreational pressure, colonisation by exotic species, collapse of the rabbit population due to the myxomatosis epidemic and deposition of atmospheric nitrogen. A last contributing factor is climate change: a longer growing season and increased CO_2 concentration possibly can enhance the succession. An advanced plant growing season by macroclimatic warming may lead to a microclimatic cooling, which has already led to the decrease of several spring-developing, thermophilous species like butterflies. Another effect of climate change will be the increased erosion and the alteration of the groundwater regime due to sea level rise (Bonte and Provoost, 2004; Maes and Bonte, 2006; Provoost et al., 2011; Vestergaard, 1991; Wallisdevries and Van Swaay, 2006).

At present, the typical dynamic dune landscape remains only in Southwestern France and Northern Denmark. Instead of the original continuous dune belt along the European coast, all that remains at other places are smaller and more isolated patches. In Belgium, there are still remnants of this landscape in the Westhoek, Flanders biggest dune reserve, but they are in danger and demand management action to be maintained (Agentschap voor Natuur en Bos, 2012; Bonte and Provoost, 2005).

As mentioned previously, the lack of constant disturbance leads to a more homogenous landscape dominated by shrubs, instead of the very diverse environment with different specific habitat types in different phases of succession. Especially the early successional and most dynamic stages (shifting dunes, blond dunes, young dune slacks) are suffering from these changes, and it are exactly these areas that are host to the most unique biodiversity. When it comes to invertebrate fauna, grey dunes are the most endangered dune habitat (Bonte and Provoost, 2005; Provoost et al., 2004; Provoost et al., 2011).

Patch size and connectivity between different patches are two crucial factors for the viability of species, and both are affected by the recent changes. Fragmentation of the dune region, even only by scrubs, leads to the decrease of the number of typical invertebrate species within each isolated patch, because colonization or exchange events between subpopulations in a metapopulation depend on connectivity. Next to this, extinction rates are related to patch size. Life in small isolated patches is thus threatened in two ways: a reduced colonization and an increased extinction rate (Bonte et al., 2002; Bonte et al., 2003; Maes and Bonte, 2006). Small patches will also be prone to significant edge effects, with atypical species entering and leading to a more instable community (Bonte et al., 2002; Provoost et al., 2004).
It is obvious that all these factors will lead to the decrease, or even the loss, of the biota associated with the specific dune habitat types.

iii. *Conservation*

There is awareness that the protection of the remaining dune area and dune quality is important. Sea dunes of the Atlantic, North Sea and Baltic coasts are included in the EU Habitats Directive and grey dunes are considered to be a priority habitat, implicating that they deserve special conservation attention. Grey dunes are ‘fixed coastal dunes with herbaceous vegetation’ according to the CORINE biotope classification (European Commission DG Environment, 2013).

In case of the fragmented dune landscape, passive protection of the remnants of the dunes will not be sufficient nor will it be efficient. Because of the relatively small size, an active management is required. In Belgium, the use of large ungulates (Scottish Highland cattle, donkeys, Konik horses and Shetland ponies) to restore the disturbance is chosen as a management tool. The animals remove redundant biomass, disperse seeds through defecation and their trampling disturbs the sand and creates conditions similar to those originating from natural sand dynamics (Bonte et al., 2006; Lamoot et al., 2005; Provoost et al., 2004). The use of grazers is an ecosystem-based measure, aiming to restore the original ecological processes. In case of the coastal dunes, the management departs from the idea that re-introducing disturbance (however not coming from the same source: wind versus trampling by grazers) will be sufficient to restore and preserve the heterogeneous habitats and the biodiversity associated with it, and stop the succession to a homogenous shrub landscape (Lamoot et al., 2005; Maes et al., 2006). The effect of grazers is thought to increase the habitat quality, by soil trampling which stimulates the aeolian dynamics, and to increase the connectivity between the fragments by removal of dense vegetation. This will be beneficial for the invertebrates that are restricted to blond and grey dunes. However, grazers prefer nutrient-rich grasslands, avoid scrubs and only use other vegetation plots as passage to their grazing habitat. In this way, the expected connectivity increase is dubious (Maes et al., 2006). Furthermore, trampling effects in stabilised dune landscapes can be very high, and can lead to the destruction of moss patches and below-ground developing eggs (Maes et al., 2006).

Thus, it is clear that not every species will benefit from an ecosystem-based approach. Although grazers create comparable conditions to wind disturbance, they also have a negative impact on certain species. The trampling and the grazing on specific places and plants can harm species with well-defined requirements, and, if no additional measures are taken, sometimes even drive them to extinction. Maes and Bonte (2006) for example demonstrated that two ground-dwelling spiders (*Alopecosa fabrilis* and *Xysticus sabulosus*) and a butterfly species (*Issoria lathonia*) were negatively affected by grazing. These species will need a more species-specific management approach, which can complement the ecosystem-based approach. Species conservation in addition to ecosystem conservation can make nature management more effective.

However, since it is rather time and resource consuming to investigate the ideal conservation plan for every separate species, this option is not realistic. A possible solution to this problem is the use of an umbrella species. This species should represent the requirements of many other species in the same biotope, so the protection of one species will benefit several others (Fleishman et al., 2001). Incorporating umbrella species into biotope restoration plans and nature management seems a good way to face conservation and management problems (Noss, 1990; Ranius, 2002). Through incorporation of the requirements of deliberately chosen specialized species into management plans (multi-species approach), the chance of successfully conserving a wider range of co-existing species would greatly increase (Maes and Van Dyck, 2005).

1.2 The digger wasp *Bembix rostrata*

The species investigated in this master's dissertation is the Common European Sand Wasp *Bembix rostrata* (Linneaus, 1758), a dune specialist. *B. rostrata* is the largest European digger wasp species and can be up to 2.5 cm large, which makes the study organism easy to observe. The species is threatened in most European countries. In Belgium, there are still a few inland populations (Geel, Kalmthout, Hamont-Achel and Oud-Turnhout), but most populations can be found at the Belgian coast, mainly in the grey dunes of nature reserve the Westhoek (Bonte, 2005).
The decrease in grey dune area has restricted the amount of suitable habitat for the species. In addition to this, *B. rostrata*, like many other ground-dwelling species, is negatively affected when grazers are present in the nesting site (Bonte, 2005).

The behaviour of *B. rostrata* has already been studied for a couple of aspects, such as homing, courtship behaviour, chemical communication and orientation (e.g. Schöne and Tengö, 1981, 1991; Schöne et al., 1993; Tengö et al., 1990). The organism has a high potential mobility, but is thought to stay very loyal to its original patch. The species nests in loose sand, although to be able to construct the nests, the soil should also provide sufficient solidity (Schöne and Tengö, 1981). To reach these conditions in a coastal dune landscape, a constant disturbance of the terrain is needed to allow an appropriate area of bare sand to remain available for nesting.

Despite this present knowledge, there are still important gaps to fill. A thorough investigation about habitat use and patch loyalty of the species is still missing, while such species-specific information is indispensable for conservation purposes. Knowledge about connectedness of and exchange between different (sub)populations can be used to obtain a metapopulation model and provide insight into methods to secure the species' survival. Moreover, an accurate description of the habitat preferences for nest building is of high importance to conserve and manage the appropriate sites. Estimates of population size can be useful to inspect whether the species is thriving, remaining constant or declining. With all this acquired information, it should be possible to get more insight into the optimal conservation measures for this valuable species.

Research on this species will add complementary information to earlier research on other typical dune invertebrates, and expand the list of possible conservation indicators for coastal dune grasslands in Belgium (Maes et al., 2006). This research fits into the Terrestrial Ecology Unit of Ghent University, where biodiversity conservation is an important topic, and several investigations about dune management and preservation have already been performed and will be executed in the future, often focussing on arthropod species.

2 Objectives

The general objective of this research is to obtain insights into how the conservation of *Bembix rostrata* can be improved. Knowledge about habitat use, dispersion of the species and the connectivity of different (sub)populations is a crucial factor in conservation management. The acquired information, which focuses on one highly adapted species, will complement the knowledge on dune conservation based on site management measures.

To achieve this general purpose, firstly, it will be investigated if *B. rostrata* has a preference for nesting on spots with a specific vegetation type, by making a comparison of the vegetation in the immediate surroundings of the burrows and the vegetation at random points in the investigation area. A potential preference to nest on a slope will be examined in the same manner.
Srba and Heneberg (2012) observed that for five closely related sphecid species, microhabitat selection was determined by vegetation cover and slope, in addition to abiotic factors. These abiotic factors include light intensity, temperature, moisture and soil compactness. The limited area of suitable habitat can play a role in the presence and the density of nest aggregations.

Secondly, the distance between the different holes of the same female, and the distribution of the burrows (scattered, clustered) will be determined. Spatial arrangements of populations can be the reflexion of intra- and interspecific interaction within communities (Holldobler, 1976; Levings and Traniello, 1981). This information can be of great help when determining conservation measures. The digger wasp is a central-place foraging species with gregarious nesting, so a clustered distribution is the most plausible hypothesis.

The third part of the work involves the investigation of site fidelity to the nesting plot, in other words if there is exchange between different patches. Knowledge about dispersal is crucial when determining the threats and the conservation possibilities.
The hypothesis investigated here assumes that, although the species is highly mobile, with adult females having a homing capability as far as three kilometres (Tengö et al., 1990), they remain very loyal to their original patch and their activity will be concentrated around the home area. In the homing experiment done by Tengö et al. (1990), a few individuals were however found again in alien nesting sites, so a small dispersion rate can be expected.

Lastly, this research will consist of a determination of population size: one of each separate study area and one of all study plots together. The amount of burrows per female will also be defined. This information will be important to define the level of decrease of and threat to the species. These data may be useful for future research as well, to compare the future sizes with the size found in the present investigation, and to evaluate the evolution of the species and the effectivity of the management measures.

3 Material and methods

3.1 Study organism

i. *General information*

The Common European Sand Wasp *Bembix rostrata* (Hymenoptera, Crabronidae) is a solitary wasp living in a sandy habitat, with a distribution in Central Asia and from Northern Africa to Southern Scandinavia. The species is active between the end of June and the beginning of September, and has a gregarious nesting pattern. The adults feed on nectar, mainly of Sea holly (*Eryngium maritimum*) (T'Jollyn F., personal communication) and Ragwort (*Senecio jacobaea)*. In the nest aggregation, females dig unicellular burrows to deposit their eggs (one burrow at a time, with a maximum of five nests per season) and feed their larvae with hoverflies, horseflies and robber flies. When the female leaves the nest, the entrance is closed with a sand plug (Ballesteros et al., 2012; Bonte, 2005; Larsson and Tengö, 1989; Nielsen, 1945; Peeters et al., 2004).

B. rostrata is one of the most threatened invertebrates of the European grey dunes due to a decrease in area of the suitable biotope (van der Meer, 2002). In Belgium, they are additionally threatened by anthropogenic disturbances: trampling by grazers and human recreation (Bonte, 2005).

The activity of the insects is positively related to sun irradiation and ambient temperature. There is no activity below 22° C (Evans and O'Neill, 2009), but especially insolation has an important effect: when the irradiance lowers, the level of activity drops instantly. Females are less sensitive to these climatic variables than males and are found hunting even during a moderate cloudiness. A possible explanation for this observation is that females have to continue the feeding of their larvae. For male individuals, this factor does not apply, as they do not have this external drive (Schöne and Tengö, 1981, 1992; Tengö et al., 1990).

ii. *Behavioural stages and seasonal activities*

In the article of Schöne and Tengö (1981), the different stages of the behavioural activity of the wasps were described. The seasonal activity can be divided into three different phases: the male swarming/copulation phase, the male swarming/female digging phase and the female nest building phase.

Male swarming/copulation phase

Male digger wasps start to emerge from the end of June, and immediately start patrolling the nesting area. Frequently, male aggregations are formed around a certain spot, where they start digging intensely into the sand. In this manner, they unearth conspecifics, which are situated 3 cm below the surface. The activity is non sex-specific, and indicates that the males are attracted by a specific evaporated odour, that penetrates through the soil and is sustained by the sun-heated sand (Schöne and Tengö, 1981). Larsen et al. (1986) described that animals also produce a faint buzzing sound when digging their way to the soil surface.

Normally, females emerge one to five days after the first males. When a female is unearthed by the males in the digging aggregation, she is seized by the nearest male, who tries to copulate. The male tries to carry the female away in flight, while the other males form a flight aggregation to escort them. The escorting males compete to replace the carrying male, and their attempts can lead to the pair falling down (Schöne and Tengö, 1981).

Not every female is discovered by the digging aggregation. However, even when she is not unearthed, the patrolling males will probably detect her within minutes (Schöne and Tengö, 1981).

Newly emerged females quickly start to dig small holes (sleeping holes). Only the virgin female is receptive to the males, digging (mated) females will reject approaching males (Schöne and Tengö, 1981).

Male swarming/female digging phase

About two to six days after their emergence, females start to build nesting burrows. At the same time, the intensity of the male patrolling is attenuated to a more gentle patrolling. Males often rest and sunbathe, and often appear to have a (not defended) home area (Schöne and Tengö, 1981).

Male animals sometimes land close to a female and inspect her by antennation (touching alternately with left and right antenna). One female can gather up to five males. When the female flies off or is forced to fly by a pouncing male, the males will form small flight aggregations to follow at short distance (within 10 cm). Nearby males that are passed by, will often join the flight. During the flight, males try to catch the female, but mostly females in the digging phase will reject males (Schöne and Tengö, 1981).

Female nest building phase

The females start to bring flies to their nests four to eight days after their emergence. From that moment on, brood care activities form the main occupation of the population. The normal lifespan of males is normally about two to three weeks, so during this phase, the number of males starts to decrease. The female activity can last until the beginning of September (Schöne and Tengö, 1981).

iii. *Orientation and homing behaviour*

Like many other Hymenoptera, digger wasps orientate by means of a sun compass for longer distances and with landmark orientation for the vicinity (Chmurzynski, 1967). Using the digger wasp *Philanthus triangulum* as his study object, Niko Tinbergen contributed enormously to the knowledge in this field (Tinbergen, 1932; Tinbergen, 1935; Tinbergen and Kruyt, 1938; Tinbergen and van der Linde, 1938 as in Tengö et al., 1990).

With experiments to test the homing rate when displacing *B. rostrata,* either in an open or a closed box, to an unknown or a familiar environment, it became clear that this species also uses a path integration system under certain conditions (Schöne et al., 1993).

Tengö et al. (1990) demonstrated that the homing efficiency increases during the female's life, from emerging females being worst, to digging females, to provisioning females being the best homers. In homing time as well as in the ability to cover large distances, provisioning females are superior. This can be explained by gained experience, but the need to return to the nest to take care for the offspring can provide an additional stimulation. In male individuals, the age did not influence the homing efficiency. The overall male homing frequency is comparable to the frequency of digging females.

The homing capacity of *B. rostrata* can add up to 2500 to 3500 m. The capacity to operate over distances of more than a kilometer can be necessary to collect a sufficient amount of appropriate food (Tengö et al., 1990).

3.2 Study area

The research was executed in the Westhoek nature reserve (De Panne, Belgium), a dune reserve extending for 345 ha and situated close to the French border (Figure 1 (a)). The Westhoek is the oldest Flemish nature reserve and is managed by the 'Agentschap voor Natuur en Bos'. It is part of 'the Dunes and Forests of De Panne', the biggest connected dune area of the Belgian coast (Agentschap voor Natuur en Bos, 2012).

Within the Westhoek, we collected the data at four sites situated in the 'Krakeelduinen en Duinhoek' (Figure 1 (b)), a grey dune area (best habitat type for *B. rostrata*). According to the colour of the tags given in that area, the sites were labelled yellow, green, blue and pink (Figure 1 (c)). This part of the Westhoek is inaccessible for large grazers, which is beneficial for *B. rostrata*, as mentioned earlier. The connections between the plots were of different order: some seemed well connected, without visible barriers, others were separated by a dense forest, which was thought to be a severe barrier. In another case, a dense shrub layer was present, with only a small sandy passage (Table 1).

Table 1: Distance and barriers between the four study plots.

		Yellow	Green	Blue	Pink
Green	Distance (m)	60	/		
	Barriers	No barriers	/		
Blue	Distance (m)	225	70	/	
	Barriers	Shrubs	Shrubs	/	
Pink	Distance (m)	300	150	115	/
	Barriers	Forest	Forest	Forest	/

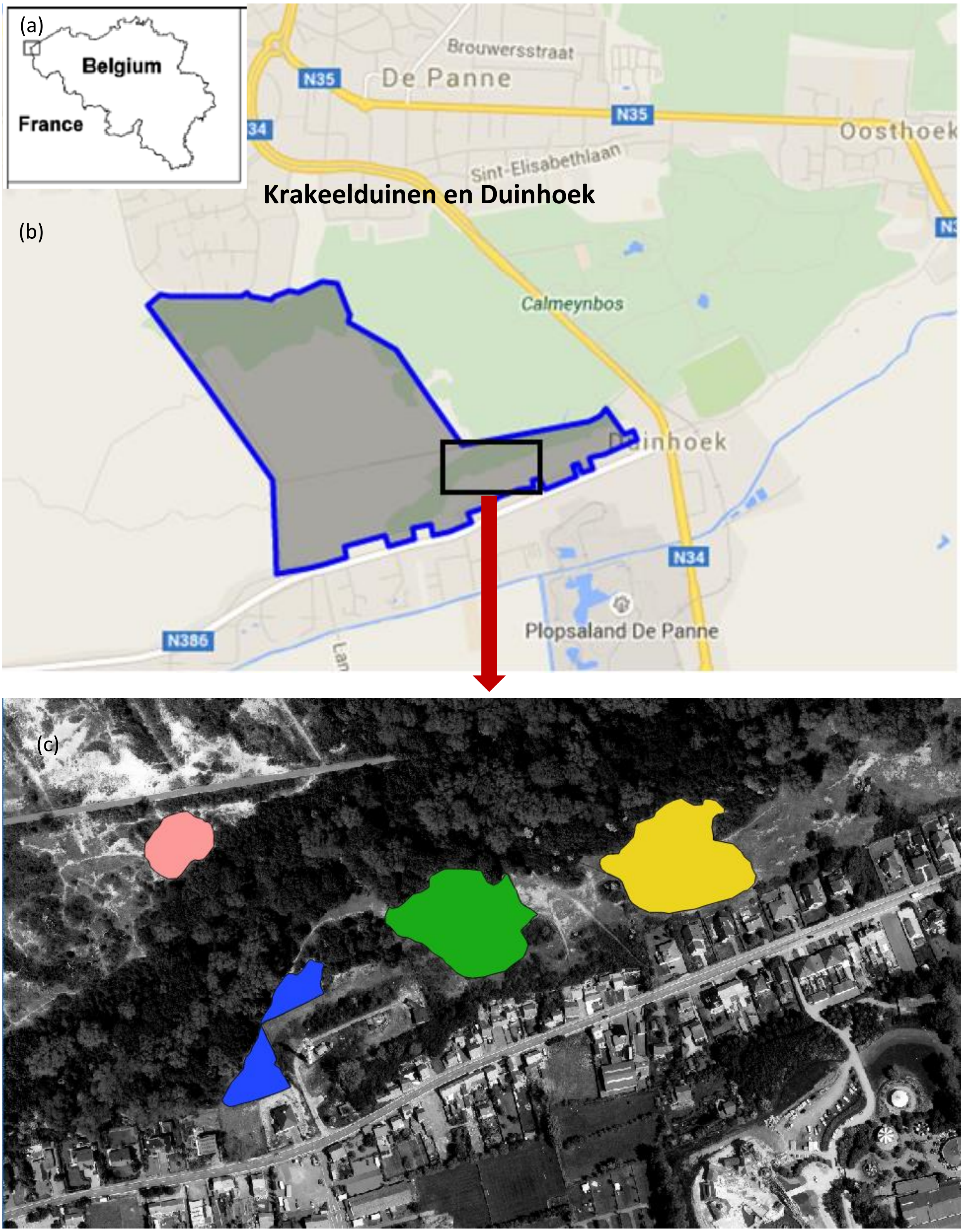

Figure 1: The location of (a) nature reserve the Westhoek (reproduced from Maes and Bonte, 2006); (b) 'Krakeelduinen en Duinhoek' (www.google.be/maps, 2015); (c) the four study plots; the colour of the plots accords to the colour of the tag given in that area.

3.3 Fieldwork

The fieldwork took place between the 23th of July and the 4th of September 2014. During this period, the plots were monitored on 25 days with acceptable weather conditions (no rain, temperature at least 18°C). Every morning, the observations started in a different plot to avoid the time of the day being a confounding factor. The daily monitoring took place between approximately 10h30 and 16h30. At the time that the research took place, all males in the population were already dead, therefore we were sure every individual caught was female. The behaviour of the males and females can be rather distinct, so only taking females into account can potentially effect the results.

i. *Capture and marking*

While walking around and observing in the different areas, every individual wasp encountered was caught with a hand net (0.35 m diameter). The wasps were manually removed from the net. With the help of a forceps, a coloured tag with a unique number was glued on the back of their thorax, whereby care was taken not to damage or glue the wings, otherwise the wasps will be left immobile and handicapped (unfortunately, this happened in three cases). The colour of the dot indicated the area where the wasps were found (the different colours were yellow, green, blue and pink). After being marked, the wasps were released.

ii. *Recapture*

Every time a digger wasp was noticed, an attempt was made to catch it. In case the animal was marked, the number and the colour were noted. Otherwise, it was marked as described above. Sometimes, we were not capable to catch a (flying) wasp, although it was still possible to read the marking (always the colour, seldom the number). In case only the colour was identified, the observation was saved nonetheless, however it was not possible to use these data for the determination of the population size. Solely for the determination of habitat fidelity, these data will be used. Every observation was entered in iObs (23th until 29th of July 2014) or in ObsMapp (30th of July until 4th of September 2014) and sent to the website waarnemingen.be.

iii. *Marking the burrows*

In case a wasp was noticed coming out of a burrow in the sand, or digging in the sand, the burrow was marked with a flag (small wooden stick with writable scotch tape, upon which a number was written with a waterproof marker). The flag was placed approximately 10 cm to the right of the entry of the burrow. In this way, the place was indicated, even if the hole was made invisible by sand cover later on.

The position of each nest was entered in iObs/ObsMapp. In addition, all nests marked before the 11th of August were also positioned with a GPS (Trimble), which was more accurate than the location system in iObs/ObsMapp (a few cm's versus approximately 25 meters).

The marked burrows were also photographed. In that way, it was not only possible to save the accurate position of the burrows, and their relative positions, but also to analyse the vegetation surrounding the burrows.

The intention to look for nests independent of wasp observations and activity did not succeed, because it was really difficult to distinguish nests of sand wasps and nests of other sand dwelling invertebrates like tiger beetles. Another obstacle was that digger wasps often closed and spread sand over their nest after delivering a prey, so the nest became invisible again. For these two reasons, we only marked the nests when we saw the immediate proximity and activity of a wasp.

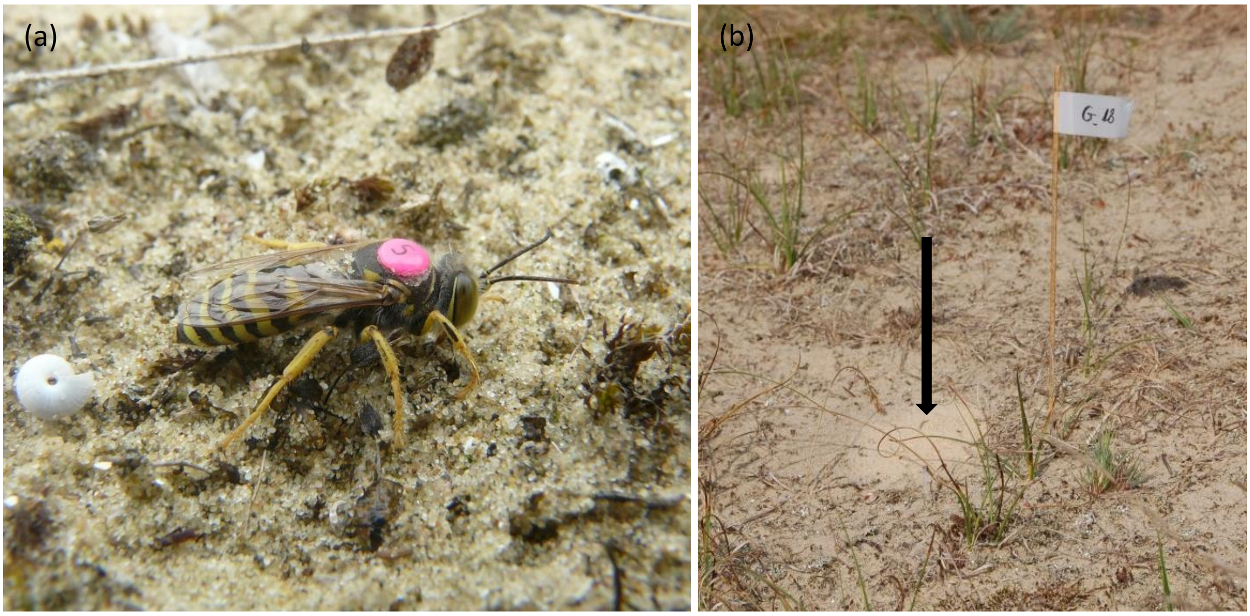

Figure 2: (a) *Bembix rostrata* with marking; (b) marked burrow, the arrow indicates the position of the burrow.

3.4 Analysis of results

i. *Microhabitat preferences*

The vegetation in the immediate surroundings of the burrow was analysed using the pictures of the marked burrows. In a radius of 25 cm around the burrow, the percentages of moss, (other) plants and sand were determined visually. Also from random points in the plots, a vegetation analysis was made in the same manner.

To test if *B. rostrata* has a preference for a specific vegetation type, the differences in vegetation between burrow and random points were compared. The focus in this test was laid on the proportion of sand. The proportion of sand surrounding the burrows was normally distributed, but the proportion at random points was not. Transformations did not succeed to make it normal. Therefore, a non-parametric Mann-Whitney-Wilcoxon test was chosen. This analysis was performed in R version 3.1.2 (R Development Core Team, 2014).

We also tested if there is a preference for nesting on a slope. A two-way contingency table was constructed and a χ^2-test with 1 degree of freedom was executed.

ii. *Spatial distribution of the burrows*

Based on the data in iObs/ObsMapp and the data collected with the GPS, it was possible to visualise the location of the burrows in a GIS (QGIS 2.8.1, QGIS Development Team, 2015)). Firstly, we coupled the names of the burrows to the corresponding coordinate, what was often rather difficult and complex, because of missing or less suitable photographs (see discussion, section ‘Remarks about the investigation and fieldwork’).

After (most of) the burrows and the coordinates had been coupled, it was possible to measure the distances between the different burrows of the same individual female.

To determine the spatial arrangement of the burrows, a nearest neighbour analysis was executed in QGIS. In this analysis, it was not possible to take the area of the plots into account. Instead of analysing the data in a well-defined area, a minimum enclosing rectangle around the data points was used. To overcome this problem, extra points were inserted at the corners of each plot. This way, the analysis used a bigger area to make the calculations. This approach however included the four non-existing burrows at the corners. The solution to this problem was to make a combination of the analysis without the area component (to determine the observed mean distance between the burrows) and the analysis with four extra nests (to determine the expected mean distance in the study plot).

iii. *Site fidelity*

Based on the number of observations of the wasps, it was possible to determine the frequency that wasps were observed in their own plot or in a foreign site.

iv. *Population sizes*

The population sizes were estimated using the Schnabel Method. This is an expansion of the Peterson estimator, in which it is possible to handle more than two samples of capture and marking (Larsen, 2014).

The formula assumes a closed population. Because the male individuals were already eliminated from the population and the normal lifespan of a female wasp accorded to the timespan of the investigation, the assumption of no mortality is made. Emigration and immigration are extremely small (see results, section 'Site fidelity'), and no new animals will be born before the next summer. All this together allowed the assumption of a constant population size, and a closed population to be made.

A second assumption is that the samples are random, and lastly, that all animals have the same capture probability within a sampling occasion (Alcoy, 2013).

Formula to determine population size:

$$\hat{N} = \frac{\sum_{t=1}^{S} C(t) * M(t)}{\sum_{t=1}^{S} R(t)}$$

Formula to determine variance:

$$Variance\,\frac{1}{\hat{N}} = \frac{\sum_{t=1}^{S} R(t)}{\left(\sum_{i=1}^{S} C(t) * M(t)\right)^{2}}$$

with S= Number of samples

C(t)= Total number of individuals caught in sample t

R(t) = Number of individuals already marked when caught in sample t

M(t) = Number of marked individuals in the population just before the current sample

With the estimation of the population size and variance of the reciprocal density, a confidence interval was calculated.

v. *Fecundity*

The reproductive rate was determined as the number of burrows of every individual female.

4 Results

4.1 Microhabitat preferences

i. *Vegetation analysis*

The vegetation in which nests were built significantly differed from those based on random expectations in the study plot. Although there were big individual differences, nests were clearly more surrounded by sand than random points, while the moss proportion was lower (Table 2 and Figure 3).

The Wilcoxon test showed that the surroundings of the nests had a significantly higher proportion of sand than the random points (W=1614.5, p-value=4.06e-7).

Table 2: Surface cover around the burrows and the random points.

	Moss		Plants		Sand	
	Burrow	Random	Burrow	Random	Burrow	Random
Min. percentage	0	0	5	2	5	0
Max. percentage	90	97	60	100	92	98
Median	20	50	20	20	50	15
Mean	23.55	45.63	23.44	24.25	53.01	30.11
Standard Deviation	21.06	28.49	14.08	21.49	18.75	31.46

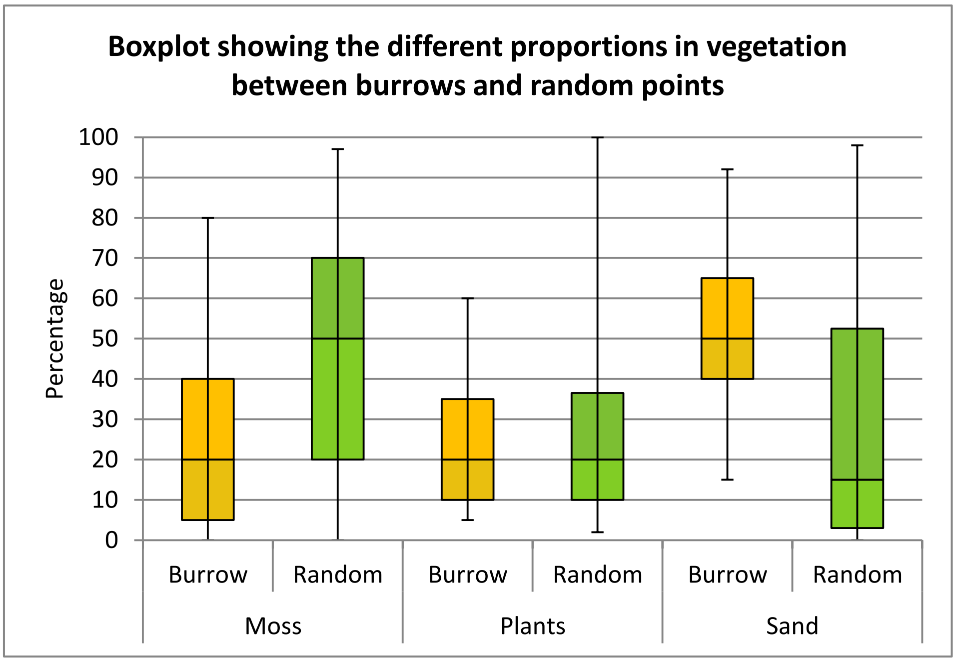

Figure 3: Boxplot visualising the differences in vegetation types between burrows and random points. The error bars indicate the minimum and the maximum value.

ii. *Slope*

The result of the χ^2-test with 1 degree of freedom on the two-way contingency table (Table 3) was highly significant (χ^2-value=12.47, p-value =0.0004). There is a preference to build nests on a slope.

Table 3: Positioning of the burrows and the random points.

	Slope	Flat	**Total**
Burrow	51	26	**77**
Random	30	49	**79**
Total	**81**	**75**	*156*

4.2 Spatial distribution of the burrows

The results of the nearest neighbour analysis indicated a clustering in every plot. The results of this analysis are given in Table 4.

The Nearest Neighbour Index indicates the level of clustering, with a value smaller than 1 suggesting clustering. The smaller the value, the more pronounced the clustering is. The biggest value in this analysis is 0.29, so the clustering is manifest.

Table 4: Results of the nearest neighbour analysis performed in QGIS.

Statistics	Yellow	Green	Blue	Pink
Observed mean distance	2.87	1.94	1.19	0.97
Expected mean distance	10.51	9.22	12.96	3.41
Nearest Neighbour Index	0.27	0.21	0.09	0.29
N	15	25	8	28

4.3 Site fidelity

i. *Recapture within site*

In total, 176 observations were made, 57 marking events included, so there were 119 recaptures. Only two times, a wasp was caught outside the site where it was marked and in these two observed dispersal events, the forest was crossed. The covered distances did not exceed 200 m (Figure 4).

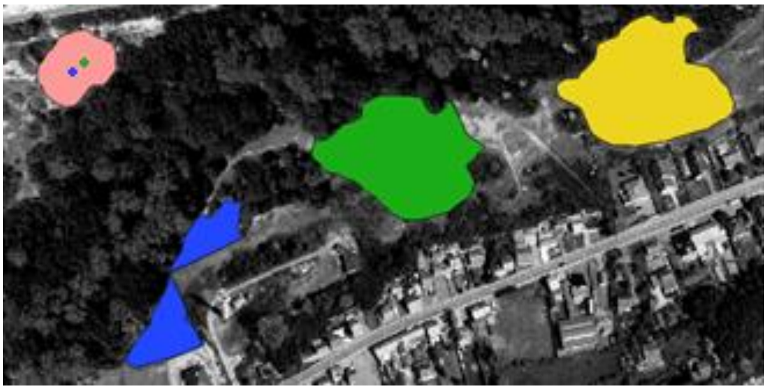

Figure 4: The four fieldwork plots. The blue and the green dot in the pink area represent an individual, marked in the plot with the respective colour, that was observed in the pink area. The blue animal crossed approximately 130 m, the green individual covered a distance of approximately 200 m .

ii. *Distances between different burrows*

In this research, there were 12 females who had at least two observed burrows, and could be used in this analysis. This resulted in only 20 distance measurements. Only in three cases, more than 20 m was covered between two nests (Figure 5). These three cases were all observations of one female, that clearly had a higher spread of her nests than all other observed individuals.

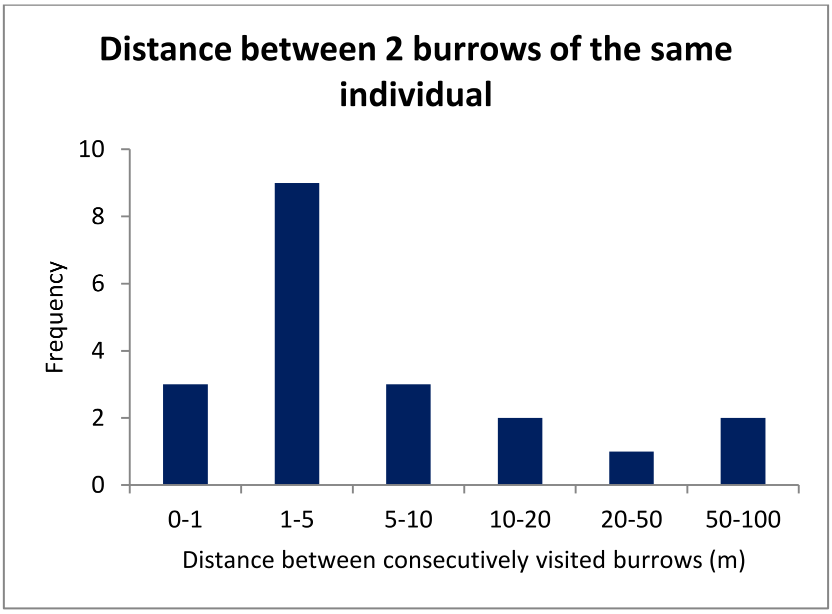

Figure 5: Distance between two consecutive burrows of the same female.

4.4 Population size and reproductive rate

i. *Population estimations*

The female population estimations according to the Schnabel method were N=15 for the yellow plot, N=22 for the green plot, N=7 for the blue plot and N=25 for the pink plot. The total estimated population size over all plots was N=70 (Figure 6).

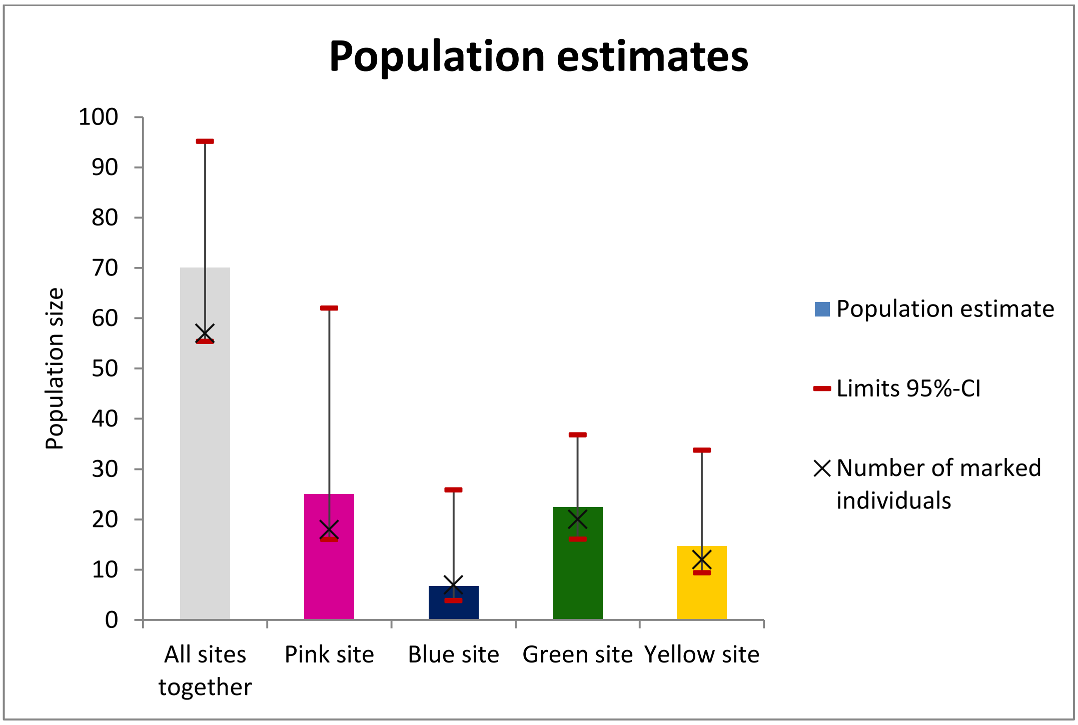

Figure 6: The estimation of the population sizes of the different plots and of the four plots together.

ii. *Number of burrows per individual*

The reproductive rate was determined as the number of burrows per female. From the 57 marked females, there were 36 found to have at least one burrow. From these 36, 24 only had one nest, and only four animals had more than two nests (Figure 7). The mean number of burrows was one per female.

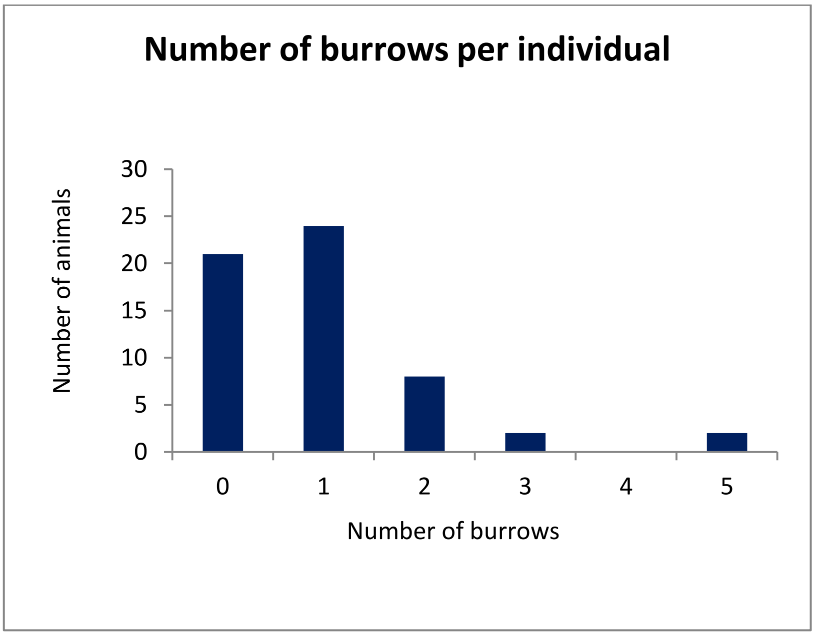

Figure 7: Observed number of burrows of an individual female.

5 Discussion

5.1 Nesting preferences

i. *Microhabitat preferences*

Bembix rostrata shows a clear preference to dig burrows on slopes where a high amount of sand is present.

In this investigation, the minimum proportion of sand that was found was 15%, and the average percentage was 53%. There is also a tendency to nest on slopes. Probably, these specific preferred habitats are the places that meet the requirements for an adequate nest best. To burrow the nests, loose sand is necessary, but the soil also needs enough solidity, and probably a limited amount of plants or moss can grant this (Schöne and Tengö, 1981). On a slope, there can be more exposure to sunlight. However, not every slope where aggregations were found was oriented in the same direction (so not all southward, as would be expected if sun exposure was the determining factor). Possibly, burrows situated on slopes will suffer less from moisture, or perhaps the soil is just looser, which can facilitate the nest building.

ii. *Spatial distribution of burrows*

Spatial arrangements of plant and animal populations can often be a reflexion of intra- and interspecific interactions within communities (Holldobler, 1976; Levings and Traniello, 1981).

In this investigation, we found that the burrows were clustered. The phenomenon of forming dense nesting aggregations seems widespread in burrowing bees and wasps (Evans and O'Neill, 2009).

Alcock (1975) suggested that at least in some lineages of solitary bees, this pattern could represent the first step towards social colonies, because gregarious nesting increases intraspecific interactions between nest building females.

To explain a non-random nesting pattern, several hypotheses can be put forward. The restriction of suitable nesting substrate and/or clustering of resources in a heterogeneous environment can be a critical factor (Brockmann, 1979; Michener, 1969). Non-random nesting can also indicate an antipredator or antiparasite strategy in a selfish herd (Hamilton, 1971), a more efficient way of foraging by hunting together with conspecifics (Creel and Creel, 1995), a decrease of the intra- or interspecific competition (Cushman et al., 1988) or a higher probability of finding a high quality mate through copying behaviour (Nordell and Valone, 1998). Using the presence of conspecifics as indication for patch suitability or quality is another form of copying behaviour that can lead to aggregation (Stamps, 1988). In general, the nesting pattern can be interpreted as the result of attraction, which would lead to clustering, or forces of repulsion, which would result in a regular pattern (Asis et al., 2014). Finally, the clustering observed at present can be the result of a selection for the own natal area to build the nests (Davis and Stamps, 2004).

Not all the previous hypotheses are applicable to *B. rostrata*: group-hunting behaviour is never observed, every female hunts individually. Mate choice seems to be the result of male scramble competition, and moreover, the nest building phase starts when the mating phase is already largely over (Schöne and Tengö, 1981).

There can also be conditions and environments where gregarious nesting would have negative consequences for certain species. In *Bembix pallidipicta*, a pattern of overdispersion was found, which indicate a negative reaction on the presence of conspecifics. In this species, the overdispersed pattern can be explained by prey stealing behaviour (Rubink, 1982) and by kleptoparasitism by conspecifics (Casiraghi et al., 2003). For nest clustering to be favourable, intraspecific competition cannot be present (Asis et al., 2014). However, in plenty of cases, the benefits of aggregated nesting will exceed the costs (e.g. Strohm et al., 2001; Wcislo, 1984).

In the article of Asis et al. (2014), it is established that for females of *Bembix merceti, B. zonata* and *B. sinuata,* the proximity of conspecifics is the main determinant when choosing a nesting site. Previous nesting behaviour, experience, and the effect of natural enemies seemed not important. Also attraction or repulsion at the heterospecific level appeared not to be significant, probably explained by an absence of competition.

In the digger wasp *Stizus continuus* as well, female-female attraction was found to be the main determinant of the spatial positioning, more important than the distance from the own natal hole and more important than the availability of substrate (Polidori et al., 2010; Polidori et al., 2008). A plausible explanation for this pattern is copying behaviour (Danchin et al., 2004). Seeing the successful nests and the successful provisioning of others females can be a cue to increase the accuracy of the own nest-site place or reduce its cost (Asis et al., 2014).

Although biotic factors provide a suitable explanation, it is difficult to exclude an influence of abiotic factors. In some species of ground-nesting Apoideae, these were found to be of high importance. For example, Wuellner (1999) described that the nest aggregations of the ground-nesting bee *Dieunomia triangulifera* were determined by abiotic factors, in particular moist, compact soil with an irregular surface, the presence of landmarks and the absence of vegetation. Bees preferred nesting in areas with warmer soil surface temperatures and brighter illumination. In this situation, nesting decisions were not influenced by the presence of conspecifics.

In a lot of cases, it is difficult to distinguish between the influence of abiotic factors and conspecific attraction. In the article of Polidori et al. (2008), it was attempted to tackle this problem. They studied the digger wasp *Stizus continuus* and tried to deduce if its clumped nesting was the result of a limited substrate availability or of female-female attraction. Their investigation showed that social attraction was the main determinant of clumping.

Of course, there will often be a general habitat preference, but within the acceptable habitats (suitable abiotic conditions), there is still a non-random spatial distribution, which cannot be explained by abiotic factors and for which biotic interactions can provide an explanation (Polidori et al., 2008; Sakagami and Hayashida, 1960).

In our investigation, we only tested for the spatial patterns, and not for the underlying causes of the clustering. But if we take all the present information together, the results probably point at an intraspecific attraction. It is clear that *B. rostrata* has specific microhabitat requirements, as described earlier. However, in the study site, not all patches with suitable conditions hosted nest aggregations, which indicates that not only abiotic factors where decisive.

Larsson (1986) pointed out that nesting density in *B. rostrata* increased with the presence of the kleptoparasitic fly *Metopia leucocephala*. Because the relative incidence per nest was declining as the nest density increased, the hypothesis of the selfish herd mechanism as a response to parasites and predators is supported.

5.2 Site fidelity

Our results show clearly that there is a very high site fidelity. 98% of the animals were caught inside the own plot, only two females were observed outside of their site.

Although two animals in 178 observations and 119 recaptures may seem very little, these two animals indicated something significant: there is connectivity between different plots, although the rate of dispersal will be very small. Dispersion between habitat patches is a key parameter to determine the viability of metapopulations (Hanski et al., 1996). Isolated populations will drift towards fixation of some alleles and thus towards a higher homozygosity. The smaller the population, the faster this will happen. However, gene flow between different populations can counteract effects of genetic drift, even at very low frequencies. One immigrant per generation is already able to keep the fixation index (F_{ST}) at 0.20 (F_{ST} ranges between 0 and 1; 1 indicates complete fixation of an allele). So, even a little dispersal can be enough to retain a high heterozygosity and to counteract genetic drift (Futuyma, 2009).

The barrier that was thought to be the most arduous to cross (the forest), proved not to be invincible, the two dispersing animals had managed to cross it. It will thus not hinder the animals from reaching new places. A similar result was also found in a study on two species of bumblebees. Although there were species-specific differences, the forest was no effective landscape barrier for foraging bumblebees, as they were able to cross 600 m of forestland (Kreyer et al., 2004).

Bembix rostrata is a central-place foraging species. The females are nest builders, who have to visit the nesting site repeatedly to provide food to their offspring. They also are large animals, with a potential to cover a distance of about 3.5 km (Tengö et al., 1990). These animals are theoretically capable of moving between various habitat fragments. However, this pattern was not observed, as *B. rostrata* stayed mostly loyal to the plot of origin.

There are several other studies where a high nest site fidelity was found (e.g. Dorchin et al., 2013; Potts and Willmer, 1997; Steffan-Dewenter and Schiele, 2004). A possible explanation for this pattern is the presence of a sufficient amount of resources (flowers) within the site, so there is no need to commute longer distances. The site fidelity can in this way rather be seen as flower/resource fidelity than as site fidelity (Dorchin et al., 2013). Maybe when resources in a patch become more scarce, the animals will be forced to go further away to satisfy their needs, but when it is not necessary to cover long distances, site fidelity is more time and energy efficient (Stephens, 1986).

In this investigation, we did not explicitly measure the amount of nectar flowers in the different patches, but a lot of Ragwort was noted. The low amount of observations, the presence of only one observer and the fact that a lot of animals were captured close to a nesting population can eventually lead to an underestimate of the number of dispersing animals, but it is difficult to believe this underestimation would be so extreme that it would lead to a different interpretation.

Sometimes, a difference is made between natal dispersal (dispersion from the natal site) and breeding dispersal (Paradis et al., 1998). We only started our research after emergence of all the animals, so we were incapable of examining natal dispersal. However, it was not possible to find references to natal dispersal in literature, although *B. rostrata* has repeatedly been studied. This supports the supposition that natal dispersal behaviour will largely be absent in this digger wasp species.

Breeding dispersal is the dispersal between different breeding attempts of a female, so in this case, between successive nest burrows. This distance remained rather small in the case of *B. rostrata*. In 75% of the cases, the distance was less than 10 m; in 85% of the cases, it was less than 20 m. All distances exceeding 20 m were of one individual. Despite the small amount of data, this already indicates that there is a preference to build new nests close to the old ones, mostly within the same nesting spot. As argued earlier, it is beneficial to nest close to conspecifics, and if the factors in the first nest were satisfactory, it is probably energy efficient to choose the second nest nearby, in an environment the individual is already familiar with.

In this thesis, only females are considered. But the behaviour of males can be rather distinct, and maybe this can also lead to a difference in dispersion? If males would prove to be active dispersers, this can obviously lead to an increased gene flow between different populations. In the case of this digger wasp species, a high dispersion from the males is not expected. The males rather stay close to the females and the nest aggregations, and have a lower homing capacity than provisioning females (Schöne and Tengö, 1981; Tengö et al., 1990).

Paxton (2005) described similar patterns for bees. The movement patterns could mainly be explained by mating strategy. In case the nesting density is high, and females emerge more or less synchronised, the male reproductive success will be maximized by searching for receptive females at the natal nest site of the females. Long distance movement will occur when there is territorial competition, but is not likely in species that practice non-territorial scramble competition for a mate, like *B. rostrata* does.

5.3 Population size and reproductive rate

The population sizes found in our plots are very small. Even when considering the four plots to be part of one big metapopulation (we described the connectedness earlier), the total size is only 70 females. For the master thesis of Sander Bruylants, observations on five arthropod species, including *Bembix rostrata*, were performed over a much bigger area of the Belgian coast. His investigation proved that there were more occupied patches, but because of the different observation method, it is difficult to make extrapolations about their total population sizes. He found wasps at three other spots in the Westhoek (3, 1 and 15 individuals), at one patch in Ter Yde, one patch in the Schipgatduinen and one patch in the Plaatsduinen (all 1 individual) (Bruylants, 2015).

We also determined the number of burrows per female. Although our observation method had its restrictions (most of the time, there was only one observer present for all four study plots) and presumably some observations were missed, more than two burrows were only found for four females out of the 57, and for 21 females no burrows were noted. The maximum number of burrows a female is able to complete is five (Larsson and Tengö, 1989), so this observations suggest a low reproductive rate.

Larsson and Tengö (1989) found a negative correlation between body size of a female and fecundity: the larger the female, the longer she needs to construct and provision a nest, consequently larger females produce less nests in a season. In our investigation, no body size measurements were executed, so we were not capable to judge whether an effect of body size was involved in the low reproductive rate of the populations in the Westhoek.

Connectivity between the plots was found, so it can be assumed that all populations in this study are part of a metapopulation instead of several small isolated patches with independent population dynamics and extinction probabilities. A classical metapopulation requires just enough migration to avoid complete isolation, but on the other hand not too much migration, to prevent a single panmictic population (Fronhofer et al., 2012). The fact that few individuals were captured outside their original plot, confirms the hypothesis of a classical metapopulation.

In most studies, the extinction dynamics of individual populations within a metapopulation are considered as being determined by the area of the patches and by isolation. Pellet et al. (2007) however discovered that local population size predicted extinction patterns more effectively than patch area. Franzen and Nilsson (2010) found a similar outcome in a study of the solitary bee *Andrena hattorfiana*. The local persistence was related to the amount of pollen (patch quality) and the local population size. Connectivity between different patches did not seem to be important.

Small populations are more susceptible to extinction from various causes (Shaffer, 1981). They risk inbreeding, with the associated deleterious effects, have a higher genetic drift, and stochastic events will have a larger impact in small populations (e.g. Bijlsma et al., 2000; Ellstrand and Elam, 1993; Shaffer, 1981). In case of *B. rostrata*, it was found that small populations are more susceptible for parasitism from the fly *Metopia leucocephala* and predation by ants (usually *Formica rufa*). This observation was not made over an entire metapopulation, but within different nesting aggregations. As the density increased, the relative parasitism per nest declined (Larsson, 1986).

However, it is often difficult to determine a minimum viable population size. In the article of Shaffer (1981), a minimum viable population for a certain habitat is defined as 'the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental and genetic stochasticity, and natural catastrophes'. The population must not only survive under normal conditions, but also be able to maintain itself during various perturbations and catastrophes and during a certain timeframe (although 1000 years is a very long timeframe in a dynamic system like the dunes).

Franklin (1980) suggested that a minimum effective population size to maintain short-time fitness (prevent severe inbreeding) should be around 50. A minimum effective population size of 500 is recommended to allow adaptation to changing conditions. However, to retain long-term evolutionary potential (at the species level) a substantially larger population is required (Soulé, 1980).

For wasps and bees, there is not a lot of knowledge about local population sizes, although for solitary bees, a low density is assumed for most species (Michener, 2000; Westrich, 1989 as in Steffan-Dewenter and Schiele, 2004).

Even in habitat patch networks supposed to support a stable population, local population size within a patch can differ strongly between years. Studies that cover only one or a few generations sometimes tend to underestimate extinction threats. In an investigation on the butterfly species *Plebejus argus* for example, metapopulation dynamics appeared trivial during the first years of the research. But as the work progressed (the investigation ran for 30 years), the number of patches involved in population turnover greatly increased (Thomas et al., 2002).

The study of Franzen and Nilsson (2013) found a very high population variability over a nine year study of a declining solitary bee (*Andrena humilis*) with two-year fluctuations between 21-48 nests and 490-1230 nests, independent of climatic variables or pollen availability in the patch. These population cycles can optionally be due to a strategy to avoid natural enemies and survive in small habitat patches.

Thus, there are different underlying factors that can cause a difference in population size between years.

In this study, we were only able to estimate the population size of *B. rostrata* during one season. However, in the literature, no references to fluctuations were found, and so we suppose that the only fluctuations in population size are due to external factors, and not inherent to the species.

5.4 Implications for conservation

To be able to determine a possible conservation management for a species, it is first of all necessary to identify the threats to the particular species. In *Bembix rostrata*, we have encountered several risks. The microhabitat requirements, the high patch fidelity, the low fecundity and small population size are all factors that increase the vulnerability to extinction.

This digger wasp species has very specific microhabitat preferences. Apart from the general decline of (grey) dune area, its specific microhabitat is endangered because of the disappearance of the natural disturbances. This can lead to an increasing sandy area becoming vegetated, whereas sand is necessary for nest building.

In addition, small populations are highly vulnerable for extinction. Small populations will always suffer more from stochastic, demographic and genetic factors (e.g. Bijlsma et al., 2000; Ellstrand and Elam, 1993; Shaffer, 1981) and in *B. rostrata*, there is the supplementary threat of increased parasitism in small populations (Larsson, 1986).

The species has a very low dispersal rate, and this will hamper possible rescue effects, because the success of rescue is based on the increase in population size (Hanski et al., 1996). In our research, rescue seems extra unlikely because there are only a few subpopulations present, all consisting of a small number of individuals. This also impedes the colonization of a new or an extinct patch. When a patch will go extinct, it is uncertain if individuals from other patches will be able to colonize it again. The limited distance between the different burrows of a female and the clustered nesting has as downside that, when a stochastic catastrophe would strike at a nesting spot, there is a high probability of all nests being destructed at once.

The most important factor to conserve this species seems to be the management and conservation of the occupied patches, and prevent, to the extent possible, a decrease in population sizes. When the size of the patches and the amount of available nectar flowers would increase, it may be possible that even larger populations can be supported.

The amount of suitable patches (grey dunes with a sufficient amount of bare sand) has decreased so drastically, that it will be difficult to find and colonize new suitable patches. However, by removing vegetation, it is possible that some previously suitable spots in the neighbourhood will become fit again to host *B. rostrata*.

The species did not have a problem to cross barriers between different sites, so the connectivity in our study area seems sufficient, although the distances between the different patches were small. The species has a high potential mobility, so connectivity with more distant populations in the Westhoek, and with other patches along the coast (e.g. Ter Yde, the Schipgatduinen), is theoretically not impossible. It is difficult to come up with management actions that would efficiently increase the connectivity.

For conservation purposes, it is essential to assure the persistence of suitable habitat by impeding succession. It appears that the best way of realising conservation is the restoration of sand dynamics in a more natural way than the use of grazers provide. The restoration of natural sand dynamics requires however a large connected area, and it is utopic to count on this realization. The current applied conservation management using grazers is associated with negative effects, because the density of nests drastically decreased when grazers were present. The presence of tourists in occupied sites resulted in a similar decline (Bonte, 2005). Ungulates normally avoid grazing in grey dunes, the only effect from their presence is trampling, what is definitely deleterious for *B. rostrata*, but also for a lot of other species.

The succession of this area should be precluded by internal removal of shrubs and plants and by prevention of invasions of new plants and shrubs from adjacent areas, while care is taken not to damage and trample below-ground nests. This is rather labour intensive, and negative effects of anthropogenic disturbance remain a threat. Nonetheless, when every factor is taken into account, this appears to be the best option.

These management measures will also benefit the conservation of a lot of other dune arthropods, like already validated for psammophilous spider species, some butterfly species and a grasshopper species (Maes and Bonte, 2006; Maes et al., 2006; Provoost and Bonte, 2004). The result of this investigation can be combined with earlier research on dune arthropods, and will result in a more comprehensive dune conservation approach when compared to a solely ecosystem-based management.

5.5 Remarks about the investigation and fieldwork

The fieldwork done in this study encountered a few difficulties and had some weaknesses. Not all of them could be avoided, but they sometimes complicated the analysis or the interpretation of the results.

i. *Weather conditions*

Digger wasp activity is heavily influenced by the weather. When it is too cold, too hot, too cloudy or too wet, activity is diminished drastically, and the wasps will rather stay inside their burrows (Schöne and Tengö, 1981, 1992). On days with bad weather predictions, the fieldwork could not be executed. Unfortunately, the weather in August 2014 did not contribute to the execution of the fieldwork: it was the coldest August in more than 20 years, it was anomalously wet, with a lot of wind and a low amount of sunshine (Koninklijk Meteorologisch Instituut van België, 2014). This would have influenced the number of observations. In total, it was only possible to make observations on 22 days from the 23th of July until the 4th of September 2014.

ii. *Removal of flags*

During the fieldwork, it was noticed on several occasions that flags placed on earlier days had disappeared. Although the fieldwork took place in an area that was inaccessible for public and behind a fence, the place was visible to people passing by. The most probable assumption is that random passers removed the flags. It was not difficult to find an entrance in the study area, and it often happened that foreign footprints and dog paw prints could be found during the period of the fieldwork. At the green plot, it happened twice that the flags were removed (two times from the same hill). In the pink plot as well, some flags were removed.

iii. *Remarks about the fieldwork*

A first point of criticism is that the photographs of the burrows were not taken immediately after the discovery and marking of a new burrow. Occasionally, there was taken a picture that was sent to iObs/ObsMapp, but the standardised pictures to perform vegetation analysis with were only taken at the end of the fieldwork. At that time, some flags had been removed, and could not be captured on a photograph. Some of these flags were luckily photographed earlier, but most were not. In addition, these pictures in iObs/ObsMapp did not always catch the right area and the right angle to make vegetation analysis possible.

A second complication happened when the GPS saved the position of the burrows. Only the coordinates, and not the names of the burrows were saved. It was sometimes quite difficult, or even inaccurate, to couple the names of the burrows to the right coordinates. It should have been better to couple the names directly to the coordinates in the GPS.

A third criticism about the data collection can be that the pictures of the random points were taken only on the 16th of April 2015, while the photographs of the burrows were already taken in the beginning of September 2014. Possibly, the difference in time can accord with a difference in vegetation cover. Although our own observations on the spot did not really support this hypothesis, there was not tested for, and we cannot entirely exclude it had an influence.

iv. *Future research*

There are several possible options for future research on this species. I have some suggestions here, but there are plenty of other subjects.

A first suggestion is to start a future investigation earlier in the season, at the time animals start to emerge (from the end of June). In that way, it is possible to investigate whether there is fidelity for the natal area or natal dispersal. In our research, only female individuals were taken into account, but because of the different behaviour of the males and the females, it could also be useful to investigate both sexes and test if there is a dispersal difference between them. The sex-ratio of this digger wasp species can also be determined.

It can also be useful to test if factors other than antiparasite behaviour are influencing the nesting behaviour. In this study, we only focussed on patterns, and not on the underlying causes of the spatial distribution.

Lastly, a multi-year monitoring of the population size can be extremely useful, to obtain a more accurate insight into the population sizes and dynamics. An estimate based on observations in a single year can be biased by several stochastic factors (bad weather conditions, for example). When monitoring for multiple years should demonstrate an evolution in population sizes, this can be used to evaluate the current management.

6 Conclusion

The European dune area is in danger. Active dune management is crucial to conserve and preserve the remaining parts. In Belgium, there is mostly chosen for an ecosystem-based management using grazers. However, several species will experience damage from this measure. To improve a conservation approach, it can be useful to include the conservation requirements of some deliberately chosen species into management plans. One of these species is the threatened digger wasp *Bembix rostrata*. It has greatly suffered from habitat loss, and in addition, tourism and animal trampling destroy its nests. In this research, several species characteristics that had an importance for conservation were examined.

This investigation shows that *B. rostrata* has a preference to nest on slopes where a high amount of bare sand is present, because sand is essential for nest construction. When looking for a nesting place, females are attracted by the presence of conspecifics, resulting in gregarious nesting. Dense nest aggregations can have multiple benefits, in this case there is at least prove of an antiparasite strategy.

Despite its high homing capacity, the species is sedentary, and prefers to stay at the same patch. Also the different burrows of a female are found within short distance of each other. Possibly, this is because the conditions in the patch are satisfactory, and thus dispersal would only be energy waste. Animals could be forced towards a higher dispersal if the conditions within the plots became less favourable or the food reserves declined.

The species has very small population sizes and a low reproductive rate, which make them vulnerable for demographic, genetic and environmental stochasticity and increased parasitism by the kleptoparasitic fly *Metopia leucocephala*.

The combination of specific nesting preferences, a high site fidelity, low fecundity and small population size makes the species very vulnerable for extinction. The most appropriate way to conserve them seems to preserve and eventually enlarge the living grounds and to prevent succession to a less sand-rich situation. A restoration of the natural sand dynamics is infeasible, and introduction of grazers is damaging. The best achievable management appears to avoid the growth of shrubs and grasses and to remove redundant biomass within the grey dunes. This measure will also benefit a high amount of other dune inhabitants.

7 Summary

European coastal dunes are a very valuable ecosystem. Aeolian dynamics are responsible for a continuous sand displacement, resulting in constant disturbance of the system. This dynamics create a very heterogeneous landscape, with a high diversity in habitat types and high species richness.

However, this valuable ecosystem is in danger. The most important reason for this is a huge areal decrease and fragmentation of the dune area caused by urbanisation, tourism and coastal defence works. In smaller dune patches, wind dynamics are not able to support the constant sand disturbance present in larger sites. This will allow soil stabilisation by plants, and lead to fixation and homogenisation of the dunes. It is obvious that this will lead to the decrease, or even the loss, of the biota associated with the specific dune habitat types. The most unique biodiversity resides in the most dynamic and early successional stages of the dunes, and especially these parts are affected by the changes.

At present, management actions are necessary to preserve the remaining dune area. Passive protection will not suffice. In Belgium, the most important management measure is the use of large grazers. The trampling of the grazers will induce sand dynamics, and their grazing will remove redundant biomass and increase connectivity between different fragments. This management is expected to benefit the entire ecosystem, and to restore and preserve the heterogeneous habitats and the biodiversity associated with it. However, the vegetation preference of the ungulates makes the expected connectivity increase dubious and trampling effects in stabilised dune landscapes can be deleterious for some specialised species, and even drive them to extinction. These animals will need a more species-specific management approach. Although it is not realistic to investigate every species separately, the incorporation of the requirements of some deliberately chosen species into management plans will greatly increase the chance of successfully conserving a wider range of species.

One of these species is the Common European Sand Wasp *Bembix rostrata,* a threatened dune specialist. The decrease in grey dune area has restricted the amount of suitable habitat for the species. In addition to this, the presence of grazers in the nesting site will be detrimental for *B. rostrata*, as well as for many other ground-dwelling species.

Some aspects of the behaviour and ecology of *B. rostrata* has already been studied, and there is already knowledge about its high homing capacity, chemical communication, courtship behaviour, stages of behavioural activity, and orientation.

Despite this present knowledge, there are still important questions to answer before a conservation attempt can be made. In this study, we performed an investigation of nesting preferences and spatial distribution of the nests, site fidelity of the species, and estimated the fecundity and population sizes of four connected (sub)populations.

The research was executed in the Westhoek nature reserve (De Panne, Belgium). Between the 23th of July and the 4th of September 2014, we collected data at four sites situated in the 'Krakeelduinen en Duinhoek', a grey dune area inaccessible for grazers.

The fieldwork consisted of the capture and recapture of every wasp noticed. To enable identification of the individuals, every wasp was marked with a coloured, numbered tag. The burrows were marked as well, and their coordinates were saved to perform a spatial analysis with. The marked burrows were photographed for the purpose of a vegetation analysis.

In the vegetation analysis, the vegetation surrounding nests was compared to random points. The outcome of this analysis showed a significant preference to nest on spots with a high amount of sand. There was also a preference for slopes found. These conditions will provide the highest nesting success. It is impossible to nest when there is no bare sand present. The increasing succession due to the disappeared aeolian disturbance will alter the relatively sandy habitat to a more vegetation-rich patch, so the specific microhabitat is in danger.

A nearest neighbour analysis indicated clustering of the burrows. An intraspecific attraction between the females seems in this case the main determinant of this aggregated pattern. Probably, once abiotic prerequisites are fulfilled, the most profitable place to nest is close to other conspecifics. Nesting in aggregations can have several benefits. In case of this digger wasp, there is at least prove that the parasitism per capita diminished with a more dense nesting aggregation.

Females remain loyal to their original site. 98% of all animals were recaptured within their own plot. The scarce amount of dispersing animals nonetheless indicated that different populations were connected, and that the barriers between different plots did not impede the dispersal. The species has a high homing capacity (up to 3.5 km), but in this investigation, rather stayed close to the nesting site. In a lot of other species, this pattern is observed as well, and probably indicates that the food supply in the nesting plot is sufficient, so going further will not grant additional yield, and will only cost more energy.

Because the fieldwork only started after the emergence of all animals, we were not able to examine natal dispersal. However, breeding dispersal, measured as the distance between the consecutive burrows of a female, was in most of the cases very small. It seems likely that the female chooses to stay in a familiar environment when the conditions in earlier nests were satisfactory. Because clustering is beneficial, this often results in nesting in the same cluster.

Population sizes were estimated using the Schnabel Method. The obtained population sizes were very small. Even when considering the four plots as one big population, we only found a population size of 70 females. A population this small will suffer from genetic and demographic effects, and will be more vulnerable to stochastic catastrophes. In addition, small populations in *B. rostrata* will suffer more from parasitism. The low amount of nests per individual also indicated a low reproductive rate.

A species with specific (and threatened) nest requirement, high site fidelity, small population size and a low reproductive rate combines four factors that increase the vulnerability for extinction. The best way to conserve it appears to be the protection of the plots occupied at present, and enlarge them when feasible. Restoring the natural sand dynamic at the landscape level is unfortunately impossible, and grazing is definitely deleterious, so the best way of conservation appears to prevent succession by manually removing redundant biomass and prevent vegetation from the surrounding matrix from entering. This management will also provide benefits to a lot of other species, and the combination of this study with the results of former investigations on other species can be included in a general conservation plan, leading to a more comprehensive conservation approach.

8 Samenvatting

De Europese kustduinen zijn uiterst waardevol vanuit ecologisch oogpunt. Winddynamieken zorgen voor voortdurende zandverstuivingen, die leiden tot een systeem met continue verstoring. Dit mechanisme resulteert in een heel verscheiden landschap, met een groot aantal verschillende habitattypes en een hoge soortenrijkdom.

Helaas wordt dit kostbare ecosysteem bedreigd. De belangrijkste oorzaak hiervan is het grote verlies aan duinoppervlakte en een verhoogde versnippering wegens verstedelijking, toerisme en kustverdedigingswerken. Wanneer duingebieden onvoldoende groot zijn, is het niet mogelijk om de winddynamiek en de zandverstuivingen in stand te houden. Het wegvallen van de verstoring zal ervoor zorgen dat toenemende plantengroei de bodem kan fixeren, en dit leidt tot een meer homogeen duingebied. Vanzelfsprekend zal dit de achteruitgang, en eventueel zelfs het uitsterven, van de biota die verbonden zijn aan bepaalde habitattypes veroorzaken. De meest unieke soorten leven in de meer dynamische, vroeg successionele duintypes, en net deze delen worden het hardst getroffen.

Om de overgebleven gebieden in stand te houden volstaat het niet om ze uitsluitend passief te beschermen. Er is actief beheer nodig. In België worden meestal grote grazers ingezet als beheersmaatregel. De vertrappeling zorgt voor zandverplaatsing en hun graasgedrag zal overmatige biomassa verwijderen en de verbondenheid tussen afzonderlijke fragmenten vergroten. Van deze maatregel wordt een positief effect voor het hele ecosysteem verwacht, met het herstel en de instandhouding van de landschapsverscheidenheid en de afhankelijke biodiversiteit tot gevolg. De graasvoorkeuren van de hoefdieren zorgen er echter voor dat de verwachte stijging in connectiviteit vrij twijfelachtig is, en vertrappeling kan voor sommige soorten dramatische gevolgen hebben, met soms zelfs uitsterven tot gevolg. Voor deze soorten is er nood aan aangepaste beheersmaatregelen. Hoewel een afzonderlijk onderzoek naar elke soort niet realiseerbaar is, kan het opnemen van de vereisten van een aantal welgekozen soorten in de beheersplannen ervoor zorgen dat de kans op een succesvol behoud van een groter aantal soorten beduidend toeneemt.

Een van deze gespecialiseerde soorten is de harkwesp (*Bembix rostrata*). Het is een duinspecialist, die door de achteruitgang van de mosduinen haar leefgebied zag verminderen en sterk bedreigd wordt. Daarenboven is de aanwezigheid van grazers in het nestgebied nefast voor de soort, net zoals voor een groot aantal andere gravende soorten.

Enkele aspecten van het gedrag en de ecologie van *B. rostrata* zijn vroeger al bestudeerd, en er is heel wat geweten over hun grote homingcapaciteit, de chemische communicatie, het paargedrag van de mannetjes, de verschillende gedragsfasen gedurende de zomer en hun oriëntatiemechanismen. Ondanks al deze kennis blijven er nog heel wat op vragen onbeantwoord die onontbeerlijk zijn om een efficiënte behoudspoging te kunnen ondernemen. In deze studie werd onderzoek verricht naar de nestvoorkeuren en de ruimtelijke spreiding van de nesten, naar de plaatstrouw van de soort, en werden er schattingen van de vruchtbaarheid en de populatiegrootte gemaakt.

Het onderzoek vond plaats in natuurreservaat de Westhoek (De Panne, België), tussen 23 juli en 4 september 2014. De data werden verzameld op vier plaatsen in de Krakeelduinen en Duinhoek, een mosduingebied waartoe grazers geen toegang hadden.

Het veldwerk bestond uit het vangen en hervangen van elke waargenomen wesp. Om identificatie mogelijk te maken werd elk individu gemerkt met een gekleurd en genummerd plaatje. Ook de holen werden gemerkt, en de coördinaten werden opgeslagen om een ruimtelijke analyse mee uit te kunnen voeren. Daarnaast werden de holen ook gefotografeerd om een vegetatie-analyse mogelijk te maken.

In de vegetatie-analyse werd de vegetatie rond de nesten vergeleken met de vegetatie op lukrake punten. De uitkomst van deze analyse maakte duidelijk dat er een significante voorkeur is om nesten te bouwen op plekken met een grote hoeveelheid zand. Ook een voorkeur voor hellingen werd gevonden. Deze condities zullen de beste omstandigheden voor succesvolle nestbouw opleveren. Met onvoldoende zand is het onmogelijk om nesten te bouwen. De toenemende successie door het verdwijnen van windverstoring zal een zandrijk gebied omvormen naar een gebied met veel meer vegetatie, dus het vereiste microhabitat is in gevaar.

Een nearest neighbour-analyse toonde clustering van de holen aan. De belangrijkste verklaring voor dit patroon lijkt een intraspecifieke aantrekking tussen de wespen te zijn. Van zodra de abiotische vereisten zijn vervuld, is het waarschijnlijk het meest voordelig om een nest te bouwen dicht bij soortgenoten. Nestaggregaties kunnen meerdere voordelen hebben. In het geval van de harkwesp is het op zijn minst al duidelijk dat parasitisme per capita afneemt als de nestdensiteit toeneemt.

Vrouwelijke wespen vertonen een heel hoge plaatstrouw. 98% van alle dieren werd hervangen binnen de eigen plot. De zeldzame dieren die wel in een andere plot teruggevonden werden, tonen aan dat de verschillende populaties wel verbonden zijn, en dat dispersie niet verhinderd wordt door de barrières tussen de verschillende plots. De soort heeft een hoge potentiële mobiliteit (homing tot 3.5 km), maar in dit onderzoek bleven ze toch liever dicht bij hun eigen nesten. In andere soorten is vergelijkbaar gedrag waargenomen. Wat mogelijk een verklaring kan zijn, is dat de voedselvoorziening binnen het eigen gebied voldoende is om aan alle noden te voldoen, in zoverre dat het afleggen van een grotere afstand geen extra voordeel oplevert, maar uitsluitend meer energie kost.

Omdat het veldwerk pas van start ging na het uitkomen van de dieren, waren we niet in staat om de dispersie weg van de geboorteplek te onderzoeken. Dispersie tussen de nestpogingen, gemeten als de afstand tussen twee opeenvolgende holletjes, was in de meeste gevallen heel klein. Waarschijnlijk kiest een vrouwtje ervoor om in haar vertrouwde omgeving te blijven wanneer eerdere condities er goed genoeg waren. Aangezien gezamenlijk nesten voordelig is, leiden dit vaak tot een nest in dezelfde cluster.

De populatiegroottes werden bepaald volgens de Schnabelmethode. De bekomen populatiegroottes waren heel klein. Zelfs wanneer we de vier plots als een grote populatie beschouwen, is de grootte ervan slechts 70 vrouwtjes. Kleine populaties hebben te lijden onder genetische en demografische effecten, en zijn ook gevoeliger aan toevallige negatieve omstandigheden. Daarnaast is er een verhoogde kans op parasitisme in kleine populaties van *B. rostrata*. Het kleine aantal nesten per vrouwtje wijst ook nog op een lage voortplanting.

Een soort met bijzondere (en bedreigde) nestvereisten, een hoge plaatstrouw, een kleine populatiegrootte en een lage voortplanting bezit meerdere eigenschappen die de gevoeligheid voor uitsterven verhogen. De beste manier om bescherming te bieden is om de huidige bezette gebieden te beschermen en, indien mogelijk, uit te breiden. Het is helaas onmogelijk om de oorspronkelijke natuurlijke zanddynamiek te herstellen, en begrazing leidt enkel tot extra achteruitgang, dus de beste beheersmaatregel lijkt in dit geval een handmatig openhouden van het gebied door het verwijderen van begroeiing en het voorkomen van invasies van vegetatie uit de omringende gebieden. Dit beheer zal ook een aantal andere soorten ten goede komen, en dit resultaat, gecombineerd met resultaten uit onderzoek op andere soorten, kan deel uitmaken van een veelomvattend beheers- en behoudsplan.

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